



**Abstract**—The aim of this study was to use a Bayesian approach to estimate age and growth parameters for the golden cownose ray (*Rhinoptera steindachneri*) in the southern Gulf of California in Mexico. Age estimates were obtained through analysis of vertebrae of 249 individuals. The von Bertalanffy growth function (VBGF) and Gompertz growth model (GM) were fit to length-at-age data by using a Markov chain Monte Carlo algorithm for parameter estimation. Prior distributions of parameters were included for an informative prior for disc width at birth ( $DW_0$ ) and uninformative priors for the theoretical maximum disc width ( $DW_\infty$ ) and growth coefficients ( $k$  and  $g$ , for the VBGF and GM, respectively). Our results indicate that the golden cownose ray lives up to 13 years. The GM for combined sexes was selected as the best model by using the Watanabe–Akaike information criterion for model selection suitable for Bayesian estimation. The mean values of the GM parameters were as follows:  $DW_\infty=101.10$  cm (95% credible interval [CI]: 94.19–110.43),  $g=0.15$  year<sup>-1</sup> (CI: 0.12–0.18), and  $DW_0=40.00$  cm (CI: 39.29–40.71). This study of the golden cownose ray contributes to the information available to develop better management and conservation strategies for this species.

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## Bayesian estimation of the age and growth of the golden cownose ray (*Rhinoptera steindachneri*) in the southern Gulf of California in Mexico

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The golden cownose ray (*Rhinoptera steindachneri*) ranges from the Gulf of California (GOC) to Peru, including the Galapagos Islands. Abundant in the GOC in summer, this species inhabits coastal waters and migrates seasonally (McEachran and Notarbartolo-di-Sciara, 1995). Bizzarro et al. (2007) investigated the biology of the golden cownose ray in the GOC and reported a maximum length of 104 cm disc width (DW) and a median length at maturity of around 70 cm DW. This species produces a single embryo at a size of 38–45 cm DW after 12 months of gestation. Low fecundity, typical of chondrichthyan species, is recognized as a limiting factor for the sustainability of the fisheries that target them and leads to the rapid overexploitation of populations.

The GOC supports the largest artisanal and multi-specific ray fishery in Mexico, and the golden cownose ray is among the most commonly captured

species (Bizzarro et al., 2007). Its dorsoventrally flattened and broad body makes it susceptible to being caught in gill-net fisheries and as bycatch by the trawlers licensed to catch shrimp and operate in the GOC (Márquez-Farías, 2002). Despite the importance of the golden cownose ray in the artisanal ray fishery of the GOC, detailed information on the life history of this species and age estimates are scarce. Aging is necessary to determine age-specific survival and reproduction rates, which are useful for assessing species productivity (Cortés, 1998). However, determining age in chondrichthyans is challenging because of the logistical problems of collecting samples that result from their seasonal migrations and because of the difficulty of identifying growth bands in hard parts (Cailliet, 2015). Growth is a fundamental component of life history, and the ability to model it is imperative for practical fishery assessments (Smart et al., 2016).

The von Bertalanffy growth function (VBGF) has been used conventionally to describe growth in elasmobranchs (Cailliet et al., 2006) and involves the assumption that variation in growth rate is determined by an individual's metabolic state, diet, and reproduction and by environmental factors (Pitcher and Hart, 1982). However, the VBGF does not always reflect the growth of elasmobranchs. Therefore, it is necessary to explore alternative models (Smart et al., 2016). Neer and Thompson (2005) evaluated various models for estimating the growth of the cownose ray (*R. bonasus*) in the Gulf of Mexico, and they found that the Gompertz model (GM) described its growth convincingly.

