REGULAR PAPER

Growth and derived life-history characteristics of the Brazilian electric ray *Narcine brasiliensis*

Fernanda A. Rolim[1] | Zachary A. Siders[2] | Fabio P. Caltabellotta[2,3] |
Matheus M. Rotundo[4] | Teodoro Vaske-Júnior[5]

[1]Elasmobranch Research Laboratory, Institute of Bioscience, Sao Paulo State University (UNESP), São Vicente, Brazil

[2]UF/IFAS SFRC Fisheries and Aquatic Sciences Program, University of Florida, Gainesville, Florida, USA

[3]Coastal Oregon Marine Experiment Station, Oregon State University, Newport, Oregon, USA

[4]Zoological Collection, University Santa Cecília (UNISANTA), Santos, Brazil

[5]Institute of Bioscience, Sao Paulo State University (UNESP), São Vicente, Brazil

Correspondence
Zachary A. Siders, UF/IFAS SFRC Fisheries and Aquatic Sciences Program, University of Florida, 136 Newins-Ziegler Hall, Gainesville, FL 32611, USA.
Email: zsiders@ufl.edu

Abstract

The majority of batoids are listed as Threatened (20.4%) or Data Deficient (41%) by the IUCN Red List. A key challenge to assessing Data-Deficient species is obtaining estimates of key life-history characteristics. Here, a Bayesian approach was used to estimate derived life-history characteristics from a growth model applied to the Data-Deficient Brazilian electric ray *Narcine brasiliensis*. The age of 170 specimens (107 females, 63 males) was estimated from vertebral centra, and total length, disc width, total weight and birth size were used in a joint estimation of sex-specific length-weight models and two-dimensional von Bertalanffy growth models. Estimates of age at length zero, age at maturity, longevity and mortality at age were derived simultaneously. The Bayesian joint modelling approach was robust to small sample sizes by adding a likelihood to constrain L_0 and sharing parameters, such as Brody growth coefficient between length measurements. The median growth parameter estimates were a shared L_0 = 38.8 mm, female L_∞ = 515 mm, = 0.125 and male L_∞ = 387 mm, = 0.194. Age at maturity was estimated to be 7.40–7.49 years for females and 4.45–4.47 years for males, whereas longevity was 22.5–22.6 years for females and 14.2 years for males depending on length measurement. Age-1 natural mortality was estimated to be 0.199–0.207 for females and 0.211–0.213 for males. The derived life-history characteristics indicate *N. brasiliensis* is earlier maturing, but slower growing relative to other Torpediniformes. These characteristics along with the species' endemism to southern Brazil and high by-catch rates indicate that one of the IUCN Red List threatened categories may be more appropriate for the currently Data-Deficient status. The Bayesian approach used for *N. brasiliensis* can prove useful for utilizing limited age-growth data in other Data-Deficient batoid species to inform necessary life characteristics for conservation and management.

KEYWORDS

age and growth, Batoidea, Bayesian, life history, Narcinidae

1 | INTRODUCTION

A main impediment in assessing the status of batoid species is the general lack of life-history characteristics used to determine a species' risk to overexploitation (Stevens *et al.*, 2000; Simpfendorfer *et al.*, 2011). For some key life-history characteristics, such as age at maturity, longevity and mortality at length (or age), estimates can be derived from age and growth models (Cailliet & Goldman, 2004; Charnov *et al.*, 2013; Fabens, 1965; Mangel, 2017). Nonetheless, obtaining sufficient sample sizes to estimate growth models can be challenging (Smart *et al.*, 2013, Heupel & Simpfendorfer, 2010). Bayesian methods offer a promising route for tackling data limitation through setting reasonable priors, inducing parameter exchangeability between submodels (Gelman *et al.*, 2013) and incorporating uncertainty into derived life-history characteristics.

The elasmobranch superorder Batoidea (skates and rays) presents a higher proportion of species designated as threatened (*i.e.*, Critically Endangered, Endangered or Vulnerable) by the IUCN Red List Categories and Criteria (hereafter IUCN Red List) than the other elasmobranch superorders (20.4% in Batoidea, 18.3% in Selachii and 13.5% in Squalomorphii) (IUCN, 2019). Forty-one per cent of Batoidea are also designated as Data Deficient (IUCN, 2019) and, if thoroughly assessed, could drastically increase the proportion of threatened species. For the electric rays in the order Torpediniformes, the proportion of threatened and Data Deficient species increases relative to Batoidea as a whole (23.2 and 51.8%, respectively). Within Torpediniformes, the numbfishes (*n* = 28, family Narcinidae) are broadly threatened with unintentional harvest, and all 10 Data-Deficient species belong to the genus *Narcine* (*n* = 19), the largest genus within the family (Carvalho & Last, 2016; IUCN, 2019).

The Brazilian electric ray, *Narcine brasiliensis* (Olfers 1831), is one of these Data-Deficient *Narcine* species (Rosa & Furtado, 2007) and is endemic from southeast Brazil to northern Argentina (Carvalho, 1999). A primarily coastal and estuarine species, it is found in muddy and fine sand substrata (Martins *et al.*, 2009; Vianna & Vooren, 2009). This small lecithotrophic species reaches a maximum size of 49 cm in total length (Gomes *et al.*, 2010; Rolim *et al.*, 2015) and produces between 4 and 15 embryos in each gestation occurring approximately every year (Gomes *et al.*, 2010; Rolim *et al.*, 2016). Individuals reach sexual maturity at approximately 28 cm in males and 32 cm in females (Gomes *et al.*, 2010; Rolim *et al.*, 2016). Other important aspects of their life history, such as age and growth, age at maturity, natural mortality and longevity, are currently unknown, representing a key data gap for the assessment of *N. brasiliensis* (Rosa & Furtado, 2007).

Like other members of Narcinidae, demersal gears rarely target *N. brasiliensis* but, in Brazil, the trawling fleet often has incidental catches (Rolim *et al.*, 2015; Rotundo *et al.*, 2019). The lack of commercial value results in the discard of most individuals at sea (Martins *et al.*, 2009; Vianna & Vooren, 2009), limiting the amount of fishery-based scientific collection. Collection of target or by-catch specimens in commercial fisheries can result in sampling issues that impact the estimation of growth models. The most pertinent is size-selective bias

that can result from gear selectivity and spatial or temporal patterning to the fishery.

This size-selective bias has consequences for the parameters of interest in the commonly used von Bertalanffy growth model (VBGM) (Beverton & Holt, 1957; von Bertalanffy, 1934): asymptotic size (L_∞) and the Brody growth coefficient (k) (Gwinn *et al.*, 2010). In the case of missing small specimens, L_∞ biases high, whereas k biases low resulting in assuming later maturity at age, lower natural mortality and a longer longevity. One solution proposed by Cailliet *et al.* (2006) is to return to the original size at birth (L_0) formulation proposed by von Bertalanffy (1934). In elasmobranchs, L_0 is a frequently measured quantity, and it is common practice to fix L_0 at the mean for the species or bootstrap over a suite of possible parameter values. Neither approach takes advantage of directly including data on birth size into the estimation of the VBGM.

Another potential avenue for overcoming limited age-growth data can be to use multiple length measurements to better inform shared parameters in the VBGM. For instance, many species in Batoidea grow in both disc width and total length. It is of minor consequence to jointly estimate VBGM parameters to describe disc width at age and total length at age in a Bayesian framework. Given that the Brody growth coefficient, k, is the proportional rate of growth, it is reasonable to assume exchangeability in the parameter between different measurements of length at age (Beverton & Holt, 1957, p. 33). Other parameters such as L_0 can be shared between sexes, a reasonable assumption for most elasmobranchs. Thus, a hierarchy is induced to the observations of length at age.

A Bayesian framework for deriving life history for Data Deficient species has four distinct advantages: (a) in the case of limited samples, often the generative cause of Data Deficient, a Bayesian approach is exact for the sample size in question; *i.e.*, it does not rely on asymptotic behaviour to be unbiased (Kéry, 2010); (b) uncertainty in the estimation of growth model parameters can be directly propagated forward to the derivation of life-history parameters (Kéry, 2010); (c) information can be combined formally, such as data on size at birth and age-growth or restricting the Brody growth coefficient to values less than 1; and (d) the probability of model parameters given the data is obtained rather than the probability of the data given the model (Kéry, 2010). For *N. brasiliensis*, the fishery-derived nature of the biological samples precludes obtaining unbiased and high numbers of specimens for age-growth analysis. Thus, using additional information on the size at birth helps to reduce biases from missing smaller specimens, sharing parameters between length measurements can improve model accuracy and precision, and any modelling uncertainty is passed directly to derived life-history parameters.

