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# Age and growth of three endemic threatened guitarfishes *Pseudobatos horkelii*, *P. percellens* and *Zapteryx brevirostris* in the western South Atlantic Ocean

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## Abstract

The age and growth of three endemic threatened guitarfish species were analysed using vertebrae of *Pseudobatos horkelii*, *P. percellens* and *Zapteryx brevirostris*. Edge and marginal-increment analyses were used to evaluate the periodicity of the formation of the band-pairs, suggesting deposition of one band-pair per year, from late winter to late spring. The von Bertalanffy growth model was used to describe the growth of these species with the following parameters, for pooled sexes: *P. horkelii* $L_\infty$ = 126.93, $k$ = 0.19 and $t_0$ = −1.51; *P. percellens* $L_\infty$ = 109.31, $k$ = 0.16 and $t_0$ = −1.78; *Z. brevirostris* $L_\infty$ = 60.37, $k$ = 0.24 and $t_0$ = −1.42. Our results are essential to understanding the resilience and vulnerability of these species to harvest, which can contribute to management and conservation actions of these species.

**KEYWORDS**
fisheries management, growth modelling, life history, population dynamics, shark-like batoids

## 1 | INTRODUCTION

Age and growth studies of fishes are regarded as the central basis of population dynamic models, ranging from a simple estimation of growth coefficients to their use in stock-assessment models (Cailliet & Goldman, 2004; Goldman *et al*., 2012). Considering the common life-history characteristics of elasmobranchs (*i.e.* relatively slow growth, low fecundity, late sexual maturity and relatively long life spans), data on age and growth associated with other biological traits are crucial for assessing their risk of overexploitation (Simpfendorfer *et al*., 2011; Stevens *et al*., 2000).

The guitarfishes (Rhinopristiformes) are a diverse group of small to large-bodied coastal benthic shark-like batoid elasmobranchs

distributed worldwide, comprising four families and about 55 species (Last *et al*., 2016). Fins of large species are highly prized by the international shark-fin markets and, in general, the group is typically caught as by-catch in many fisheries. As a result, guitarfishes are currently one of the most globally threatened elasmobranch groups (Dulvy *et al*., 2014; Moore, 2017) but there is relatively little information on the life histories of this group compared with other elasmobranchs (Frisk, 2010).

In the western Atlantic Ocean, two families and four species have been recorded. In the family Rhinobatidae, the Atlantic guitarfish *Pseudobatos lentiginosus* (Garman 1880), in the western North Atlantic; Brazilian guitarfish *Pseudobatos horkelii* (Müller & Henle 1841), endemic and restricted in the western South Atlantic Ocean, from south-eastern

Brazil (Rio de Janeiro) to Argentina; Southern or Chola guitarfish *Pseudobatos percellens* (Walbaum 1792) endemic and widely distributed in the western Atlantic Ocean, from Panama to Santa Catarina in southern Brazil (both species genus *Rhinobatos* until recently). The second family, the Trygonorrhinidae (until recently as Rhinobatidae), includes Shortnose guitarfish *Zapteryx brevirostris* (Müller & Henle 1841), endemic and restricted in the western South Atlantic Ocean, from south-eastern Brazil (Santa Catarina) to northern Argentina (Last *et al.*, 2016; Menni & Stehmann, 2000).

In Brazilian waters, *P. horkelii*, *P. percellens* and *Z. brevirostris* are usually found sympatrically over the south-east continental shelf, from Rio de Janeiro to Santa Catarina, between 20 and 110 m depth (Figueiredo, 1977; Menni & Stehmann, 2000). These lecithotrophic species exhibit maximum sizes of 138 cm total length ($L_T$; Lessa *et al.*, 1986), 100 cm $L_T$ (Figueiredo, 1977; McEachran & de Carvalho, 2002) and 65 cm $L_T$ (Colonello *et al.*, 2011), respectively. Although these guitarfishes are not targeted by demersal fisheries that exploit sciaenid fishes (*e.g.*, *Micropogonias furnieri* (Desmarest 1823), *Macrodon ancylodon* (Bloch & Schneider 1801) and *Cynoscion jamaicensis* (Vaillant & Bocourt 1883)), they are generally caught as by-catch in the small-to-large-scale commercial fisheries; *e.g.*, double-rig trawl, pair and single bottom trawls and bottom gillnets (Costa & Chaves, 2006; Martins & Schwingel, 2003; Mazzoleni & Schwingel, 1999). In addition, the occurrence of these species in multispecies commercial fisheries has been considered a current threat to their status (Di Dario *et al.*, 2015; Pinheiro *et al.*, 2015), contributing to their global IUCN classification of Critically Endangered (CR) for *P. horkelii*, Near Threatened (NT) for *P. percellens* and Vulnerable (VU) for *Z. brevirostris* (Casper & Burgess, 2016; Lessa & Vooren, 2016; Vooren *et al.*, 2006).

Despite the occurrence and distribution of these species along the south-east to south coast of Brazil, most of the few studies undertaken to date have focused on reproduction (Abilhoa *et al.*, 2007; Batista, 1991; Colonello *et al.*, 2011; Lessa *et al.*, 1986; Martins *et al.*, 2018; Rocha & Gadig, 2012) and feeding habits (Bornatowski *et al.*, 2010; Carmo *et al.*, 2015; Marion *et al.*, 2011). The knowledge of other aspects of their basic biology, including age and growth parameters, is fairly limited and only available for *P. horkelii* and *Z. brevirostris* in southern Brazil (Carmo *et al.*, 2018; Lessa, 1982; Vooren *et al.*, 2005) and for *P. Percellens* in north-eastern Brazil (Nunes, 2012).

Considering the variation of the life-history characteristics of elasmobranchs and the occurrence of illegal trade of some species (de-Franco *et al.*, 2012), accurate age and growth information is fundamental to effective conservation and management actions. In south-eastern Brazilian waters, life-history information on these three guitarfish species is currently unknown. Therefore, the objective of the present study was to provide the first detailed assessment of age and growth parameters of *P. horkelii*, *P. percellens* and *Z. brevirostris* for the western South Atlantic Ocean, based on the interpretation of vertebral growth bands and periodicity of the band-pair formation.

## 2 | MATERIALS AND METHODS

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

### 2.1 | Study area and sampling

Specimens were collected throughout the year, between September 2007 and September 2009, as incidental by-catch from bottom pair-trawling in commercial fisheries operating on the continental shelf (between 15–55 m depth) off south-eastern Brazil, between 24° 00′ S, 45° 15′ W and 25° 10′ S, 47° 52′ W (Figure 1). Fishing operations averaged 4.5 h trawling day$^{-1}$, using nets that ranged from 40 to 50 m in length, 6 to 8 m in width and with mesh sizes of 150 mm in the body and 100 mm in the codend. Most of these fishing operations (81%) occurred between 15 and 30 m depth. Specimens were transported to the laboratory for sampling that included determining sex, $L_T$ and disc width ($W_D$, mm) and mass ($M$, g).

### 2.2 | Age determination

Vertebrae were removed from the abdominal region of the vertebral column, manually 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, Aremco; www.aremco.com) and sectioned using a low-speed saw with two diamond wafering blades 102 mm (4 in.) in diameter separated by a 0.4 mm spacer. Each vertebral centrum was cut along the mid-sagittal axis through the focus, resulting in one bowtie section 0.35–0.40 mm thick. Each section was observed and photographed under transmitted light using a stereomicroscope at a magnification of x10–20. 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.; www.motic.com).