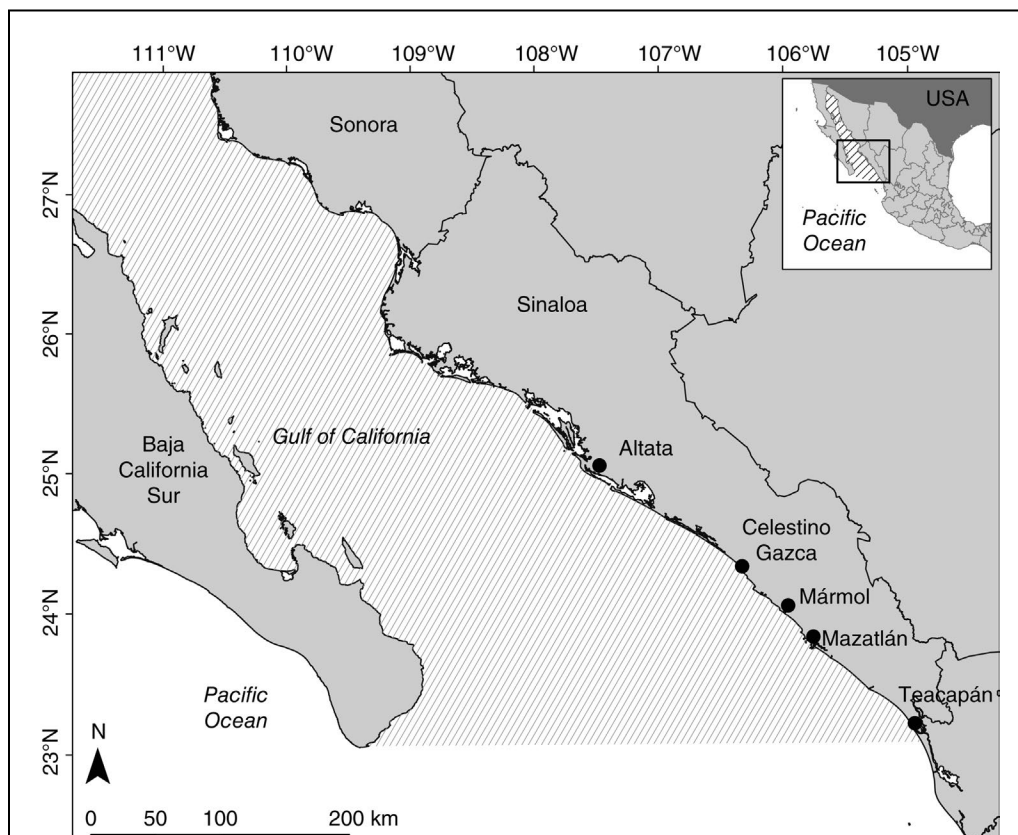
In our study, we estimated age by using counts of growth bands on vertebrae of golden cownose rays collected in the artisanal ray fishery of the GOC. We evaluated the ability of 2 models (VBGF and GM) to describe growth. We used a Bayesian approach to estimate the posterior probability of the growth parameters (marginal posteriors). The availability of marginal posteriors of growth parameters allows the explicit incorporation

of the uncertainty of parameters into further demographic or stock assessment studies to obtain more realistic estimates.

## Materials and methods

Samples of golden cownose rays were collected in 2008–2014 from landings of the artisanal fishery and from bycatch of the commercial shrimp trawl fishery in the southern GOC (Fig. 1). We recorded the sex of each sampled ray and measured the DW (in centimeters), avoiding the curvature of the body. A section of 8–10 cervical vertebrae was extracted from each specimen (Natanson et al., 2018). Excess tissue and neural arches were excised from the vertebral segments, and vertebrae were exposed to sodium hypochlorite (5%) to remove the remaining fascial tissue (Anislado-Tolentino et al., 2008).

A single vertebra was removed from each section by using a blade to expose the surface of the centrum and



**Figure 1**

Map showing the primary locations (black circles) where golden cownose rays (*Rhinoptera steindachneri*) were sampled from landings of the artisanal fishery and from bycatch of the shrimp trawl fishery in the southern Gulf of California in Mexico between 2008 and 2014. The area with the diagonal lines indicates the Gulf of California.

was fixed to a flat piece of wood with synthetic resin. Each vertebral centrum was sectioned in a sagittal plane through the focus with an IsoMet Low Speed Saw<sup>1</sup> (Buehler Ltd., Lake Bluff, IL) that had double blades separated by 0.24 mm. Each section was mounted on a slide and photographed with transmitted light on an Olympus SZ61 stereomicroscope (Olympus Corp., Tokyo, Japan) equipped with an OptixCam S7N digital camera (Microscope LLC, Roanoke, VA). We created a database of section images for the interpretation and counting of growth bands.