Life-history characteristics are fundamental for assessing conservation risk and guiding conservation actions, especially in elasmobranchs (Simpfendorfer *et al.*, 2011). Often the collection of elasmobranch specimens is opportunistic and prevents sufficient certainty on life-history characteristics necessary for management (Hammerschlag & Sulikowski, 2011). The purpose of this study was to fill in this data gap for the Brazilian electric ray, *N. brasiliensis* by (a) estimating length-weight and age-growth VBGM parameters; and

(b) deriving estimates of age at maturity, longevity and mortality at age. Considering the high degree of Data-Deficient elasmobranchs, an additional goal was to present a methodological approach that could be used readily on other elasmobranch species.

2 | MATERIALS AND METHODS

This work was authorized by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio): survey permit SISBIO/13893.

2.1 | Study area and sampling

Specimens were collected opportunistically, between November 2010 and March 2012, as an incidental by-catch from commercial bottom pair trawlers that operate on the continental shelf (between the depths of 25 and 50 m) off southeastern Brazil, between 23°08′09″ S–25°24′23″ S and 44°23′25″ W–47°39′04″ W (Figure 1a). Fishing operations averaged four trawling hours per day, using nets 40–50 m

in length, 6–8 m in width and mesh-sizes of 150 mm in the body and 100 mm in the cod end. Specimens were transported to the laboratory and identified according to Carvalho *et al*. (1999) (Figure 1b). Sampling included determining sex, total length and disc width (l_{TL} and l_{DW} respectively, in mm) and mass (w, in g).

2.2 | Sample processing

In each specimen, 10 vertebrae were removed from the central region of the disc, just posterior to the synarcual process, cleaned and stored frozen following standard protocols (Cailliet & Goldman, 2004). One vertebral centrum from each specimen was air-dried and then mounted on a microscope slide using thermoplastic resin (Crystalbond 509, Electron Microscopy Sciences, Hatfield, PA, USA) and sectioned using a low-speed saw with two diamond wafering blades 102 mm in diameter separated by a 0.25 mm spacer. Each vertebral centrum was cut along the mid-sagittal axis, resulting in one 0.20–0.25 mm-thick "bowtie" section (Figure 1c). All sections were then stored in vials containing 100% isopropyl alcohol.
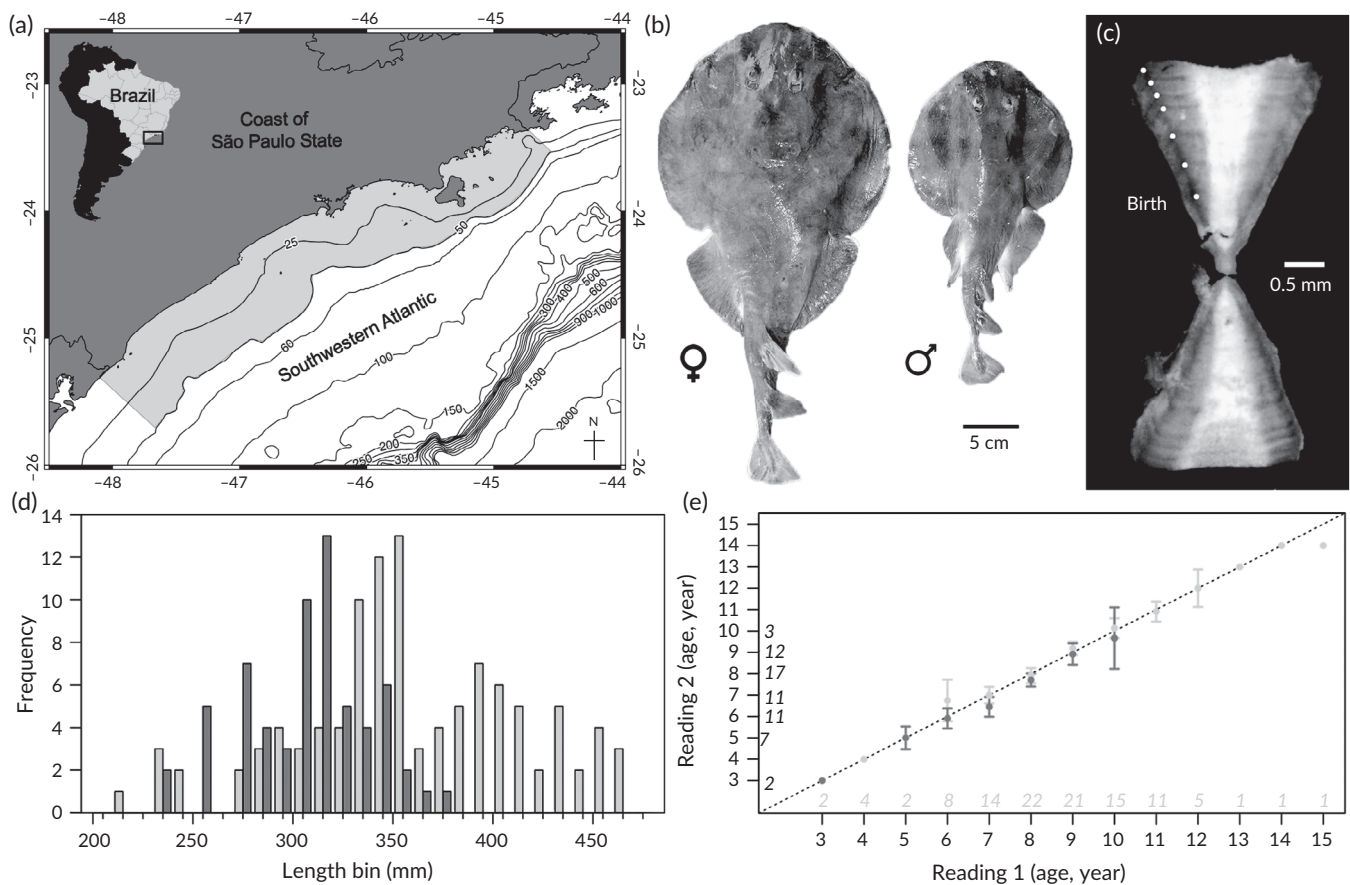

FIGURE 1 (a) Map of sampling localities in southeastern Brazil. The grey polygon indicates where individuals of *Narcine brasiliensis* were captured as by-catch from pair trawl fisheries fleet used in the present study. (b) Photos of representative male and female specimens. (c) An example of the sagittal cut from the vertebrae of a female individual detailing the birth band and nine subsequent growth bands. (d) Frequency of total lengths in 1 cm length bins for female (□) and males (■). (e) Mean and 95% C.I. of bias in the age estimation between the two readers for ○ Female (μ & 95% CI) and ● Male (μ & 95% CI) with the number of females at age along the x-axis and males along the y-axis

2.3 | Age determination

Each section was observed and photographed under reflected light using a stereomicroscope at a magnification of 10–20×. Mineral oil was applied before viewing to enhance banding patterns, and the resulting images were analysed using Motic Image Plus 2.0 imaging software (Motic China Group Co., Ltd. 1999–2010). Linear regressions between total length l_{TL} and vertebral radius (VR, the distance from the focus to the outer edge) and disc width l_{DW} and VR were estimated for both sexes to check if vertebral centrum growth remained proportional to somatic growth. Differences between sexes were examined using ANCOVA (Zar, 1999).

Band pairs consisting of one wide band (opaque) and one narrow band (translucent) were identified following Cailliet et al. (2006) and counted. A random sub-sample was selected and read by two independent readers to ensure a consensus on the interpretation of the band patterns. The birthmark was considered to be the first distinct band after the focus and occasionally associated with a slight change in the angle of the corpus calcareum (Figure 1c). After establishing ageing criteria, the primary reader read all vertebral sections twice, without prior knowledge of a specimen's size, sex or previous band-pair counts. Band-pairs were compared and those that differed were re-read by the primary reader; if an agreement between the re-reads was not reached, the sample was discarded and excluded from the age analysis following the recommendation of Goldman et al. (2012). Counts were conducted in different months to ensure the readings were independent. Band counts were converted to ages by assuming the band-pair formation followed an annual deposition pattern as described in other Batoids (i.e., Rioraja agassizii, Pseudobatos horkelii, Pseudobatos percellens and Zapteryx brevirostris) in the same area of the present study (Caltabellotta et al., 2019a; Caltabellotta et al., 2019b). The precision of ageing between reads (reads 1 and 2) was calculated using the average percent error (APE) (Beamish & Fournier, 1981) and the C.V. (Chang, 1982). Differences in ages were evaluated using an age-bias plot (Campana et al., 1995) and Bowker's test of symmetry (Bowker, 1948; Hoenig et al., 1995), which determines whether ageing differences are systematic or a result of random error.