Band-pairs consisting of one wide band (opaque) and one narrow band (translucent; Figure 2) were identified following the description and terminology detailed in Cailliet *et al.* (2006). A subsample comprising all size ranges of both sexes was randomly 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. After establishing ageing criteria, all bowtie sections were read by the primary reader twice, without prior knowledge of the size of the individual, sex, or previous band-pair counts. Age readings were compared and ages that differed were re-read by the primary reader; if an agreement could not be reached on the third reading, the sample was discarded and excluded from the age analysis. Counts were conducted in different months to ensure independence of the readings.
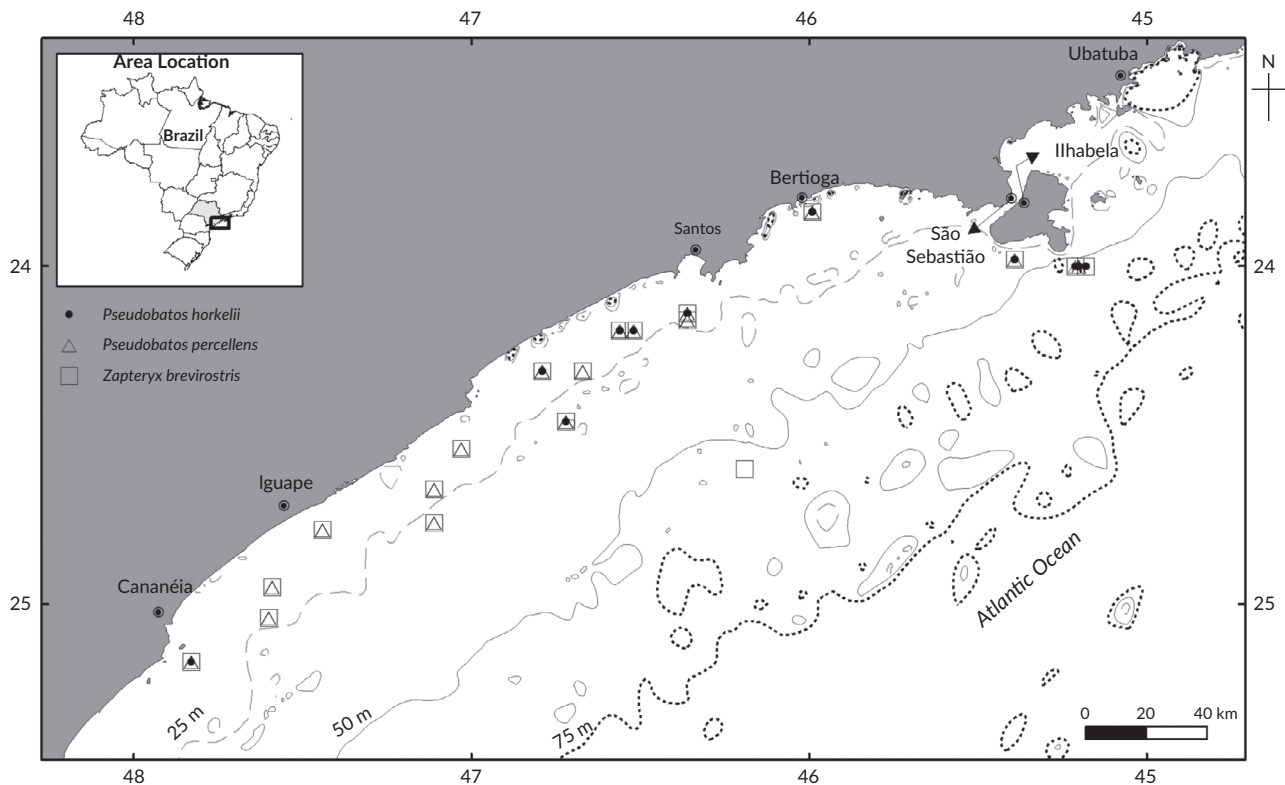
**FIGURE 1** Sampling locations for *Pseudobatos horkelii*, *P. percellens*, and *Zapteryx brevirostris* off the coast of south-eastern Brazil, western Atlantic Ocean. Depth contours are 25, 50 and 75 m
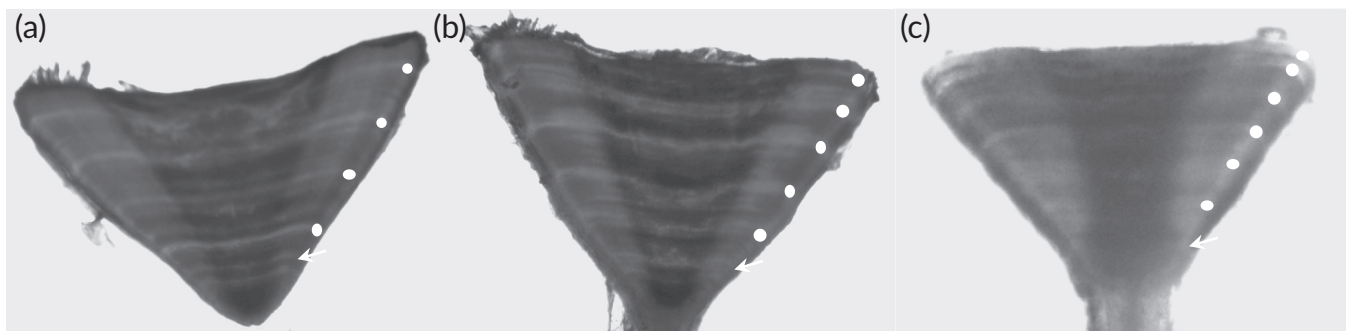


**FIGURE 2** Annual band-pairs formed on the sectioned vertebral centra of female (a) *Pseudobatos horkelii* 84.0 cm total length ($L_T$), (b) *P. percellens* 72.5 cm $L_T$ and (c) *Zapteryx brevirostris* 49.5 cm total length. The white dots indicate translucent bands; the white arrowhead indicates the birthmark

Regressions between $L_T$ and centrum radius ($R_C$; the distance from the focus to the outer edge) were fitted for each species for both sexes to check if vertebral centrum growth remained proportional to somatic growth. Differences between sexes were examined using analysis of covariance (ANCOVA) (Zar, 1999).

## 2.2.1 | Precision and error analysis

Within-reader precision of ageing between reads (reads 1 and 2) was calculated using average percent error (APE; Beamish & Fournier, 1981) and the CV (Chang, 1982). Low values for APE and CV indicate high ageing precision. Differences in ages were also 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.

## 2.2.2 | Edge and marginal-increment analysis

Periodicity of band-pair formation was verified using centrum edge analysis and marginal increment ratio ($I_{MR}$; Cailliet *et al.*, 2006; Smith *et al.*, 2007). Centrum edge analysis was used to classify the edge type of the vertebral centra according to four categories: (1) narrow translucent, (2) broad translucent, (3) narrow opaque and (4) broad opaque. Narrow bands were classified as having a bandwidth <50% of the previously fully-formed like band and broad bands with a bandwidth

≥50% of the previously fully-formed like band. Proportion of each edge type was then plotted against month of collection to evaluate the seasonality of the formation of the band-pairs following the recommendations of Smith *et al.* (2007). The number of translucent bands observed was interpreted as being the number of band-pairs formed in a 12 month period.

The annual periodicity of band formation was also quantified using $I_{MR}$ according to Conrath *et al.* (2002): $I_{MR} = W_M W_{PB}^{-1}$, where $W_M$ is the margin width and $W_{PB}$ is the previous band-pair width. Age 0 year individuals were excluded from these analyses due to the lack of a fully formed band-pair. For $I_{MR}$ analysis, sexes and age classes were pooled after visually verifying that there were no apparent differences in the trends of monthly averages by sexes and age classes following the recommendation of Campana (2001). Mean $I_{MR}$ was calculated for each month of capture with the difference in $I_{MR}$ among months tested using a non-parametric Kruskal–Wallis one-way analysis of variance (Smith *et al.*, 2007).