### Age estimation

Opaque and translucent bands form annually, and under transmitted light, these bands appear dark and light, respectively (Beamish, 1979). Age estimates were made by counting these band pairs (one dark and one light band) along the corpus calcareum after identifying the birthmark, the first distinct band after the focus (Cailliet et al., 2006). The distance from the focus to the edge of a vertebra and the thickness of each band were recorded by using Image-Pro Plus image analysis software (vers. 6.0, Media Cybernetics Inc., Rockville, MD). Images were projected onto a screen for the identification of growth bands. We used several vertebrae for defining reading criteria, and 3 independent readers counted the growth bands along the corpus calcareum on each vertebral section. We considered only age estimates with which at least 2 readers coincided. Otherwise, readings were discarded. We used a Bayesian *t*-test by using reference (uninformative) priors for the mean ( $\mu$ ) and standard deviation ( $\sigma$ ) of DW (Suppl. Table 1) to determine the support for the difference in mean DW between sexes, as previously described by Doll and Jacquemin (2018). We fit a Bayesian linear regression with reference priors (Suppl. Table 1) to assess the proportionality of growth between vertebral diameter (VD) and DW.

The agreement of growth band counts was evaluated by using a bias plot (Campana et al., 1995). Reproducibility and precision of growth band counts were assessed by using the index of average percent error (IAPE), the coefficient of variation (CV), and the precision index (*D*) for readings of all 3 readers together and between readers (Beamish and Fournier, 1981; Chang, 1982; Goldman and Musick, 2006):

$$IAPE = 100 \left[ \frac{1}{N} \sum_{j=1}^N \left( \frac{1}{R} \sum_{i=1}^R \frac{|x_{ij} - \bar{x}_j|}{\bar{x}_j} \right) \right]; \quad (1)$$

$$CV = 100 \left[ \frac{1}{N} \left( \sqrt{\sum_{i=1}^R \frac{(x_{ij} - \bar{x}_j)^2}{\bar{x}_j}} \right) \right]; \text{ and} \quad (2)$$

<sup>1</sup> Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

$$D = \left[ 100 \left( \frac{A}{B} \right) \right], \quad (3)$$

where *N* = the number of vertebrae;

*R* = the number of readers;

$x_{ij}$  = the age *i* determined for individual *j*;

$\bar{x}_j$  = the mean age calculated for individual *j*;

*A* = the numbers of agreements; and

*B* = the number of readings done.

### Periodicity of band formation

We performed and compared 2 methods to infer the period of band formation: edge percentage analysis and relative marginal increment (MI) analysis following Cailliet (2015). We categorized the edge type of each section of a vertebra as *opaque* or *translucent*, and the relative frequency of each edge type was tabulated in bimesters (2-month intervals).

The MI analysis was conducted over bimesters by using vertebrae from rays at the ages of 1–3 years (number of rays=94) to reduce bias that can be caused by the inclusion of older individuals with many bands (Lessa et al., 2006). Bimesters with mean MI values close to 1 were interpreted to be the time of year when the growth cycle is about to be completed (Cailliet et al., 2006):

$$MI = \left( \frac{VR - r_n}{r_n - r_{n-1}} \right), \quad (4)$$

where *MI* = the marginal increment;

*VR* = the vertebral radius;

$r_n$  = the distance from the focus to the last band pair; and

$r_{n-1}$  = the distance from the focus to the penultimate band pair.

To evaluate differences in the MI values among bimesters, we used a Bayesian one-way analysis of variance (Gerronette, 2011). First, we estimated the posteriors of the mean MI for each bimester ( $\mu_i$ ), using reference priors to nullify their influence on posterior distribution of mean MI. Then, we estimated the difference between bimesters (*d*) by subtracting the entire posterior mean MI of one bimester from another (i.e.,  $\mu_1 - \mu_2$ ,  $\mu_1 - \mu_3$  . . . ,  $\mu_5 - \mu_6$ ). We used the odds of difference,  $P(d < 0) / P(d > 0)$ , as an informative statistic of the effect of mean MI (Suppl. Table 1).