2.4 | Bayesian life-history model

An integrated model was used to jointly estimate length-weight relationships and von Bertalanffy growth models for N. brasiliensis from disc width (l_{DW}), total length (l_{TL}), weight (w), age (t) and size at birth (p). For the weight at length relationship, an exponential model was used (Ricker, 1979):

$$\hat{w}_{i,j} = a_j l_{i,j}^{b_j} \tag{1}$$

where for a given specimen, i, the predicted weight, $\hat{w}_{i,j}$ was assumed to follow an exponential model as a function of the observed length, $l_{i,j}$, for a given measurement j (either disc width or total length). The scaling parameter, a_j, converts units of l_j to weight, and b_j is exponential rate of increase. The error of the length-weight relationship was assumed to have a lognormal error structure (Ricker, 1979):

$$w_i \sim \text{lognormal}\left(\log(\hat{w}_{i,j}), \sigma_{w,j}\right) \tag{2}$$

where the observed weight at length w_i is distributed using a lognormal distribution with mean $\log(\hat{w}_{i,j})$ and standard deviation, $\sigma_{w,j}$. [Correction added on 25 June 2020, after first online publication: Equations 2, 4, 5 and 8 were rendered incorrectly and have been amended in the current version of the article.]

The von Bertalanffy growth model was parameterized following the original formulation (von Bertalanffy, 1934):

$$\hat{l}_{i,j} = L_{\infty,j} - (L_{\infty,j} - L_{0,j})e^{-kt_i} \tag{3}$$

where the predicted length, $\hat{l}_{i,j}$, is conditioned on a specimen's age, t_i, $L_{\infty,j}$ is the species asymptotic length, k is the Brody growth coefficient expressed in years^{-1} and $L_{0,j}$ is the size at birth for a given length measurement j. It was assumed that the observed length at age $l_{i,j}$ was described by a lognormal distribution (Millar, 2002):

$$l_{i,j} \sim \text{lognormal}\left(\log\left(\hat{l}_{i,j}\right), \sigma_{l,j}\right) \tag{4}$$

with mean $\log\left(\hat{l}_{i,j}\right)$ and a standard deviation of $\sigma_{l,j}$. Departing from the standard VBGM estimation procedure, an additional likelihood was added to constrain the posterior distribution of L_0 using data on the size at birth, $p_{i,j}$:

$$p_{i,j} \sim \text{lognormal}\left(\log(L_{0,j}), \sigma_{L_0,j}\right) \tag{5}$$

where a lognormal distribution with mean $\log(L_{0,j})$ and a standard deviation of $\sigma_{L_0,j}$ describes the observed size at birth.

Using the von Bertalanffy growth model parameters and rearranging the VBGM equation (Equation (1) in terms of half-lives (Cailliet et al., 2006), the three ages at specific proportions of L_∞ were calculated: (a) the x-intercept or the theoretical age at length zero (t_0), (b) the age at maturity $\left(t_{\frac{2}{3}}\right)$ (Beverton & Holt, 1959; Jensen, 1996) and (c) longevity ($t_{0.95}$) (Ricker, 1979).

$$t_{x,j} = \frac{1}{k}\log\left(\frac{L_{\infty,j} - L_{0,j}}{L_{\infty,j}(1-x)}\right) \tag{6}$$

where x is the specific proportion of L_∞ in question and $t_{x,j}$ is the age at that specific proportion for a particular length measurement. Although t_0 is a relatively common parameter to either estimate directly or derive post hoc, the use of $t_{\frac{2}{3}}$ as the age at maturity is less common in elasmobranchs. Nonetheless, the use of Beverton-Holt life-history invariants, such as length at maturity is approximately two-thirds proportional to L_∞ (Beverton & Holt, 1959), is relatively

common in teleosts (Jensen, 1996; Prince et al., 2015). Mortality at length (or age), M_l, was derived from the VBGM parameters as shown in Charnov et al. (2013).

$$M_{l_t} = k \left(\frac{l_{t,j}}{L_{\infty,j}} \right)^{-1.5} \tag{7}$$

It is important to note that there are other analytical solutions for age at maturity, longevity and M_l (Fabens, 1965; see Mangel, 2017 for a synopsis of maturity and mortality derivations), but given the constraints of the sampling in this study, the previous assumptions for maturity, longevity and mortality at length were used. Lastly, the ratio of total length to disc width at age was calculated based on the mean length at age predicted by the respective VBGMs.

For the pooled specimens (regardless of sex), all parameters were estimated irrespective of their length composition data with the exception of the Brody growth coefficient, k, which was shared between the VBGMs for each length composition type. The same parameterization was held for the sex-specific models with the exception of L_0 which was shared between sexes. In this manner, data from both size composition types and both sexes informed parameters shared between the submodels.

The priors for the all parameters were assumed to be half-Normal (a normal distribution truncated at zero). For the length-weight relationships and von Bertalanffy growth model parameters, an *optim* routine implementing both models in *R 3.6.2* (R Core Team, 2019) was used to generate maximum likelihood estimates (MLE) to be used as the prior mean following Caltabellotta et al. (2019a). An assumed C.V. (0.8) was used to scale these ML estimates to standard deviations to be used as the prior standard deviation (Equation 8). The result was to generate priors roughly centred on the central tendency of the data but diffuse enough to not strongly impact the posterior. All standard deviation parameters, σ_X, were assumed to follow a half-Normal with mean 0 and standard deviation of 2. The expression $T(0)$ indicates a truncation in the distribution at zero.

$$\theta \sim N(\theta_{MLE}, \theta_{MLE} * CV) T(0) \tag{8}$$

All priors were specified using weakly informative priors, such that minor structural information was provided and the inference was weakly regularized (Gelman et al., 2017). The pooled and sex-specific models were implemented using the *rstan* package (STAN Development Team, 2020) separately using the No-U-Turn variant of the Hamiltonian sampling algorithm over four chains with 5000 warmup iterations that were discarded and 2500 samples per chain resulting in a total of 10,000 samples per model. Convergence was assessed visually using trace plots and the potential scale reduction statistic (Gelman-Rubin Diagnostic) (Gelman & Rubin, 1992) with $\hat{R} < 1.1$ indicating convergence (Gelman et al., 2013).

From each model, each parameter's median $(\tilde{\theta})$ and 90% credible interval ($\alpha = 0.1$) was calculated from the posterior distribution. A posterior predictive check was conducted using a lognormal random number generator (Gelman & Hill, 2006, p. 158) as well as used to generate median model estimates, $\hat{l}_i$, and 90% credible intervals across a vector of ages (0 to the maximum observed age). For the sex-specific models, residuals were calculated for each observation conditioned on the observed sex. The estimated age at maturity was also compared using the length at maturity for females (length at 50% maturity: 318.9 mm) and males (279.8 mm) estimated by Rolim et al. (2016). For this, Equation (6 was modified such that denominator was $L_\infty - L_m$. For parameters that varied between sexes, the difference between the parameter estimates (e.g., $\theta_F - \theta_M$) was calculated within the model and sampled along with the other parameters. Sex-specific parameters were significantly different when the 90% credible interval of the difference between parameters did not contain zero (Kéry, 2010). By taking the average of parameter differences that were less than zero, the probability of the difference was calculated (Equation (9), where n is the number of posterior samples (Kruschke, 2013). Parameter differences were significant if $\frac{\alpha}{2} < p(\theta_F - \theta_M)$ or $p(\theta_F - \theta_M) > 1 - \frac{\alpha}{2}$.

$$p(\theta_F - \theta_M) = \frac{\sum (\theta_F - \theta_M < 0)}{n} \tag{9}$$

3 | RESULTS

3.1 | Sample size

In total, 170 specimens were sampled and analysed with 107 females ranging in total length from 215 to 470 mm (Figure 1d) and disc width from 110 to 250 mm as well as 63 males ranging in total length from 236 to 380 mm (Figure 1d) and disc width from 126 to 177 mm. For both sexes, most of the sample was composed of medium- to large-sized individuals (300–470 mm), although some small individuals (<300 mm) were also recorded (Figure 2a).

3.2 | Age determination

Age precision estimates were high at 2.75% (Index of Average Percent Error) and 3.89% (C.V.). First and second reads agreed ±1 year in 61.17% of the samples. Bowker's test of symmetry and age-bias plots identified no systematic bias in ageing counts between reads 1 and 2 for *N. brasiliensis* (χ^2 = 13.45, df = 15, P = 0.568; Figure 1e).

A significant linear relationship was found between VR *vs.* l_{TL} and VR *vs.* l_{DW} (P < 0.01) for pooled sexes (l_{TL} = 13.18 + 8.99 * VR, r^2 = 0.64; l_{DW} = 5.85 + 4.87 * VR, r^2 = 0.65). Nonetheless, the relationship was different between sexes (l_{TL}: $F_{1,167}$ = 12.601, P = 0.0005; l_{DW}: $F_{1,167}$ = 12.031, P = 0.0007); therefore, the linear relationship for males was l_{TL} = 20.81 + 4.96 * VR, r^2 = 0.31; l_{DW} = 10.04 + 2.50 * VR, r^2 = 0.37, and for females was l_{TL} = 12.02 + 9.58 * VR, r^2 = 0.63; l_{DW} = 6.35 + 4.82 * VR, r^2 = 0.60.