## 2.3 | Growth modelling

The von Bertalanffy growth model (VBGM) parameterized following Beverton and Holt (1957), was used to model the growth of the three guitarfish species. A given specimen's length at age $t$ ($L_t$) was assumed to follow the von Bertalanffy growth equation: $L_t = L_\infty(1 - e^{-k(t - t0)})$, where $L_\infty$ is the species asymptotic length (mean maximum length), $k$ is the Brody growth coefficient per year and $t_0$ is the theoretical age where the species would be length zero. The VBGM was implemented in a Bayesian framework in STAN (STAN Development Team, 2018a) in R (R Development Core Team, 2018; www.r-project.org) using RStan. To do so, the observed specimen lengths, $L_t$, were assumed to belong to a log-normal distribution with mean $L_t$ and error $\sigma_{obs}$: $L_t \sim$ log-normal(log $L_t, \sigma_{obs}$).

The priors for the parameters were assumed to be half-normal for $L_\infty$, $k$ and $\sigma_{obs}$ and normal for $t_0$. For the VBGM parameters, an optim routine in *R* was used to generate maximum likelihood (ML) estimates to be used as the prior mean. An assumed CV of 0.8, was used to scale these ML estimates to SD to be used as the prior SD (Equations 1–4). The observation error, $\sigma_{obs}$, was assumed to follow a half-normal with mean 0 and SD = 1 (Equation 4). The expression $T(0)$ indicates a truncation in the distribution at zero.

$$L_\infty \sim N(L_{\infty MLE}, CV(L_{\infty MLE})) T(0) \tag{1}$$

$$k \sim N(k_{MLE}, CV(k_{MLE})) T(0) \tag{2}$$

$$t_0 \sim N(t_{0,MLE}, CV(t_{0,MLE})) \tag{3}$$

$$\sigma_{obs} \sim N(0,1) T(0) \tag{4}$$

The result of these prior distributions was weak, diffuse priors but still with the majority of the probability mass within reasonable values as recommended for use in STAN (STAN Development Team, 2018b).

The basic VBGM was modified to estimate sex-specific VBGM parameters for each species conditioned on the specimen's sex ($s_i$): ($s_i$): $L_t = L_\infty[s_i]\{1 - e^{-k[s_i](t - t_0[si])}\}$, where $s_i$ was an identity vector to indicate a specimen's sex. All parameter prior distributions were assumed to be the same as the pooled model (Equations 1–4).

Each model was implemented separately for each species using the No-U-Turn Sampler (NUTS) with 5000 warmup iterations that were discarded, 2500 samples per chain, with four chains for a total of 10,000 samples per species per model. Convergence was assessed using the Gelman-Rubin diagnostic potential scale-reduction statistic (Gelman & Rubin, 1992), $\hat{R} < 1.1$ suggested by Gelman *et al.* (2013).

The median and 90% credible interval ($\alpha = 0.1$) for each parameter in each model was calculated from the posterior distribution. A log-normal random number generator was used to do a posterior predictive check (Gelman & Hill, 2006) as well as generate median model estimates, $L_T$ and 90% credible intervals across a vector of ages (0 to maximum age observed of each species). Residuals were calculated based on the pooled model median estimates for each observation. A one-dimensional kernel density estimator was used to generate the posteriors of each parameter estimate from each model for each species. The joint posterior distributions for all VBGM parameters was visualised using the correlated sampling draws and calculating the 5% and 50% probability masses using a two-dimensional kernel density estimator in the MASS package (Venables & Ripley, 2002). The Pearson correlation coefficient was calculated between all VBGM parameters.

To assess whether males and females had different parameter estimates, the difference between the sex-specific parameters (*e.g.*, $\theta_F - \theta_M$) was sampled as part of the sex-specific model. The posteriors of these parameter differences were visualised and the 90% credible interval (CI) was calculated. Following Kéry (2010), sex-specific parameters were significantly different when the 90% CI did not contain zero. Additionally, the probability of the parameter differences was calculated by taking the average of parameter differences that were less than zero (Kruschke, 2013): $\rho(\theta_F - \theta_M) = $ mean ($\theta_F - \theta_M < 0$). Parameter differences were significant if $0.5\alpha < \rho(\theta_F - \theta_M)$ or $\rho(\theta_F - \theta_M) > 1-0.5\alpha$.

## 3 | RESULTS

### 3.1 | Sampling

In total, 118 vertebrae from *P. horkelii*, 318 from *P. percellens* and 388 from *Z. brevirostris* were used. Male and female *P. horkelii* ranged in size from 45.5 to 100.0 cm $L_T$, with the majority of females 50–70 cm $L_T$. Unfortunately, small individuals (*i.e.*, neonates) were not sampled (Figure 3a). For *P. percellens* we observed similar sizes compared with *P. horkelii*, with the majority of females 40–70 cm $L_T$. However, we also observed some small individuals of both sexes (< 40.0 cm $L_T$; Figure 3b) that were caught during the austral autumn. Individuals of *Z. brevirostris* were the smallest specimens sampled and
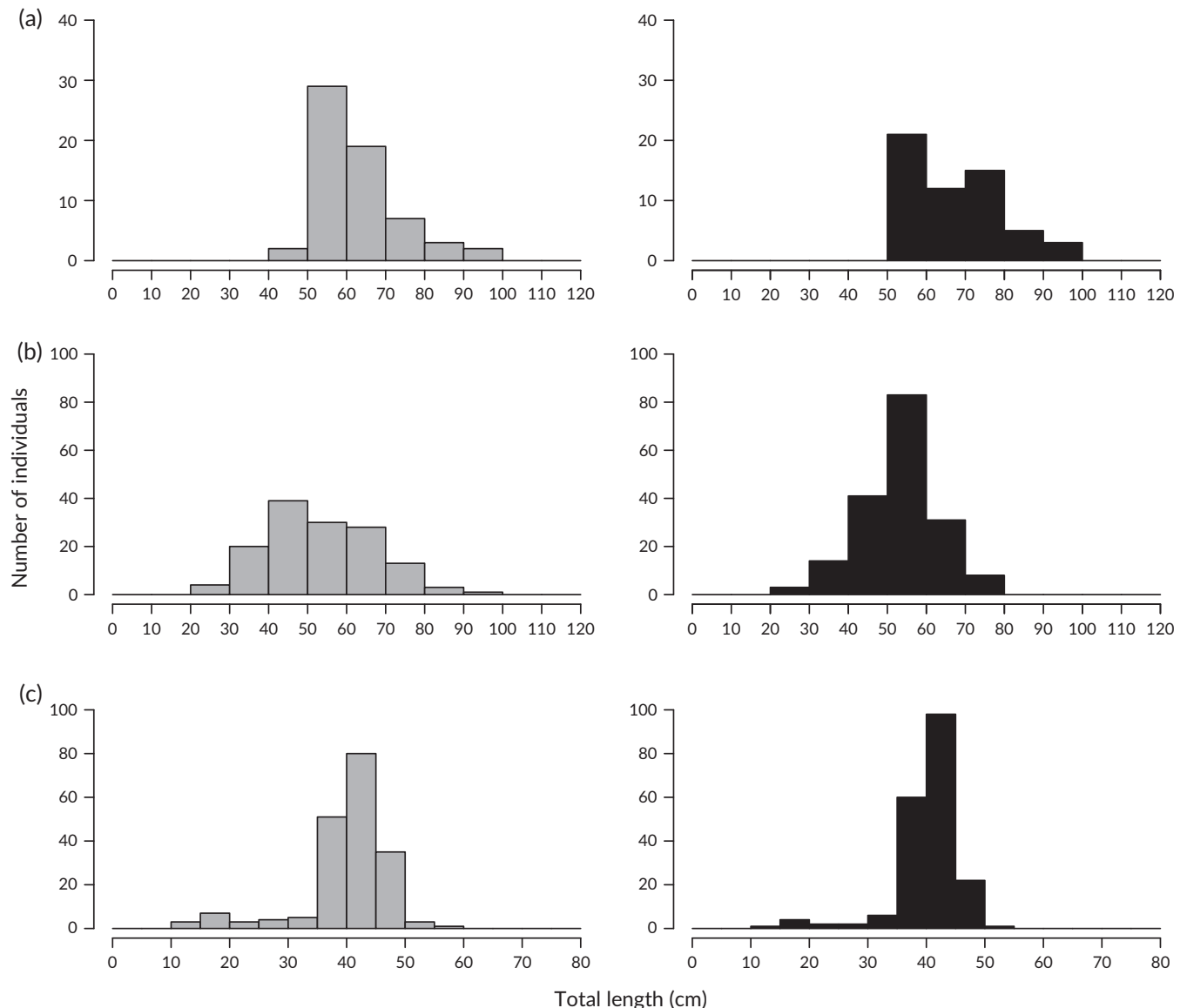
**FIGURE 3** Length-frequency distributions of female (F; (▨)) and male (M; (■)): (a) *Pseudobatos horkelii* (F, *n* = 62; M, *n* = 56); (b) *P. percellens* (F, *n* = 138; M, *n* = 180); (c) *Zapteryx brevirostris* (F, *n* = 192; M, *n* = 196)