### Growth models

Two models were fit to the observed age–length data. The first was the VBGF (von Bertalanffy, 1938), described as follows:

$$DW_t = DW_\infty - (DW_\infty - DW_0)e^{-kt}, \quad (5)$$

where  $DW_t$  = the estimated disc width (in centimeters) at a given age *t* (in years);

$DW_\infty$  = the theoretical maximum disc width (in centimeters);

$DW_0$  = disc width at birth (in centimeters); and

*k* = the growth coefficient (year<sup>-1</sup>).

The second model was a modified version of the GM (Ricker, 1975), described as follows:

$$DW_t = DW_0 e^{-\log\left(\frac{DW_0}{DW_\infty}\right)(1-e^{-gt})}, \quad (6)$$

where  $g$  = the completion growth parameter (Smart and Grammer, 2021).

Model fitting was done by using the software JAGS (vers. 4.3.0; Plummer, 2003). An additive error was assumed, indicating that, for individual  $i$  at given age  $t$ ,  $DW_i$  follows a normal distribution expressed by a mean of zero, and its precision ( $\tau$ ), which is the inverse of its variance, is expressed as  $\tau=1/\sigma^2$  (Doll and Jacquemin, 2018).

It is necessary to specify a prior distribution for the parameters to fit the growth models by using Bayesian methods. The priors for the parameters  $DW_\infty$ ,  $k$ , and  $g$  were chosen to be relatively uninformative, expressed as a uniform distribution (UD) based on growth estimates and information about maximum size in waters of Mexico (Villavicencio-Garáyzar, 1996; Gámez-Moedano et al., 2006): UD(80,200) and UD(0,1), respectively. The prior for size at birth  $DW_0$  was informative and normally distributed (ND): ND(41.5,1.0) based on the reported range of  $DW_0$  (38–45 cm; Bizzarro et al., 2007; Burgos-Vázquez et al., 2018). The prior for  $\sigma^2$  was UD(0,100). The posterior distribution for the parameters of the 2 growth models (Equations 5 and 6) was computed by using Bayes formula (Smart and Grammer, 2021):

$$P(\theta | d) = \left( \frac{P(d | \theta)P(\theta)}{\int_1^n P(d | \theta)P(\theta) \partial \theta} \right). \quad (7)$$

Given the complexity of this multiparameter equation, the evaluation of the denominator requires numerical methods. The posterior probability distribution is summarized by drawing random samples from the vector of all parameters with the Markov chain Monte Carlo algorithm (Robert and Casella, 2004). A total of 1 million runs were completed after an initial burn-in of 20,000 runs. Every tenth iteration was saved to test convergence (Gerrodette and Eguchi, 2011).

The growth models (VBGF and GM) were fit to data and then compared by using the Watanabe–Akaike information criterion (WAIC). The WAIC is considered a better version of the deviance information criterion, which is commonly used to assess Bayesian models because it uses the entire posterior distribution to make an inference (Coll et al., 2019). The best model was chosen by considering a difference of at least 2 units in WAIC as is typically done for the Akaike information criterion (Burnham and Anderson, 2002). Once the best model was selected, we compared 2 versions of the best model, with and without sex variation, and the WAIC was used to choose the best model. All statistical analyses were performed by using Microsoft Excel 2015

(Microsoft Corp., Redmond, WA) and R, vers. 3.6.1. (R Core Team, 2019).