Most of vertebral growth bands were identified along the intermedialia and in the corpus calcareum of the vertebral centrum; nonetheless, band-pair counts were based on the corpus calcareum. The
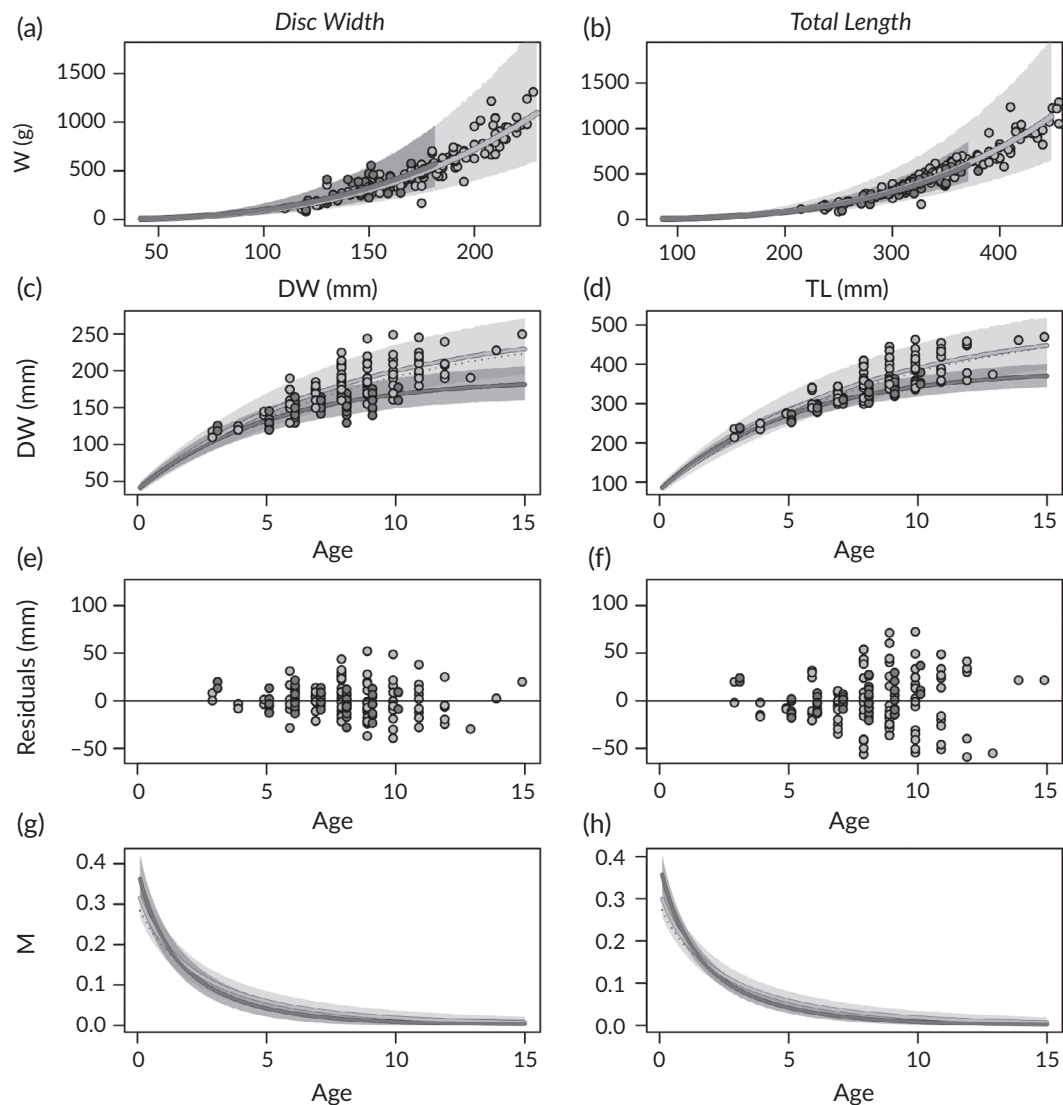
FIGURE 2 (a, b) Predicted length-weight, (c, d) von Bertalanffy growth models, (e, f) residuals of the von Bertalanffy growth model, and (g, h) predicted mortality at age for disc width (left panels) and total length (right panels). Median predictions are indicated by lines, data by points and 90% credible intervals by shaded polygons. Dark grey indicates model predictions specific to males and light grey to females. ◯ ObsF, ● ObsM, —— Med. F, —— Med. M, ······ Median, ▫ 90% CI F, ▪ 90% CI M

birthmark was measured at a distance of 0.47 ± 0.01 mm ($\mu \pm \sigma$) from the focus. Age readings included individuals from age-3 to age-15 in females (with most between age-7 and age-12) and from age-3 to age-10 in males (most between age-6 and age-9).

3.3 | Bayesian life-history modelling

The trace plots visually indicated that the sampling algorithm converged (Supporting Information Figure S1), and the Gelman-Rubin convergence diagnostic, which considers the within and between variances from each chain, indicated that pooled and sex-specific integrated models approached a value of $\hat{R} < 1.1$ and converged to stable posterior distributions. Marginal posterior and prior distributions for each parameter in the pooled and sex-specific submodels were normal and shrunk relative to the prior (Supporting Information Figures S2

and S3). From the posteriors, it is readily apparent that the more abundant females in the data set swamped any male-specific signal in the pooled model (pooled posteriors overlapped more frequently with the sex-specific female posteriors).

For the length-weight relationship, the pooled model estimated isometric growth for disc width (90% CI of b_{DW} contains 3) and positive allometric growth for total length $\left(\tilde{b}_{TL} = 3.21\right)$ (Table 1). In the sex-specific model, males presented negative allometric growth for disc width $\left(\tilde{b}_{DW} = 2.5\right)$ and isometry for total length $\left(\tilde{b}_{TL} = 3.02\right)$, whereas females showed isometric growth for disc width $\left(\tilde{b}_{DW} = 3.01\right)$ and for total length $\left(\tilde{b}_{TL} = 3.12\right)$ (Table 1). Nonetheless, none of the sex-specific length-weight parameters were significantly different between sexes ($P = 0.707$ for a and $P = 0.407$ for b).

For the von Bertalanffy growth model, the pooled model predicted $\tilde{L}_{\infty,DW}$ and $\tilde{L}_{\infty,TL}$ higher than either sex-specific estimate and correspondingly a lower k. As expected the size at birth, $\tilde{L}_0$, was

TABLE 1 Summary of the median posterior value and 90% credible interval for length-weight, von Bertalanffy growth model and derived parameters

$f(x)$	Θ	Disc Width Median Estimate (90% C.I.)	Total Length Median Estimate (90% C.I.)
Length–weight	a	1.32e-04 (6.51e-05–2.32e-04)	3.08e-06 (1.58e-06–5.33e-06)
	F	8.39e-05 (3.24e-05–1.87e-04)	3.65e-06 (1.77e-06–6.42e-06)
	M	1.33e-04 (3.59e-05–2.74e-04)	3.19e-06 (1.07e-06–6.33e-06)
	b	2.93 (2.82–3.07)	3.23 (3.14–3.34)
	F	3.01 (2.86–3.20)	3.20 (3.11–3.33)
	M	2.94 (2.79–3.20)	3.22 (3.10–3.41)
von Bertalanffy growth model	L_∞	267 (248–290)	527 (491–572)
	F	264[a] (247–286)	515[a] (481–556)
	M	190[a] (181–200)	387[a] (370–408)
	k	0.112 (0.0961–0.128)	
	F	0.125[a] (0.108–0.145)	
	M	0.194[a] (0.170–0.222)	
	L_0	38.6 (36.6–40.8)	80.7 (77.3–84.4)
	F/M	38.8 (36.8–41.1)	80.5 (77.2–84.1)
Derived	t_0	−1.40 (−1.54–−1.27)	−1.49 (−1.63–−1.36)
	F	−1.27 (−1.41–−1.14)	−1.36[a] (−1.49–−1.23)
	M	−1.18 (−1.31–−1.06)	−1.20[a] (−1.33–−1.08)
	$t_{\frac{2}{3}}$	8.44 (7.25–9.94)	8.35 (7.16–9.85)
	F	7.49[a] (6.39–8.86)	7.40[a] (6.30–8.76)
	M	4.47[a] (3.87–5.19)	4.45[a] (3.85–5.17)
	$t_{0.95}$	25.4 (22–29.7)	25.3 (21.9–29.6)
	F	22.6[a] (19.4–26.5)	22.5[a] (19.4–26.4)
	M	14.2[a] (12.4–16.4)	14.2[a] (12.4–16.3)

Note: Separate parameters for disc width and total length were estimated for all parameters but k and for both sexes (F = females, M = males) for all parameters but L_0, which was shared in the sex-specific models.
[a]denotes a parameter that is significantly different ($\alpha = 0.1$) between sexes (Kruschke, 2013).

similar between pooled and sex-specific models given that L_0 was shared between sexes in the sex-specific model. In the sex-specific model, females were predicted to have median asymptotic disc widths 1.4 times larger than those of males ($\tilde{L}_{\infty,DW} = 265$ mm for females and 189 mm for males). Similarly, females were predicted to have median asymptotic total lengths 1.33 times larger than those of males ($\tilde{L}_{\infty,TL} = 515$ mm for females and 387 mm for males). Correspondingly, females were predicted to grow slower than males ($\tilde{k} = 0.125$ for females and 0.195 for males). As a result of these sex-specific differences in length at age, both asymptotic size and the Brody growth coefficient were significantly different between sexes ($P = 0$ for L_∞ and $P = 1$ for k).