ranged from 14.8 to 59.3 cm $L_T$ with the majority 35–50 cm $L_T$ (Figure 3c).

## 3.2 | Age determination

For all three guitarfish species, vertebral growth bands were clearly distinguished along the intermedialia and in the corpus calcareum of the vertebral centrum; however, band-pair counts were based on the corpus calcareum. The birthmark was primarily identified as the first distinct band after the focus, occasionally associated with a slight change in the angle of the corpus calcareum and was measured at a mean (± SD) distance of 1.03 ± 0.04 mm from the focus for *P. horkelii* (*n* = 118), 0.92 ± 0.03 mm from the focus for *P. percellens* (*n* = 318) and 0.63 ± 0.04 mm from the focus for *Z. brevirostris* (*n* = 388). *Pseudobatos horkelii* had band counts ranging from 1 to 7 in females and 2 to 7 in males; no age 0 year fish were collected. Band-pair counts of

*P. percellens* and *Z. brevirostris* ranged between 0 to 11 in females and 0 to 6 in males and 0 to 9 in females and 0 to 7 in males, respectively.

No significant difference was found in the relationship of $R_C$ with respect to $L_T$ between sexes for *P. horkelii* ($F_{1,113}$ = 1.46, $P$ > 0.05) and the pooled regression was $L_T$ = 13.84 + 18.37$R_C$, $r^2$ = 0.96. The relationship was different between sexes for *P. percellens* ($F_{1,314}$ = 4.01, $P$ < 0.05), therefore, for males was $L_T$ = 13.73 + 16.68$R_C$, $r^2$ = 0.94 and for females was $L_T$ = 14.38 + 15.85$R_C$, $r^2$ = 0.96. *Zapteryx brevirostris* $R_C$ with respect to $L_T$ was not different between sexes ($F_{1,384}$ = 3.78, *df* = 385, $P$ > 0.05) and was therefore pooled as $L_T$ = 11.24 + 13.55$R_C$, $r^2$ = 0.91.

## 3.3 | Precision and error analysis

Ageing precision was high for all three species, with low APE (3.42%, 3.49% and 2.60%) and CV (4.84%, 4.94% and 3.69%)

values for *P. horkelii*, *P. percellens* and *Z. brevirostris*, respectively. First and second reads agreed ±1 year in 79.7%, 78.9% and 85.0% of the three species, respectively. Bowker's test of symmetry and age-bias plots identified no systematic bias in ageing counts between reads 1 and 2 for *P. horkelii* ($\chi^2$ = 5.24, *df* = 5, *P* > 0.05; Figure 4a), *P. percellens* ($\chi^2$ = 9.60 *df* = 11, *P* > 0.05 = 0.567; Figure 4b) and *Z. brevirostris* ($\chi^2$ = 12.92, *df* = 8, *P* > 0.05; Figure 4c).
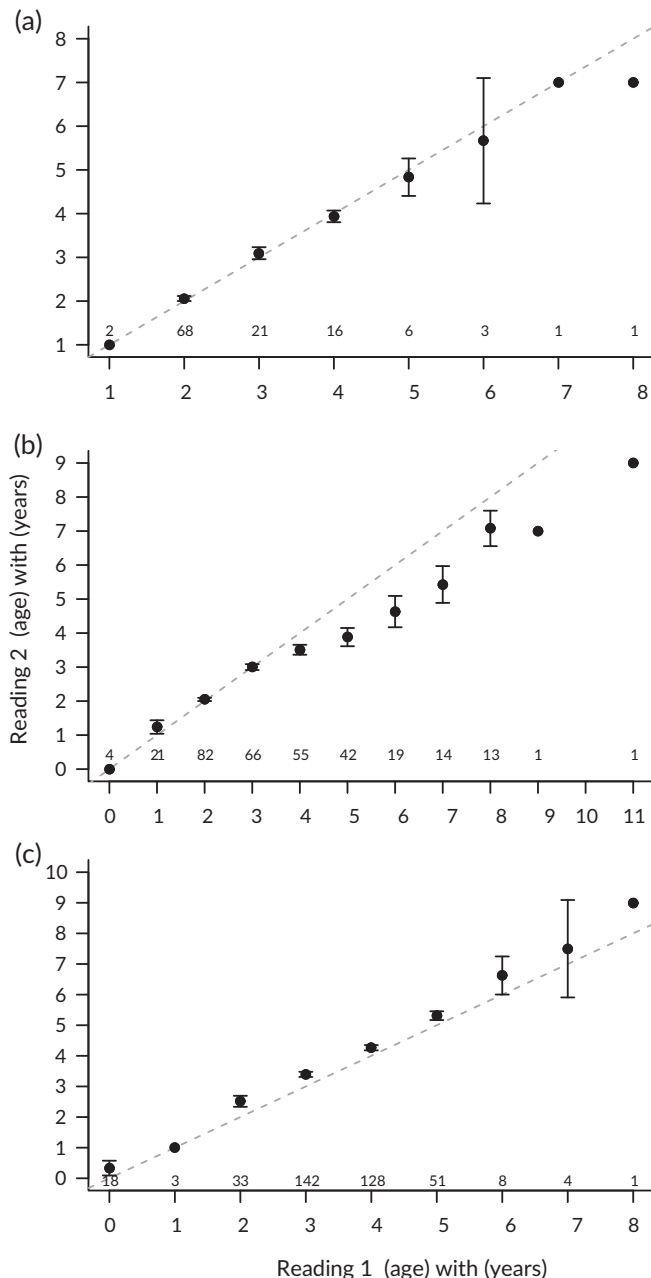


**FIGURE 4** Age-bias plot of annual band-pair counts of reading 1 *v.* mean (± 95% CI) reading 2 for (a) *Pseudobatos horkelii*, (b) *P. percellens*; and (c) *Zapteryx brevirostris*. (-----), Equality line indicating a one-to-one relationship

## 3.4 | Edge and marginal-increment analysis

Centrum-edge analysis and $I_{MR}$ suggested that a single translucent band is formed annually on the vertebral centra of *P. percellens* and *Z. brevirostris*. In the *P. percellens* and *Z. brevirostris* samples, translucent bands (both narrow translucent (NT) and broad translucent (BT)) were primarily observed during October–December, but also showed up as early as June–August in some specimens (Figure 5b–c). In *P. horkelii*, both analyses were hampered due to the lack of samples during the winter and the low number of monthly samples available for spring and early summer. NT and BT bands were only observed during November–January, of the 7 months sampled (Figure 5a). Since both analyses were inconclusive about the periodicity pattern in growth band deposition for *P. horkelii*, we suggested an annual pattern of band-pair formation based on the general trend observed in the other two closely-related species.