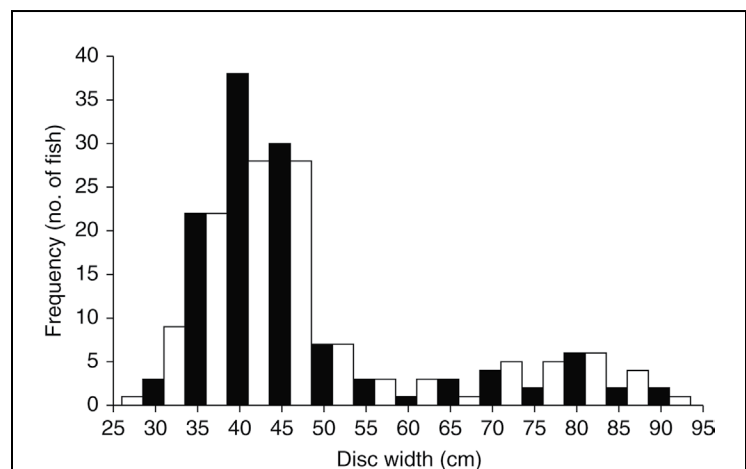
## Results

### Age estimation

A total of 256 specimens of golden cownose rays (129 females and 127 males) were analyzed. Seven vertebrae were discarded because the band pairs were unreadable. The size range for females was 29.4–96.9 cm DW (mean: 49.20 cm DW [standard deviation (SD) 14.62]), and males ranged in size from 21.5 to 92.9 cm DW (mean: 49.69 cm DW [SD 15.71]). A higher proportion of organisms were observed in the 10-cm-DW interval of 35–45 cm DW (Fig. 2). The difference in mean size between sexes was 0.49 cm DW, and the mean difference in DW between sexes was  $-0.15$  cm (SD 1.93), with a 95% credible interval (95% CI) of  $-1.49$ – $1.27$  cm. This difference in mean DW is considered irrelevant because the probabilities of males being larger ( $P=0.53$ ) or smaller ( $P=0.47$ ) than females are almost equal (odds=1.13).

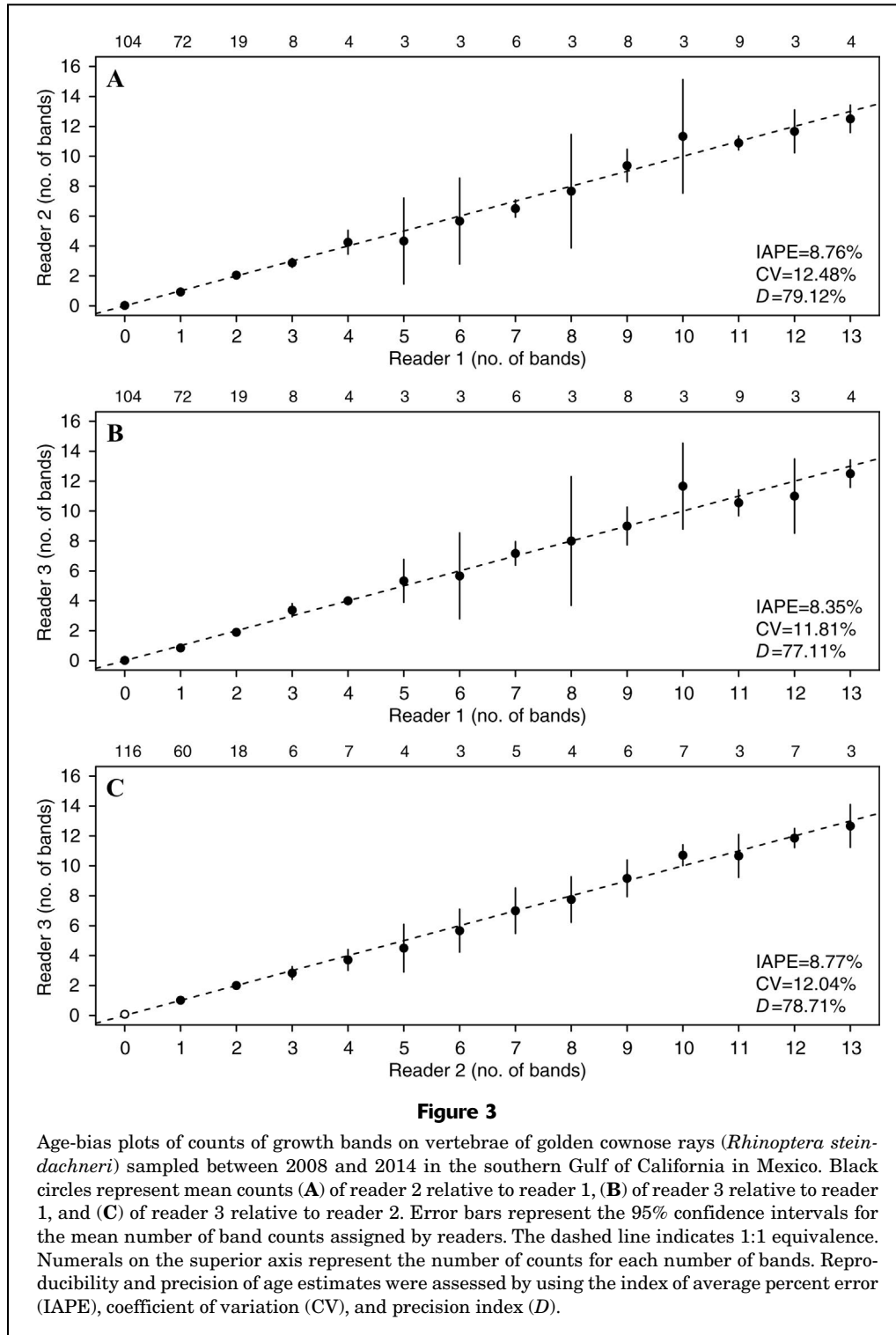
We found strong evidence of a linear relationship between VD and DW, given that the 95% CI of 12.49–13.52 for the marginal posterior of the slope did not include zero. The equation that describes the relationship is as follows:  $DW=1.98+12.98(VD)$ . The bias plot shows 13 growth bands identified by the 3 readers, indicating that variability increases with the number of growth bands. For the readings of the 3 readers, the overall IAPE was 12.11%, the CV was 15.73%, and the precision index was 67.47%. The precision of readings between each pair of readers is shown in Figure 3.