The derived VBGM parameter for theoretical age at length zero, t_0, was similar between the disc width and total length submodels (Table 1; $\tilde{t}_{0,DW} = -1.54$ and $\tilde{t}_{0,TL} = -1.63$). Between sexes, only $t_{0, TL}$ was significantly different ($P = 0.9715$). Age at maturity, $t_{\frac{2}{3}}$, was similar between length measurement submodels and was significantly different between sexes ($P = 0$). Females were estimated to mature around 7.5 years, approximately 1.6 times later than males that were estimated to mature around 4.5 years (Table 1). Using the length at 50%

maturity from Rolim *et al.* (2016), females were estimated to mature at a median of 6.3 years and males at a median of 5.4 years. Similar to age at maturity, longevity was similar between submodels and significantly different between sexes ($P = 0$). Estimated females' longevity was approximately 22.5 years, whereas males' estimated longevity was approximately 14 years.

As assessed by the insignificant differences between the sex-specific length-weight, both sexes had similar length-weight relationships for both length measurements (Figure 2a,b). The significant differences between sexes in the VBGM are apparent with females growing larger than males for both length measurements (Figure 2c,d). For disc width, the residuals of the sex-specific VBGM are symmetrically distributed (Figure 2e) but for total length, large females appear to fall into two groups with one group continuing to grow in TL (with positive residuals) and another group that ceases growing around age 10 (with negative residuals; Figure 2f). Variability in the residuals was correlated with the number of specimens per age for both length measurements ($R = 0.37$ and $R = 0.17$ for disc width and total length, respectively). For disc width, the age with the highest variability was age 10, and for total length, it was age 12. There was only one female

specimen > age 12, so variability could not be assessed for these ages. Mortality at age was similar between sexes and length measurements with a negative exponential relationship between age and mortality (Figure 2g,h).

The predicted ratio between l_{TL} and l_{DW} for males and females decreased as a function of age but more rapidly for females. The result is that females are predicted to grow proportionally wider than males as a function of age (Figure 3). The observed median ratio by age for females visually matches the predicted ratio. For males, the observed median ratios are similar to females for ages 3–6 and then the observed ratio increases above the predicted ratio for ages 7–9, reflecting a lengthening of males relative to their width.

4 | DISCUSSION

The life history of Torpediniformes is poorly known (Frisk, 2010) but essential for assessing their conservation status. Relative to other batoids, *N. brasiliensis* females grow slower, mature later and live longer; whereas males grow faster, mature earlier and live shorter (Frisk, 2010). Along with a small endemic range and low reproductive capacity, it is very likely that *N. brasiliensis* is highly at risk from external impacts. The ongoing impact of by-catch in the Brazilian pair trawl fishery along with a skewed sex ratio towards females in the by-catch is likely to put the species in jeopardy. The integrated Bayesian modelling framework applied here was a useful tool for incorporating multiple length measurements, sharing data between sexes and propagating uncertainty into derived life-history characteristics in *N. brasiliensis* and is likely to be useful for other Data-Deficient Batoids.
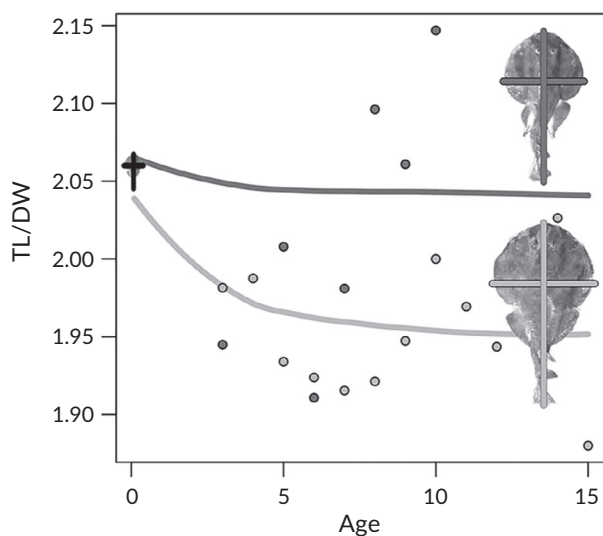

FIGURE 3 The ratio of total length (TL) to disc width (DW) for females (light grey) and males (dark grey) as function of age initializing at the size of birth, L_0 (black). Observed median ratios are in points and predicted are in lines. Pictograms indicate the relative size of the disc width and total length for females and males at L_∞ based on predictions. ● Obs., —— Pred., —— L0, —— Female, —— Male

Compared to other members of the order Torpediniformes, *N. brasiliensis* has a maximum age (15 years for females and 11 years for males) similar to that observed for the giant electric ray *Narcine entemedor* (Jordan & Starks 1895): 15 years for females and 11 years for males (Villavicencio-Garayzar, 2000); the Pacific electric ray *Torpedo californica* (Ayres 1855): 16 years for females and 14 years for males (Neer & Cailliet, 2001); and the marbled electric ray *Torpedo marmorata* (Risso 1810): 20 years for females and 13 years for males (Mellinger, 1971) (Table 2). Within the genera *Narcine*, *N. brasiliensis* is above the median (400 mm) (Carvalho *et al.*, 1999; Moreno *et al.*, 2010; Villavicencio-Garayzar, 2000) for maximum observed length but smaller than *Narcine bancroftii* (Griffith & Smith 1834; 600 mm TL; females; Moreno *et al.*, 2010; Carlson *et al.*, 2016) and about half the size of *N. entemedor* (930 mm TL; females; Villavivencio-Garayzar, 2000). The exponential rate of increase of the length-weight relationship, *b*, was higher for females (3.2) and males (3.22) than that observed for other members of the order Torpediniformes, which with the exception of females of *T. californica* (3.02, Neer & Cailliet, 2001) and females of *T. marmorata* in Turkish waters (3.04, Duman & Başusta, 2013) had *b* less than 3 when measured (Villavivencio-Garayzar, 2000; Consalvo *et al.*, 2007; Estalles *et al.*, 2011; El Kamel-Moutalibi *et al.*, 2013; Cruz-Aguero *et al.*, 2018) (Table 2).

Only three other members of the order Torpediniformes (*N. entemedor*, *T. californica* and *T. marmorata*) had von Bertalanffy growth models to compare to *N. brasiliensis* (Duman & Başusta, 2013; Neer & Cailliet, 2001; Villavicencio-Garayzar, 2000). Of these four, *N. brasiliensis* had the smallest asymptotic length, L_∞ – not surprising, considering that, with the exception of *T. marmorata* from Turkish waters (Duman & Başusta, 2013), it had the smallest observed maximum TL within this sub-set (Table 2). Similarly, the size at birth L_0 was smaller than that observed for *N. entemedor* and the extrapolated for *T. californica* but larger than the extrapolated L_0 for the *T. marmorata* population from Turkish waters (40.5, Duman & Başusta, 2013) (Table 2). The female Brody growth coefficient, *k*, for *N. brasiliensis* was the second lowest among the four species with VBGMs (only *T. californica* was lower; Neer & Cailliet, 2001). The male *k* was only lower than *N. entemedor* (Villavicencio-Garayzar, 2000), but the *k* estimated for *T. marmorata* was from a pooled model for both sexes (Duman & Başusta, 2013).