Marginal increment ratios were significantly different among months for the three species (*P. horkelii* Kruskal-Wallis: $\chi^2$ = 17.82, *df* = 5; *P* < 0.01; *P. percellens* $\chi^2$ = 86.02, *df* = 11, *P* < 0.001; *Z. brevirostris* $\chi^2$ = 89.88, *df* = 11, *P* < 0.001). In general, there was an increasing trend in $I_{MR}$ from January to September for *P. percellens* and then a minimum during October–December (Figure 5b), indicating that one complete band-pair was deposited in a 12 month period. Similarly, $I_{MR}$ in *Z. brevirostris* increased from January to August and then was at its lowest during October–December (Figure 5c).

## 3.5 | Growth modelling

Gelman-Rubin convergence diagnostic (G-R), which considers the within and between variances and expectations from each chain sequence, indicated that all the models approached a value of $\hat{R} = 1$ and converged to stable posterior distributions.

The VBGM provided a good description of the overall pattern between the observed and generated quantiles from the Bayesian posterior median lengths at age for pooled sexes in each model, with a reliable fit within the 90% CI, up to ages 5–6 years. At older ages, data were more sparse and posterior probability intervals were slightly wider (Figure 6a–c). The posterior medians and the 90% CI of each growth parameter in each model, for pooled and sex-specific data, are presented in Table 1. Plots of residuals verified the model assumption that residual error variance is normally distributed given the log-normal distribution of the observations and indicated a slight increase in the variability of estimated $L_T$ over the first years for *P. horkelii* and *P. percellens* (Figure 6d–f). Posterior predictions of the Bayesian fit for the VGGM showed a similar growth pattern between growth curves fitted for pooled and sex-specific data, in *P. horkelii* and *Z. brevirostris* (Figure 6g, i); however, differences in the growth pattern between males and females was observed for *P. percellens*, starting around age 5 (*c*. 80 cm $L_T$) (Figure 6h).

Marginal posterior and prior distributions for each growth parameter in each model, for pooled and sex-specific data, are
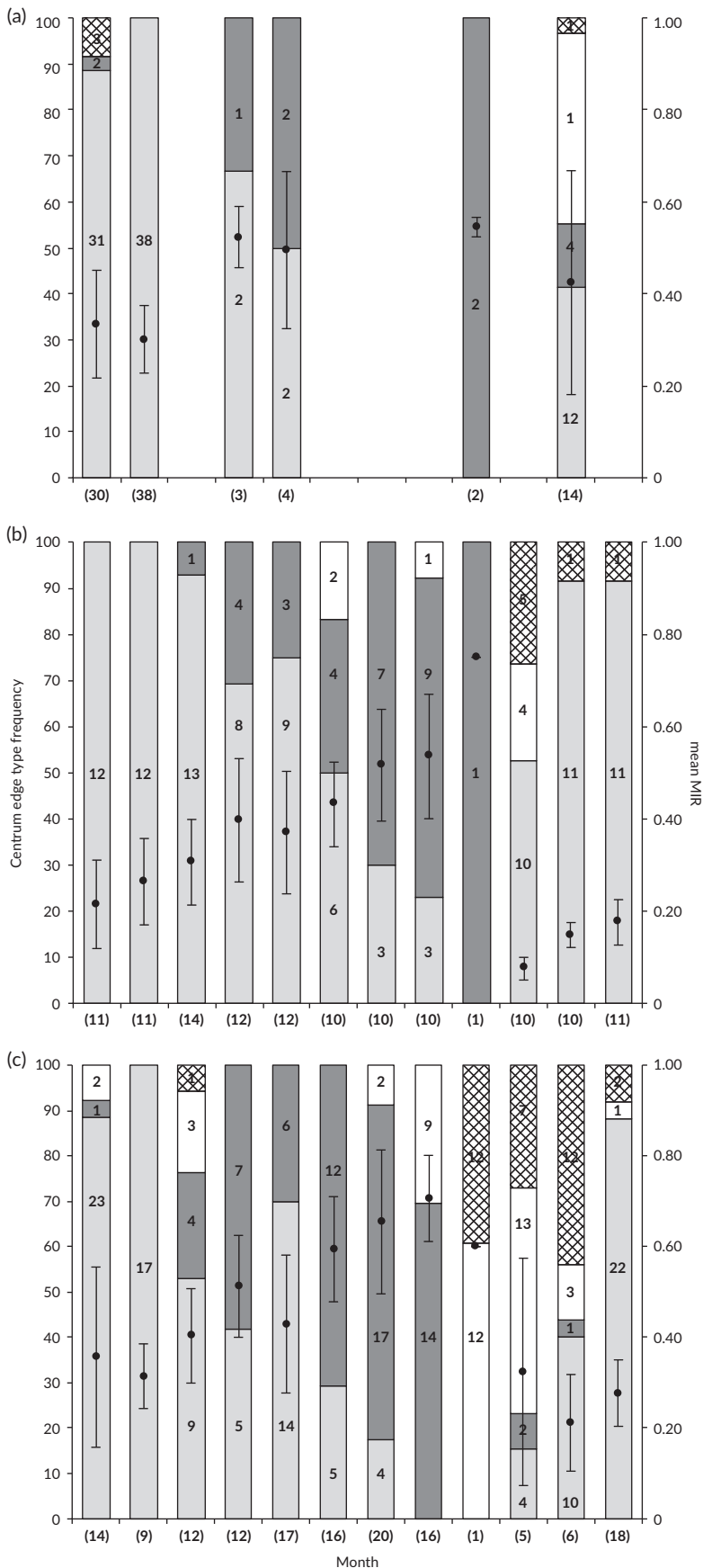
**FIGURE 5** Monthly variation in centrum edge type ((⬜), narrow opaque; (⬛), broad opaque; (□), narrow translucent; (⊠), broad translucent) and mean ((●), ± SE) monthly marginal increment ratios determined from pooled sexes and size classes for (a) *Pseudobatos horkelii* (b) *P. percellens* and (c) *Zapteryx brevirostris*. Sample sizes for edge analysis are given within the histogram and in parentheses beneath columns for marginal increment ratios
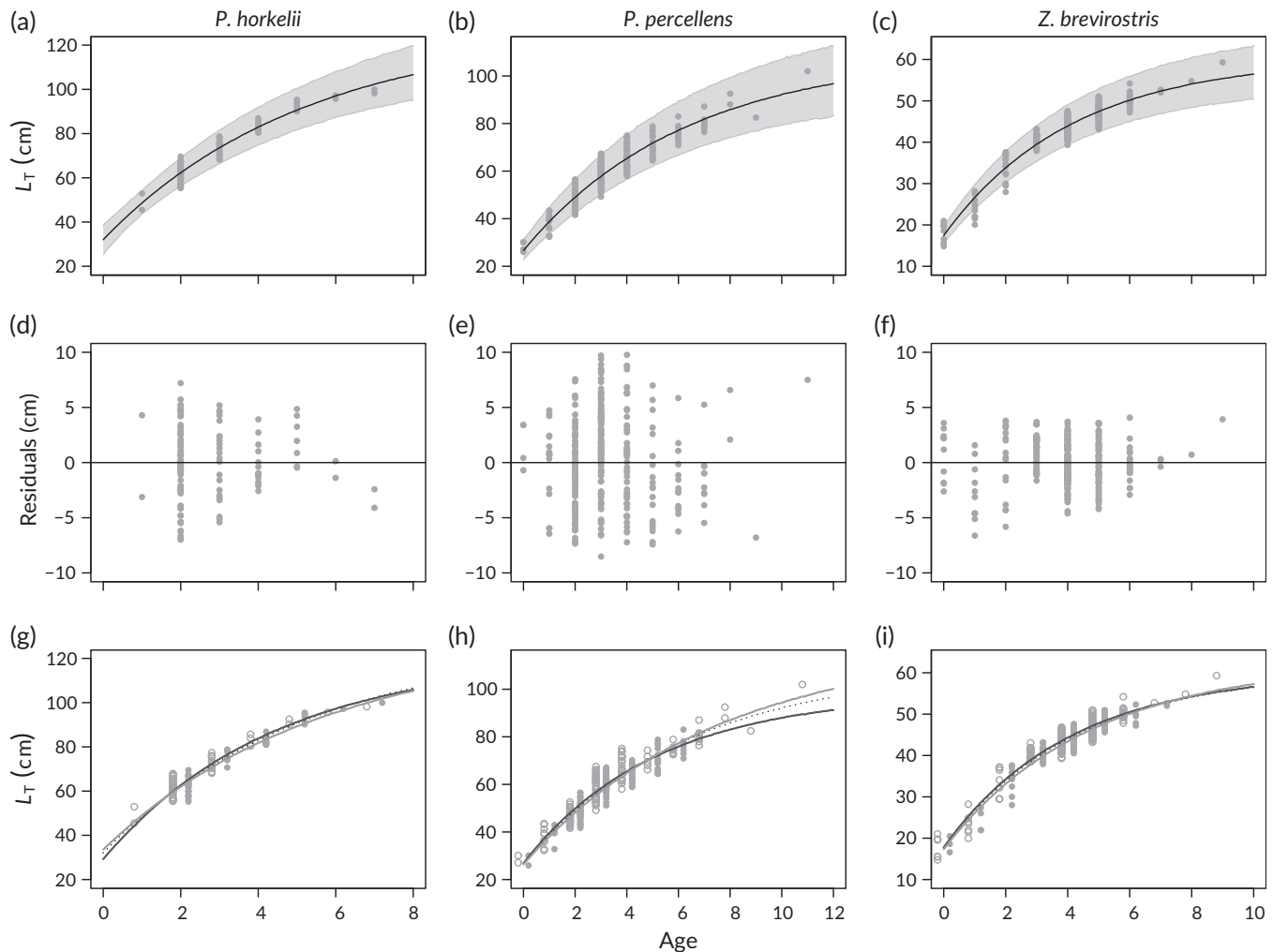
**FIGURE 6** (a–c) Posterior von Bertalanffy growth curves ((------), Median) fitted to observed total length ($L_T$)-at-age data ((●), Obs.) for pooled sexes of *Pseudobatos horkelii*, *P. percellens* and *Zapteryx brevirostris*. ((■), 90% CI), 90% Credible interval. (d–f) Residuals from the pooled model median estimates for each species. (g–i) Posterior predictive von Bertalanffy growth curves fitted for pooled sexes, males and females for each species (Estimates- (·········) Pooled, (——) Female, (——) Male, Obs.- (○) Female, (●) Male)