Female and male age at maturity in *N. brasiliensis* was lower than that in *T. californica* (9 years for females, 6 years For males; Neer & Cailliet, 2001) and *T. marmorata* (12 years for females, 5 years for males; Mellinger, 1971). Though it was not estimated by Villavicencio-Garayzar (2000), the extrapolated age at maturity (based on Beverton & Holt, 1959; Jensen, 1996) for *N. entemedor* is much earlier than that for the other species (2.4 years for females and 2.6 years for males). This is not surprising given the much higher *k* estimated for females and males than the other Torpediniformes with VBGMs (Table 2). Interestingly, with the exception of the much larger *N. entemedor* and *T. californica*, the length at maturity was similar among many other members of Torpediniformes (Table 2). Based on the maximum age observed and the derived age at maturity of *N. brasiliensis* females reproduce during 40% of their life span and

TABLE 2 Summary of maximum observed age (T_{max}), maximum observed length (L_{max}, mm), exponential rate of increase for the length-weight relationship (b), asymptotic length (L_∞, mm), Brody growth coefficient (k), size at birth (L_0, mm), length at maturity (L_{mat}, mm), theoretical age at length zero (t_0) and age at maturity ($t_{\frac{2}{3}}$), and longevity ($t_{0.95}$) for the females (F), males (M) or both sexes (centred between the columns) for the order Torpediniformes from literature

Species	T_{max} F	T_{max} M	L_{max} F	L_{max} M	b F	b M	L_∞ F	L_∞ M	k F	k M	L_0 F	L_0 M	L_{mat} F	L_{mat} M	t_0 F	t_0 M	$t_{\frac{2}{3}}$ F	$t_{\frac{2}{3}}$ M	$t_{0.95}$ F	$t_{0.95}$ M
Narcine brasiliensis[a]	15	11	470	380	3.2	3.22	515	387	0.125	0.194	81		343	258	−1.36	−1.2	7.4	4.5	22.5	14.2
Narcine bancroftii[b]			600	450							115		310	216						
Narcine entemedor[c]	15	11	930	670	2.89	2.54	812	612	0.372	0.315	150		541†	408†	−0.55†	−0.89†	2.4†	2.6†	7.5†	8.6†
Torpedo californica[d]	16	14	1020	842	3.02	2.88	1373	921	0.073	0.137	181†	170†	731	645	−1.93	−1.48	8.4†	7.3†	47.3	25.3
Torpedo marmorata[e]	20	12.5																		
T. marmorata[f]			553	364	2.85	2.72							312	251			12	5		
T. marmorata[g]	6		400	303	3.04	2.82	573		0.187		41		382		−0.39				15.6	
Torpedo torpedo[h]			477	445	2.86	2.72							258	249						
T. torpedo[i]			435	400	2.81						98									
Diplobatis ommata[j]			218		2.82															
Discopyge tschudii[k]			380	430	2.84	2.90							210	300						

Note. Derived quantities from: $L_0 = L_\infty \left(1 - e^{kt_0}\right)$; $L_{mat} = \frac{2}{3}L_\infty$; $t_0 = \left(\frac{1}{k}\right)\left(\frac{L_\infty - L_0}{L_\infty}\right)$; $t_{\frac{2}{3}} = \left(\frac{1}{k}\right)\left(\frac{L_\infty - L_0}{L_\infty\left(1 - \frac{2}{3}\right)}\right)$; $t_{0.95} = \left(\frac{1}{k}\right)\left(\frac{L_\infty - L_0}{L_\infty(1 - 0.95)}\right)$.

[a] This study.
[b] Moreno et al. (2010).
[c] Villavicencio-Garayzar (2000).
[d] Neer and Cailliet (2001).
[e] Mellinger (1971).
[f] Consalvo et al. (2007).
[g] Duman and Başusta (2013).
[h] Consalvo et al. (2007).
[i] El Kamel-Moutalibi et al. (2013).
[j] Cruz-Aguero et al. (2018).
[k] Estalles et al. (2011).

males 44%. Late sexual maturity, common among Batoids, decreases a population's turnover capability and hinders resilience in response to fishing mortality (Frisk, 2010).

Similar to many elasmobranchs, *N. brasiliensis* females were estimated to grow larger and slower, mature later and live longer than their male counterparts (Cailliet & Goldman, 2004; Cortés, 1998; Hamlett, 2005). Within Torpediniformes, this form of sexual dimorphism is common with only one measured species, *Discopyge tschudii* Heckel 1846, exhibiting the opposite phenomenon with larger males than females (Estalles *et al.*, 2011). These characteristics are concerning when considering this study's fishery-derived sample composed of over 40% more females than males. Fisheries impact two life stages of the species in southeastern and South Brazil. The pair trawl fleet, which captured the study sample, frequently captures the species (Rotundo *et al.*, 2019) and, with a 90 mm diamond mesh-size, selects larger individuals (>30 cm), which are predominantly female (Rolim *et al.*, 2015). Shrimp trawl fisheries also capture the species but, with a 30 mm mesh-size, select smaller individuals (Branco *et al.*, 2015). Generally, the pair trawl fleet operates in deeper regions of the coast (Imoto *et al.*, 2016; Rolim & Ávila-da-Silva, 2016), whereas the shrimp trawl fishery operates in shallow coastal areas. Exacerbating the potential risk to the species is its endemism to southern Brazil and northern Argentina (Carvalho, 1999) and, aggregating these risks results in a very high likelihood that the species is in one of the IUCN Red List threatened categories. Moreover, because of the lack of commercial value, limited information is available on the fisheries' catch rates of the species and its population status over time.

Common data availability issues in elasmobranchs, such as the analytical challenges of biased length frequency, and the multidimensional nature of Batoidea growth motivated the integrated Bayesian framework applied, herein. Low data availability is a common issue in elasmobranch growth studies, and techniques have been put forward to ameliorate the issue (Cailliet, 2015; Smart *et al.*, 2013). These loosely fall into two categories: back-calculation and fixing parameters in the VBGM such as L_0 as suggested by Cailliet *et al.* (2006) or, less commonly, fixing L_∞. Neither solution is truly desirable. The former relies on a proportionality assumption regarding the width of growth bands to the growth increment (recent evidence disputes the linkage between the band and the increment entirely; Natanson *et al.*, 2018) as well as induces biased standard errors by artificially increasing the sample size. The latter has the undesirable property of fixing parameters as well as results in issues with information criterion-based model selection techniques. It was beyond the scope of this study to evaluate back-calculation techniques, but the fixing of parameters is solved in the Bayesian framework by including additional data on size at birth (though this certainly can be accomplished with degrees of freedom correction in a maximum likelihood framework). An additional likelihood is added to the model, and L_0 is jointly estimated based on the size at birth data as well as length at age data. This is the natural extension to Cailliet *et al.*'s (2006) suggestion of incorporating the abundant size at birth information as well as allows the addition of a prior on both L_0 and σ_{L_0}. The latter also allows specific information to be encoded about the range in size at birth, which may be important in some species but is unlikely to be a factor in the order Torpediniformes. An important

caveat to including size at birth information is that it is likely important to collect the data from similar regions as the length at age data, especially for wide-ranging species.

Low data availability often results in biased length frequencies. Even among Actinopterygii growth studies, length frequencies are frequently biased against small or large fish (Myers & Hoenig, 1997; Pope *et al.*, 1975). This is largely dependent on the fishing (or sampling) gear but can also result from spatial or temporal autocorrelation (Maunder & Punt, 2013; Sampson, 2014). The result of this sampling is biased growth model parameters (Gwinn *et al.*, 2010; Pardo *et al.*, 2013) of which fixing parameters has been an ameliorating method (Cailliet *et al.*, 2006; Gwinn *et al.*, 2010). Estimating L_0 based on size at birth and length at age achieves the same as fixing parameter without the biases. Concordantly, issues resulting from low data availability and bias are exacerbated when sex-specific VBGMs are estimated. A second feature of the integrated Bayesian model helps to amend this issue: sharing information between sexes. In the *N. brasiliensis* model, L_0 was shared between sexes inducing exchangeability in the size at birth data. In this manner, some minimization of the biases occurs, although simulation is needed to understand the relative magnitude of this impact.

Lastly, in the case of Batoidea, many members grow in two dimensions. For the Myliobatiformes, this is likely in disc width and disc length, and for Rajiformes, it is disc width and disc length or disc width and total length. For Torpediniformes as well as Rhinopristiformes, members are likely to grow in disc width and in total length. In the case of *N. brasiliensis*, changes in body scaling by sex and over ages likely reflect differences in energetic allocation for reproduction. A relative lengthening may allow males higher movement rates in search for mates or relative wider bodies may generate more lift for heavier gestating females. Other studies have estimated VBGM separately for multiple growth measurements (*e.g.*, Caltabellotta *et al.*, 2019b; Neer & Cailliet, 2001; Villavicencio-Garayzar, 2000) but, for data-limited species, estimating k with low uncertainty is extremely important for estimating derived life-history characteristics. An integrated Bayesian framework is exceptionally useful in these circumstances as parameters can be shared between length measurements, such as the Brody growth coefficient, and uncertainty in either measurement is translated to any derived life-history characteristics.

There are caveats to using derived life-history characteristics with the most obvious being that there are no direct observations of age at maturity, mortality or longevity. A secondary concern is the underlying assumptions of the derivations. Beverton and Holt (1959) estimated that age at maturity equals the time to reach $\frac{2}{3}L_\infty$ but, with the exception of one rajiform, is based entirely on Actinopterygii. Jensen (1996) further derived the two-thirds Beverton-Holt life-history invariant and, recently, Prince *et al.* (2015) estimated a mean ratio of 0.64 for Chondrichthyes with $M/k > 1$ indicating this assumption is perhaps not entirely without merit. The only Torpediniformes member with both L_∞ and length at maturity estimates is *T. californica* with a ratio of 0.53 for females and 0.70 for males (Neer & Cailliet, 2001), further indicating that the assumption is not entirely inappropriate for *N. brasiliensis*.