shown in Supporting Information Figure S1. True values lay well within the estimated marginal posterior distribution for those parameters. Posterior distributions showed a slight asymmetry with the 90% CI wider for *P. horkelii*; while for *P. percellens* and *Z. brevirostris*, the posterior distributions were symmetric with narrower intervals. The joint posterior distributions and the Pearson correlation coefficient between all VBGM parameters, for pooled and sex-specific data, are shown in Supporting Information Figures S2–S4. Correlations among the parameters $L_\infty$ and $k$, which are, in general, assumed to be negative in most studies of age and growth of fishes, were indeed estimated to be highly negatively correlated for all the three guitarfish species.

Differences in growth parameters ($L_\infty$ and $k$) between sexes were significant for *P. percellens* with the 90% CI not containing zero and $P < 0.05$ and $> 0.05$, respectively (Figure 7; Table 2). The observation error, $\sigma_{obs}$, also showed significant differences between sexes for *P. percellens* and *Z. brevirostris*.

## 4 | DISCUSSION

In the present study, we describe the age and growth assessment for three guitarfish species in the western South Atlantic Ocean. Sample sizes were 45.5–100.0 cm $L_T$ for *P. horkelii*, 26.0–100.0 cm $L_T$ for *P. percellens* and 14.8–59.3 cm $L_T$ for *Z. brevirostris*. The size range observed in the sample was slightly smaller for *P. horkelii* than the 22.0–138.0 cm $L_T$ reported by Vooren *et al.* (2005) in southern Brazil, but slightly larger (17.2–72.6 cm) $L_T$ for *P. percellens* (Carmo *et al.*, 2015) and 35–56 cm $L_T$ for *Z. brevirostris* (Carmo *et al.*, 2018) in southern Brazil. Based on the size distribution, all size classes were represented for *P. percellens* and *Z. brevirostris* (*i.e.*, neonates, juveniles and adults), including near-term embryos for *Z. brevirostris*. No small individuals (*i.e.*, neonates) were observed in the sample for *P. horkelii*. Differences between the size range distribution observed in the present study and those reported in the literature may have occurred due to methodological variations in gear selectivity (Stevens *et al.*, 2000), life-

**TABLE 1**  Posterior medians of von Bertalanffy growth parameters estimates for *Pseudobatos horkelii*, *P. percellens* and *Zapteryx brevirostris* for pooled sexes, males and females

| Parameters | Sexes | *P. horkelii* | | | *P. percellens* | | | *Z. brevirostris* | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Estimate | S.D | 90% CI | Estimate | S.D | 90% CI | Estimate | S.D | 90% CI |
| $L_\infty$ (cm) | Pooled | 126.93 | 14.61 | (112.62–156.52) | 109.31 | 6.15 | (100.89–120.78) | 60.37 | 1.52 | (58.13–63.06) |
| | Male | 120.65 | 18.37 | (104.90–158.95) | 97.87 | 7.13 | (89.20–111.89) | 60.15 | 2.15 | (57.12–64.13) |
| | Female | 128.67 | 22.99 | (107.89–176.93) | 118.44 | 10.79 | (105.10–139.27) | 62.44 | 2.58 | (58.76–67.26) |
| $k$ (year$^{-1}$) | Pooled | 0.19 | 0.04 | (0.12–0.27) | 0.16 | 0.02 | (0.13–0.19) | 0.24 | 0.01 | (0.22–0.26) |
| | Male | 0.23 | 0.07 | (0.12–0.36) | 0.2 | 0.03 | (0.15–0.24) | 0.25 | 0.02 | (0.21–0.28) |
| | Female | 0.18 | 0.05 | (0.09–0.27) | 0.13 | 0.02 | (0.10–0.17) | 0.22 | 0.02 | (0.18–0.25) |
| $t_0$ (years) | Pooled | −1.51 | 0.36 | (−2.16 to −1.01) | −1.78 | 0.14 | (−2.03 to −1.57) | −1.42 | 0.07 | (−1.53 to −1.32) |
| | Male | −1.22 | 0.52 | (−2.20 to −0.52) | −1.64 | 0.19 | (−1.98 to −1.38) | −1.42 | 0.1 | (−1.60 to −1.27) |
| | Female | −1.71 | 0.46 | (−2.59 to −1.08) | −1.87 | 0.2 | (−2.24 to −1.58) | −1.50 | 0.1 | (−1.68 to −1.36) |
| $\sigma_{obs}$ | Pooled | 0.05 | 0 | (0.05–0.06) | 0.07 | 0 | (0.07–0.08) | 0.06 | 0 | (0.05–0.06) |
| | Male | 0.05 | 0 | (0.04–0.06) | 0.07 | 0 | (0.06–0.07) | 0.05 | 0 | (0.04–0.05) |
| | Female | 0.05 | 0.01 | (0.05–0.06) | 0.08 | 0 | (0.07–0.09) | 0.06 | 0 | (0.06–0.07) |