Regarding the other derived values, Charnov et al.'s (2013) mortality at length relationship uses data from Gislason et al. (2010), and of the 168 studies analysed, only three report elasmobranchs. Prince et al. (2015) revisited the Beverton-Holt invariant of $M/k = 1.5$, supported by Jensen (1996) and Charnov et al. (2013), and found a mean of 2.04 for Chondrichthyes with $M/k > 1$. With so few batoids with age-growth, maturity and mortality estimates coming from direct observations (only one species was in the Prince et al., 2015 study), the $M/k = 1.5$ Beverton-Holt life-history invariant should be tenuously applied to members. Taylor (1958) and Ricker's (1979) longevity relationship also highlights that the lack of elasmobranchs is ubiquitous as it is entirely based on gadiforms despite the ubiquity of applying the invariant to studies. Although concerning for their broader use, the lack of elasmobranchs is not surprising, as few studies have measured elasmobranch maturity and even fewer still have measured mortality (Cortés, 1998). Nonetheless, some estimate of life-history characteristics, even if based on derivations from length at age observations, is critical for assessing the threatened status of elasmobranchs. Future studies should revisit these relationships between growth and life-history characteristics to either support or refute the scaling for elasmobranch species.

The life-history characteristics and low reproductive output of *N. brasiliensis* reduce the species' resilience to external threats (Gomes et al., 2010; Rolim et al., 2016). Frequent captures of mature females by the pair trawl fishery likely put the species in jeopardy and could establish a threatened IUCN Red List listing. With similar body morphology and similar habitats (Carvalho et al., 1999), many other members of Narcinidae likely possess similar life-history characteristics and are at risk to persistent external impacts. The integrated Bayesian framework applied, herein, was a useful tool for combining the multiple length measurements in Batoidea, circumventing some undesirable aspects of common parameter fixing, as well as propagating uncertainty into derived life-history characteristics. The latter is important for evaluating sex-specific risks as in *N. brasiliensis* but also for progressing beyond point estimates (or ranges) into probabilistic space.

All data and scripts are available at https://doi.org/10.17605/OSF.IO/S9TPC.

CONFLICT OF INTEREST
The authors declare that they have no conflict of interest.

ORCID
Fernanda A. Rolim https://orcid.org/0000-0003-3761-3970
Zachary A. Siders https://orcid.org/0000-0002-0798-9515
Fabio P. Caltabellotta https://orcid.org/0000-0001-8174-2249

REFERENCES

Beamish, R. J., & Fournier, D. A. (1981). A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences*, *38*, 982–983.

Beverton, R. J. H., & Holt, S. J. (1957). *On the dynamics of exploited fish populations, reprint of* (1st ed.). Caldwell, NJ: The Blackburn Press.

Beverton, R. J. H., & Holt, S. J. (1959). A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. In *Ciba foundation symposium - the lifespan of animals (colloquia on ageing)* (pp. 142–180). Hoboken, NJ: John Wiley & Sons, Ltd.

Bowker, A. H. (1948). A test for symmetry in contingency tables. *Journal of the American Statistical Association*, *43*, 572–574.

Branco, J. O., Freitas Júnior, F., & Christoffersen, M. L. (2015). Bycatch fauna of seabob shrimp trawl fisheries from Santa Catarina state, southern Brazil. *Biota Neotropica*, *15*, e20140143.

Cailliet, G. M. (2015). Perspectives on elasmobranch life-history studies: a focus on age validation and relevance to fishery management. *Journal of Fish Biology*, *87*, 1271–1292.

Cailliet, G. M., & Goldman, K. J. (2004). Age determination and validation in Chondrichthyan fishes. In J. C. Carrier, J. A. Musick, & M. R. Heithaus (Eds.), *Biology of sharks and their relatives* (pp. 404–453). CRC Press: Boca Raton, FL.

Cailliet, G. M., Smith, W. D., Mollet, H. F., & Goldman, K. J. (2006). Age and growth studies of Chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. *Environmental Biology of Fishes*, *77*, 211–228.

Caltabellotta, F. P., Silva, F. M., Motta, F. S., & Gadig, O. B. F. (2019a). Age and growth of a threatened endemic skate, *Rioraja agassizii* (Chondrichthyes, Arhynchobatidae) western South Atlantic. *Marine and Freshwater Research*, *70*, 84–92.

Caltabellotta, F. P., Siders, Z. A., Murie, D. J., Motta, F. S., Cailliet, G. M., & Gadig, O. B. F. (2019b). Age and growth of three endemic threatened guitarfishes *Pseudobatos horkelii*, *P. percellens* and *Zapteryx brevirostris* in the western South Atlantic Ocean. *Journal of Fish Biology*, *95*, 1236–1248.

Campana, S. E., Annand, M. C., & McMillan, J. I. (1995). Graphical and statistical methods for determining the consistency of age determinations. *Transactions of the American Fisheries Society*, *124*, 131–138.

Carlson, J., Castro, J., Driggers, W., Lee, J.L., & Brame, A. (2016). Lesser electric ray status review report: lesser electric ray (*Narcine bancroftii*). Report to National Marine Fisheries Service, SERO, Protected Resources Division, September, Vol. 45, pp. 2.

Carvalho, M. R. (1999). *A systematic revision of the electric ray genus Narcine (Chondrichthyes: Torpediniformes: Narcinidae), and the higher-level phylogenetic relationships of the elasmobranch fishes (Chondrichthyes: Elasmobranchii)*. PhD thesis, The City University of New York - American Museum of Natural History.

Carvalho, M. R., Compagno, L. J. V., & Last, P. R. (1999). Batoid fishes: Order Torpediniformes. In K. E. Carpenter & V. H. Niem (Eds.), *The Living Marine Resources of the Western Central Pacific: Batoid fishes, chimaera and bony fishes part 1 (Elopidae to Linophrynidae)* (pp. 1398–1409). Food and Agriculture Organization of the United Nations: Rome.

Carvalho, M. R., & Last, P. R. (2016). Narcinidae. In P. Last, W. White, M. de Carvalho, B. Séret, M. Stehmann, & G. Naylor (Eds.), *Rays of the World* (pp. 278–340). CSIRO Publisher, Corney University Press: Ithaca, NY.

Chang, W. Y. B. (1982). A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences*, *39*, 1208–1210.

Charnov, E. L., Gislason, H., & Pope, J. G. (2013). Evolutionary assembly rules for fish life histories: natural mortality in fish life-history evolution. *Fish and Fisheries*, *14*, 213–224.

Consalvo, I., Scacco, U., Romanelli, M., & Vacchi, M. (2007). Comparative study on the reproductive biology of *Torpedo torpedo* (Linnaeus, 1758) and *T. marmorata* (Risso, 1810) in the Central Mediterranean Sea. *Scientia Marina*, 71, 213–222.

Cortés, E. (1998). Demographic analysis as an aid in shark stock assessment and management. *Fisheries Research*, 39, 199–208.

Cruz-Aguero, J. D. L., García-Rodríguez, F. J., & Cota-Gómez, V. M. (2018). Length-weight relationships of five elasmobranch species from the pacific coast of Mexico. *Turkish Journal of Fisheries and Aquatic Sciences*, 18, 1005–1007.

Duman, Ö. V., & Başusta, N. (2013). Age and growth characteristics of marbled electric ray *Torpedo marmorata* (Risso, 1810) inhabiting Iskenderun Bay, North-Eastern Mediterranean Sea. *Turkish Journal of Fisheries and Aquatic Sciences*, 13, 541–549.

El Kamel-Moutalibi, O., Mnasri, N., Boumaïza, M., Ben Amor, M. M., Reynaud, C., & Capapé, C. (2013). Maturity, reproductive cycle and fecundity of common torpedo, *Torpedo torpedo* (Chondrichthyes, Torpedinidae) from the lagoon of Bizerte (northeastern Tunisia, Central Mediterranean). *Journal of Ichthyology*, 53, 758–774.

Estalles, M., Coller, N. M., Di Giácomo, E. E., & Perier, M. R. (2011). Distribution and reproductive biology of the electric ray *Discopyge tschudii* Heckel, 1846 in san Matías gulf, northern Patagonia, Argentina. *Neotropical Ichthyology*, 9, 831–838.

Fabens, A. J. (1965). Properties and fitting of the von Bertalanffy growth curve. *Growth*, 29, 265–289.

Frisk, M. G. (2010). Life history strategies of Batoids. In J. C. Carrier, J. A. Musick, & M. R. Heithaus (Eds.), *Sharks and their relatives II* (pp. 299–332). CRC Press: Boca Raton.

Gelman, A., Carlin, J. B., Stern, H. S., Dunson, D. B., Vehtari, A., & Rubin, D. B. (2013). *Bayesian data analysis* (3rd ed.). New York, NY: Chapman and Hall/CRC.

Gelman, A., & Hill, J. (2006). *Data analysis using regression and multilevel/hierarchical models* (1st ed.). New York, NY: Cambridge University Press.

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, 7, 457–472.

Gelman, A., Simpson, D., & Betancourt, M. (2017). The prior can often only be understood in the context of the likelihood. *Entropy*, 19, 555.

Gislason, H., Daan, N., Rice, J. C., & Pope, J. G. (2010). Size, growth, temperature and the natural mortality of marine fish. *Fish and Fisheries*, 11, 149–158.

Goldman, K. J., Cailliet, G. M., Andrews, A. H., & Natanson, L. J. (2012). Assessing the age and growth of chondrichthyan fishes. In J. C. Carrier, J. A. Musick, & M. R. Heithaus (Eds.), *Biology of sharks and their relatives* (2nd ed., pp. 419–447). Boca Raton, FL: CRC Press.

Gomes, U. L., Signori, C. N., Gadig, O. B. F., & Santos, H. R. S. (2010). *Guia para identificação de tubarões e raias do Rio de Janeiro*. Rio de Janeiro: Technical Books.

Gwinn, D. C., Allen, M. S., & Rogers, M. W. (2010). Evaluation of procedures to reduce bias in fish growth parameter estimates resulting from size-selective sampling. *Fisheries Research*, 105, 75–79.

Hamlett, W. C. (2005). *Reproductive biology and phylogeny of Chondrichthyes: Sharks, Batoids and chimaeras*. Enfield, NH: Science Publishers.

Hoenig, J. M., Morgan, M. J., & Brown, C. A. (1995). Analysing differences between two age determination methods by tests of symmetry. *Canadian Journal of Fisheries and Aquatic Sciences*, 52, 364–368.

Imoto, R. D., Carneiro, M. H., & Ávila-da-Silva, A. O. (2016). Spatial patterns of fishing fleets on the southeastern Brazilian bight. *Latin American Journal of Aquatic Research*, 44, 1005–1018.

IUCN. (2019). The IUCN Red List of Threatened Species. Version 2019-1. International Union for Conservation of Nature and Natural Resources, & IUCN Species Survival Commission. https://www.iucnredlist.org

Jensen, A. L. (1996). Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 820–822.

Kéry, M. (2010). *Introduction to WinBUGS for ecologists: Bayesian approach to regression, ANOVA, mixed models and related analyses*. London: Academic Press.

Kruschke, J. K. (2013). Posterior predictive checks can and should be Bayesian: comment on Gelman and Shalizi, philosophy and the practice of Bayesian statistics. *The British Journal of Mathematical and Statistical Psychology*, 66, 45–56.

Mangel, M. (2017). The inverse life-history problem, size-dependent mortality and two extensions of results of Holt and Beverton. *Fish and Fisheries*, 18, 1192–1200.

Martins, R. R. M., Assunção, R., & Schwingel, P. R. (2009). Distribuição e abundância de *Narcine brasiliensis* (Olfers, 1931) (Elasmobranchii, Narcinidae) no litoral norte do estado de Santa Catarina, Brasil. *Pan-American Journal of Aquatic Sciences*, 4, 423–435.

Maunder, M. N., & Punt, A. E. (2013). A review of integrated analysis in fisheries stock assessment. *Fisheries Research*, 142, 61–74.

Mellinger, J. (1971). Croissance et reproduction de la torpille (*Torpedo marmorata*) I. Introduction, ecologie, crossance generale et dimorphisme sexual, cycle, fecundite. *Bulletin Biologique de la France et de la Belgique*, 105, 165–218.

Millar, R. B. (2002). Reference priors for Bayesian fisheries models. *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 1492–1502.

Moreno, F., Acevedo, K., Grijalba-Bendeck, M., Acero, A., & Paramo, J. (2010). Reproducción de la raya eléctrica *Narcine bancroftii* (Torpediniformes: Narcinidae) en Santa Marta, Caribe colombiano. *Latin American Journal of Aquatic Research*, 38, 27–36.

Myers, R. A., & Hoenig, J. M. (1997). Direct estimates of gear selectivity from multiple tagging experiments. *Canadian Journal of Fisheries and Aquatic Sciences*, 54, 1–9.

Natanson, L. J., Skomal, G. B., Hoffmann, S. L., Porter, M. E., Goldman, K. J., & Serra, D. (2018). Age and growth of sharks: do vertebral band pairs record age? *Marine and Freshwater Research*, 69, 1440–1452.

Neer, J. A., & Cailliet, G. M. (2001). Aspects of the life history of the Pacific electric ray, *Torpedo californica* (Ayres). *Copeia*, 2001, 842–847.

Pardo, S. A., Cooper, A. B., & Dulvy, N. K. (2013). Avoiding fishy growth curves. *Methods in Ecology and Evolution*, 4, 353–360.

Pope, J. A., Margetts, A. R., Hamley, J. M. & Akyuz, E. F. (1975) *Manual of methods for fish stock assessment. Part 3-Selectivity of Fishing Gear*. FAO Fisheries Technical Papers (FAO). Rome: Food and Agriculture Organization of the United Nations.

Prince, J., Hordyk, A., Valencia, S. R., Loneragan, N., & Sainsbury, K. (2015). Revisiting the concept of Beverton–Holt life-history invariants with the aim of informing data-poor fisheries assessment. *ICES Journal of Marine Science*, 72, 194–203.

R Core Team. (2019). *R language for statistical computing. R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Ricker, W. E. (1979). Growth rates and models. In W. S. Hoar, D. J. Randall, & J. R. Brett (Eds.), *Fish Physiology* (pp. 677–743). Academic Press: New York.

Rolim, F. A., Rotundo, M. M., & Vaske-Júnior, T. (2016). Notes on the reproductive biology of the Brazilian electric ray *Narcine brasiliensis* (Elasmobranchii: Narcinidae). *Journal of Fish Biology*, 89, 1105–1111.

Rolim, F., Caltabellotta, F., Rotundo, M., & Vaske-Júnior, T. (2015). Sexual dimorphism based on body proportions and ontogenetic changes in the Brazilian electric ray *Narcine brasiliensis* (von Olfers, 1831) (Chondrichthyes: Narcinidae). *African Journal of Marine Science*, 37, 167–176.

Rolim, F. A., & Ávila-da-Silva, A. O. (2016). Effects of marine protected areas on fisheries: the case of São Paulo state, Brazil. *Latin American Journal of Aquatic Research*, 44, 1028–1038.

Rosa, R. S.; Furtado, M. (2007). *Narcine brasiliensis*. In IUCN Red List of Threatened Species. Version 2019.3. 2007: e.T63157A12602819. doi: 10.2305/IUCN.UK.2007.RLTS.T63157A12602819.en. (last accessed January 31, 2020).

Rotundo, M. M., Severino-Rodrigues, E., Barrella, W., Petrere Junior, M., & Ramires, M. (2019). Checklist of marine demersal fishes captured by the pair trawl fisheries in southern (RJ-SC) Brazil. *Biota Neotropica*, *19*, e20170432.

Sampson, D. B. (2014). Fishery selection and its relevance to stock assessment and fishery management. *Fisheries Research*, *158*, 5–14.

Simpfendorfer, C. A., Heupel, M. R., White, W. T., & Dulvy, N. K. (2011). The importance of research and public opinion to conservation management of sharks and rays: a synthesis. *Marine and Freshwater Research*, *62*, 10.

Smart, J. J., Harry, A. V., Tobin, A. J., & Simpfendorfer, C. A. (2013). Overcoming the constraints of low sample sizes to produce age and growth data for rare or threatened sharks. *Aquatic Conservation*, *23*, 124–134.

STAN Development Team (2020). *RStan: the R interface to Stan*.

Stevens, J. D., Bonfil, R., Dulvy, N. K., & Walker, P. A. (2000). The effects of fishing on sharks, rays, and chimaeras (Chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science*, *57*, 476–494.

Taylor, C. C. (1958). Cod growth and temperature. *ICES Journal of Marine Science*, *23*, 366–370.

Vianna, G. M. S., & Vooren, C. M. (2009). Distribution and abundance of the lesser electric ray *Narcine brasiliensis* (Olfers, 1831) (Elasmobranchii: Narcinidae) in southern Brazil in relation to environmental factors. *Brazilian Journal of Oceanography*, *57*, 105–112.

Villavicencio-Garayzar, C. J. (2000). Taxonomia, abundancia estacional, edad y crecimiento y biologia reproductiva de *Narcine entemedor* (Chondrichthyes; Narcinidae), en Bahia Almejas, B.C.S, Mexico. PhD thesis, Universidad Autonoma de Nuevo Leon.

von Bertalanffy, L. (1934). Untersuchungen ueber die Gesetzlichkeit des Wachstums. *Wilhelm Roux' Archiv für Entwicklungsmechanik der Organismen*, *131*, 613–652.

Zar, J. H. (1999). *Biostatistical analysis* (4th ed.). Upper Saddle River, NJ: Prentice-Hall/Pearson.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.