$L_\infty$, asymptotic total length; $k$, growth coefficient; $t_0$, theoretical age at zero length; $\sigma_{obs}$, the observation error; 90% CI, 90% credibility interval.
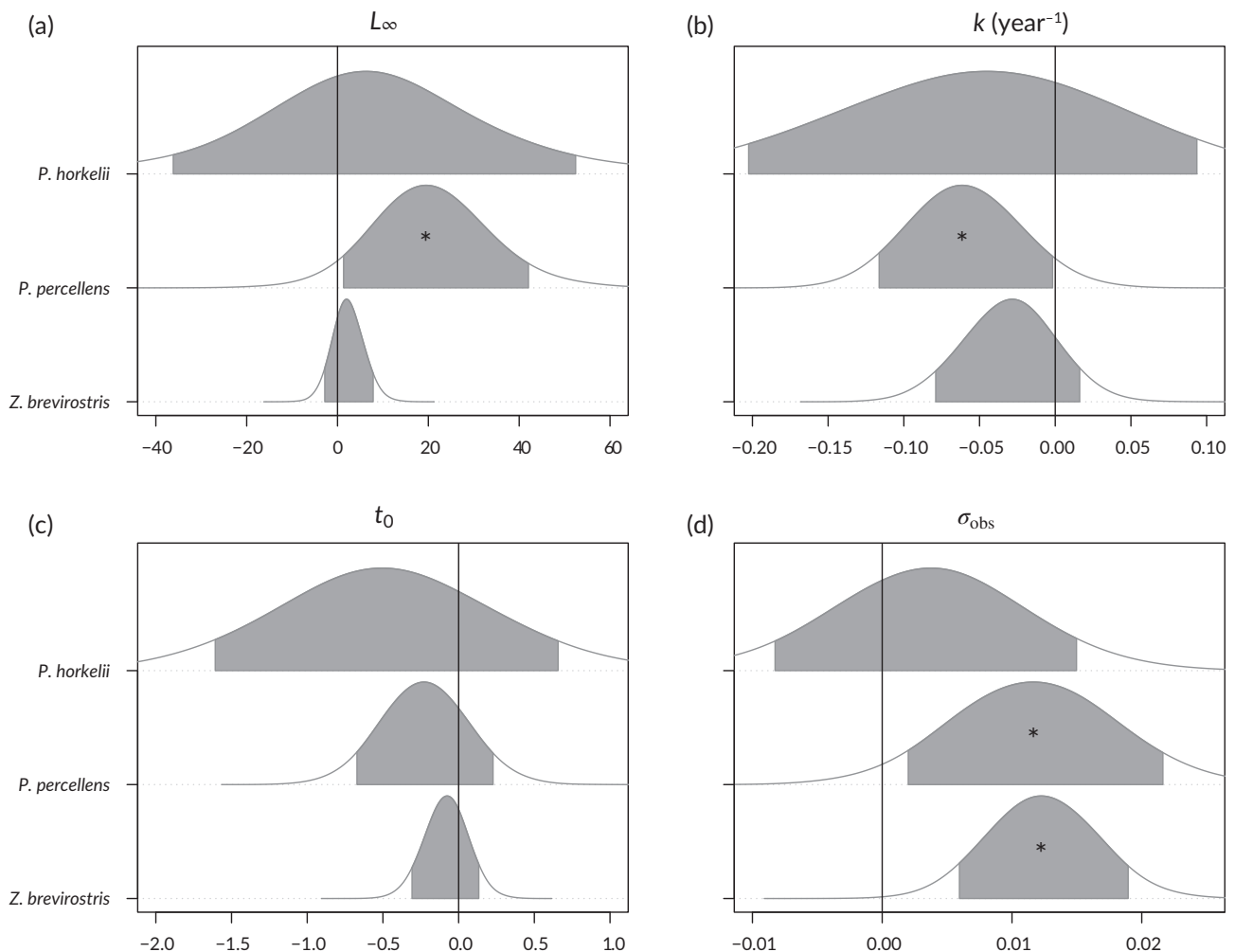


**FIGURE 7**  Posteriors of the parameter differences for sex-specific *Pseudobatos horkelii*, *P. percellens* and *Zapteryx brevirostris*. (a) asymptotic length, $L_\infty$; (b) $k$: Brody growth coefficient, $k$; (c) $t_0$: theoretical age where the species would be length zero, $t_0$; (d) observation error, $\sigma_{obs}$. *, Parameters that were significantly different ($P < 0.05$) between sexes (*i.e.*, the 90% CI did not contain zero)

history patterns (Ebert *et al.* 2008), water temperature and latitudinal differences (Yamaguchi *et al.* 2000).

In general, growth banding patterns observed in the present study were relatively easy to interpret in most of the samples. Similar growth patterns were also observed in *Rhinobatos rhinobatos* (L. 1758)

**TABLE 2**  Probability of differences between sexes in the estimated von Bertalanffy growth parameter ($L_\infty$, $k$, $t_0$ and $\sigma_{obs}$, the observation error) for *Pseudobatos horkelii*, *P. percellens* and *Zapteryx brevirostris*

| Species | $L_\infty$ | $k$ | $t_0$ | $\sigma_{obs}$ |
|---|---|---|---|---|
| *P. horkelii* | 0.372 | 0.706 | 0.759 | 0.309 |
| *P. percellens* | 0.031* | 0.965* | 0.811 | 0.022* |
| *Z. brevirostris* | 0.242 | 0.842 | 0.713 | 0.001* |

$L_\infty$, asymptotic total length; $k$, growth coefficient; $t_0$, theoretical age at zero length; $\sigma_{obs}$, the observation error; 90% CI, 90% credibility interval. *estimates that were significantly different between sexes ($P < 0.05$ and $P > 0.95$).

(Başusta *et al.*, 2008), *Trygonorrhina fasciata* Müller & Henle 1841 (Izzo & Gillanders, 2008), *Glaucostegus cemiculus* (Geoffroy St. Hilaire 1817) (Enajjar *et al.*, 2012) and *Zapteryx exasperata* (Jordan & Gilbert 1880) (Cervantes-Gutiérrez *et al.*, 2018). In terms of precision analysis, APE and CV were < 5% for all three species examined here, indicating that our ageing method was reliable for assessing their ages (Campana, 2001). These values are similar to those reported for other guitarfish species, Izzo and Gillanders (2008) estimated an APE of 3.56% for *T. fasciata*, whereas Cervantes-Gutierrez *et al.* (2018) obtained an APE of 3.77% for *Z. exasperata*. Conversely, Carmo *et al.* (2018) have reported a higher value of APE (9.71%) and CV (13.7%) for *Z. brevirostris*.

The edge analysis and $I_{MR}$ used to indirectly validate the periodicity of band-pair formation in the vertebral centra for all three species suggested an annual deposition. The annual formation of the translucent band occurred in the Brazilian spring, between October to December for *P. percellens* and between September to November for *Z. brevirostris*. Unfortunately, both analyses were hampered for

**TABLE 3**  Comparison of von Bertalanffy growth parameters among guitarfish species

| Species | Location | Sex | Model | $L_\infty$ (cm) | $k$ (year$^{-1}$) | $t_0$ (years) | $L_0$ (cm) | $n$ | Author |
|---|---|---|---|---|---|---|---|---|---|
| *Pseudobatos horkelii* | South-eastern Brazil | Pooled | VBGM | 126.93 | 0.19 | −1.51 | – | 118 | Present Study |
| | | Male | | 120.65 | 0.23 | −1.22 | – | 56 | |
| | | Female | | 128.67 | 0.18 | −1.71 | – | 72 | |
| *P. percellens* | South-eastern Brazil | Pooled | VBGM | 109.31 | 0.16 | −1.78 | – | 318 | Present Study |
| | | Male | | 97.87 | 0.20 | −1.64 | – | 180 | |
| | | Female | | 118.44 | 0.13 | −1.87 | – | 138 | |
| *Zapteryx brevirostris* | South-eastern Brazil | Pooled | VBGM | 60.37 | 0.24 | −1.42 | – | 388 | Present Study |
| | | Male | | 60.15 | 0.25 | −1.42 | – | 196 | |
| | | Female | | 62.44 | 0.22 | −1.50 | – | 192 | |
| *P. horkelii* | Southern Brazil | Pooled | VBGM | 135.51 | 0.19 | −1.08 | – | – | Lessa (1982) |
| *P. percellens* | Northern Brazil | Pooled | VBGM | 69.45 | 0.24 | −1.23 | – | 291 | Nunes (2012) |
| *Zapteryx brevirostris* | Southern Brazil | Pooled | VBGM* | 56.40 | 0.12 | – | 14 | 162 | Carmo *et al.* (2018) |
| | | Male | | 54.90 | 0.13 | – | 14 | 91 | |
| | | Female | | 59.50 | 0.11 | – | 14 | 71 | |
| *Rhinobatos rhinobatos* | North-eastern Mediterranean | Pooled | VBGM | 149.60 | 0.15 | −0.05 | – | 97 | Başusta *et al.* (2008) |
| | | Male | | 121.60 | 0.31 | −0.13 | – | 41 | |
| | | Female | | 154.80 | 0.13 | −1.26 | – | 56 | |
| *Glaucostegus cemiculus* | Southern Tunisia | Male | VBGM | 179.00 | 0.27 | −0.71 | – | 51 | Enajjar *et al.* (2012) |
| | | Female | | 198.70 | 0.20 | −0.81 | – | 59 | |
| *Z. exasperata* | Baja California Sur | Male | VBGM | 89.78 | 0.17 | −0.65 | – | 153 | Cervantes-Gutiérrez *et al.* (2018) |
| | | Female | | 100.71 | 0.14 | −0.39 | – | 83 | |
| *Trygonorrhina fasciata* | South Australia | Pooled | VBGM | 112.90 | 0.13 | −2.55 | – | 43 | Izzo and Gillanders (2008) |

VBGM, three-parameter von Bertalanffy growth model; VBGM*, two-parameter von Bertalanffy growth model; $L_\infty$, asymptotic total length; $k$, growth coefficient; $t_0$, theoretical age at zero length; $L_0$, length at birth; $n$, sample size.

*P. horkelii* due to the lack of sampling during the winter and the low number of monthly samples available for spring and early summer. However, the general trend of band-pair formation was identical to that observed in the other two species. Although the annual pattern of band-pair formation has been reported in several other studies of the age and growth of guitarfishes (Başusta *et al.*, 2008; Enajjar *et al.*, 2012; Ismen *et al.*, 2007; Izzo & Gillanders, 2008; Timmons & Bray, 1997; Wilson *et al.*, 2013), factors that determine the band-pair formation are still unknown. Nevertheless, some studies have related the band formation to variation in temperature, photoperiod, variations in the diet and internal mechanisms (Caltabellotta *et al.*, 2019; Sagarese & Frisk, 2010; Kerr *et al.*, 2006; Natanson 1993).

In terms of growth parameters, the values of $L_\infty$ estimated for all the three guitarfish species were closer to the maximum lengths reported in southern Brazil of 135 cm $L_T$ for *P. horkelii* (Vooren *et al.*, 2005), 102 cm $L_T$ for *P. percellens* (Bornatowski *et al.*, 2010) and 56 cm $L_T$ for *Z. brevirostris* (Carmo *et al.*, 2018); indicating that our estimates of $L_\infty$ were not overestimated. All three guitarfish species displayed consistencies and contrasts in their growth characteristics in south-eastern Brazil. Regarding the attributes common for *P. horkelii* and *Z. brevirostris*, males and females exhibited similar growth (*i.e.*, no significant differences between *k* estimates). In contrast, our parameters for *P. percellens* are markedly different between both sexes: males grow more rapidly than females (*i.e.*, displaying greater *k* estimates) and females grow larger than males (*i.e.*, displaying greater $L_\infty$ estimates).

Comparisons of the growth parameters among *P. horkelii*, *P. percellens* and *Z. brevirostris* from previous studies and other guitarfish species from other parts of the world are presented in Table 3. The parameters $L_\infty$ and *k* did not differ particularly from previous estimates for the same species in other areas. In southern Brazil, for instance, Lessa (1982) reported similar growth parameters to that observed in the present study for *P. horkelii*. On the other hand, our estimates for *P. percellens* were different from those reported in north-eastern Brazil by Nunes (2012), who observed a higher growth rate (*k* = 0.24 year$^{-1}$) and consequently smaller size for the asymptotic length ($L_\infty$= 69 cm $L_T$). In contrast, the $L_\infty$ observed in the present study for *Z. brevirostris* was similar to that reported in southern Brazil by the Carmo *et al.* (2018). However, the growth coefficient observed in the present study for *Z. brevirostris* (*k* = 0.24 year$^{-1}$) was two times higher than the value observed by those authors in southern Brazil (*k* = 0.13 year$^{-1}$; Table 3). In comparison with *T. fasciata* from South Australia, *Z. exasperata* from north-west Mexico, *G. cemiculus* southern Tunisia and *R. rhinobatos* from north-eastern Mediterranean, our estimates of the growth rate are within the range reported for these other species (Table 3).

Among batoid elasmobranchs, the growth coefficient *k* ranges from 0.2 to 0.5 (Cailliet & Goldman, 2004). In addition, longevity and asymptotic length are directly proportional to vulnerability and inversely proportional to the growth coefficient (Frisk *et al.*, 2001). Our estimates of *k* for males and females, in all three guitarfish species were > 0.10, which indicates that growth rate is moderate among the elasmobranchs (Branstetter, 1990). Although species with *k* > 0.10 are not considered at high risk of population decline (Musick, 1999),

guitarfishes are among the most threatened families, highly sensitive to fishing pressure and possibly exhibiting a low intrinsic rate of population increase (Dulvy & Forrest, 2010).

In conclusion, two of the assessed species of guitarfishes (*P. horkelii* and *Z. brevirostris*) have their fishing prohibited under normative instruction N°445 (Brazil, 2014), however, illegal catches are still observed. Considering that fisheries management remains nearly non-existent and fishing monitoring has not been carried out in Brazil for more than a decade (Barreto *et al.*, 2017), these illegal catches and incidental by-catch are extremely concerning. As 36% of guitarfish species are in threatened categories (2% Critically Endangered, 5% Endangered and 29% Vulnerable) worldwide because of their coastal habits targeted by intensive fisheries, endemism, medium-large size and high economic value (Moore, 2017), it is necessary to draw attention to the importance of the growth parameters estimated in the present study as a way of assessing their vulnerability to fishing pressure. Furthermore, the growth parameters assessed herein are essential for use in data-poor assessments (*e.g.*, demographic analyses and ecological risk assessment) with the aim of defining management and conservation actions for these species.

## AUTHOR CONTRIBUTIONS

F.P.C. contributed with ideas, data collection, data analysis and manuscript preparation; Z.A.S. contributed with data analysis and manuscript review; D.J.M. contributed with the data collection and manuscript preparation; F.S.M. contributed with manuscript preparation; G.M.C. contributed with manuscript preparation; O.B.F.G. contributed with data collection and manuscript preparation.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.