Results of the MI analysis indicate that deposition of growth bands on examined vertebrae was close to



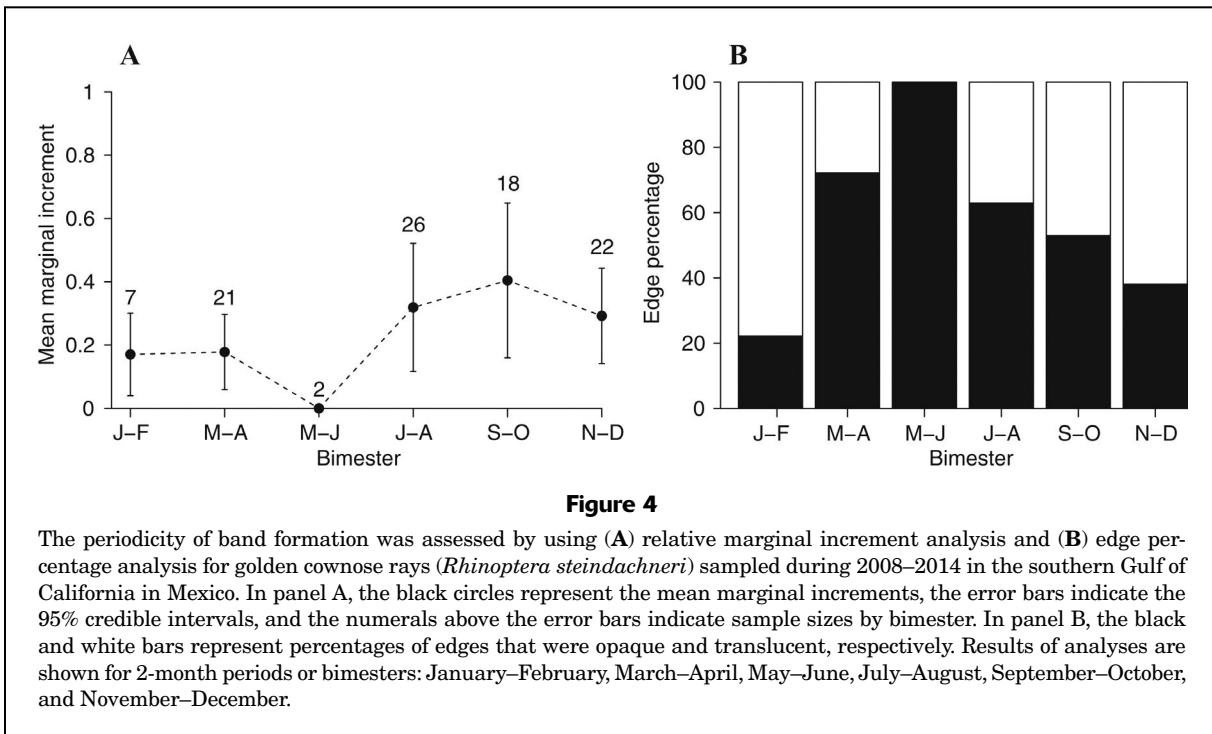
**Figure 2**

Length–frequency distributions for female (black bars) and male (white bars) golden cownose rays (*Rhinoptera steindachneri*) sampled during 2008–2014 in the southern Gulf of California in Mexico (number of rays=256).



completion in September–October when the highest mean MI value was reached (Fig. 4A). We found strong evidence for a difference in posterior mean MI between bimester 2 (March–April) and bimester 5 (September–October), a difference that could serve as support for the annual pattern of growth-band formation (Suppl. Table 2).

Results of the edge analysis indicate that opaque growth bands form during March–August (spring–summer) and translucent bands form during September–February (autumn–winter), as expected for annual formation of growth bands (Fig. 4B). Therefore, the age structure of the golden cownose rays sampled in the study area

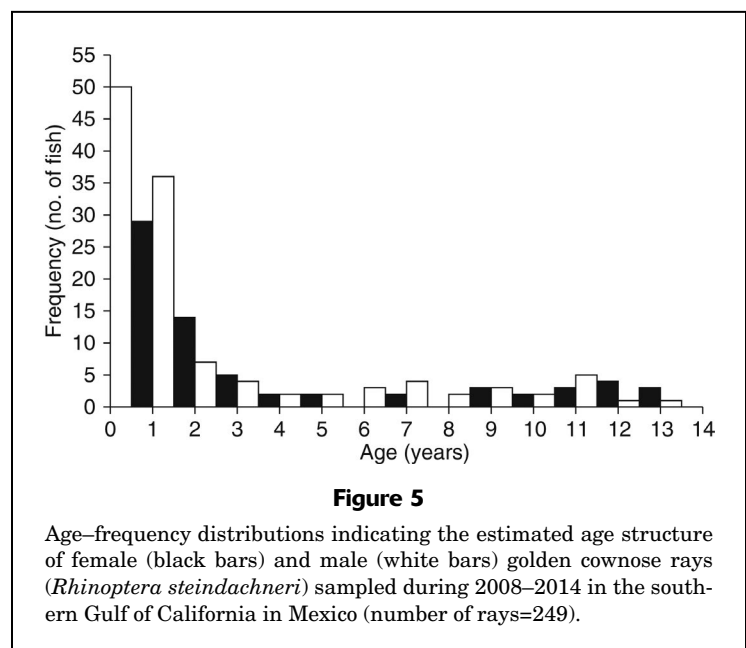


ranged from 0 to 13 years for both sexes combined, with 69.1% of individuals assigned ages of 0–1 years (Fig. 5). The oldest individuals were 13 years old for both females (92.9 cm DW) and males (96.6 cm DW).

### Growth estimation

The results of the process in which the WAIC was used for model selection indicate that the GM was better at explaining the growth of golden cownose rays, given the reduction of 2.44 units of WAIC from the WAIC of the VBGF (Table 1). Similarly, there was no gain in the model fitting from the inclusion of sex variation in the GM. When sex was included in the GM, the WAIC increased by 7.85 units (from 1459.82 to 1467.67). Therefore, we selected the model for both sexes combined.

Results from use of the GM indicate that the golden cownose ray grows rapidly during its first 4 years of life, and its growth rate decreases after age 4 as it approaches its asymptotic size at the age of 13 years (Fig. 6). After the burn-in period, the simulations generated the marginal posterior probability distributions of the GM (Fig. 7, A–C). The predicted mean values of growth parameters of the GM were more realistic than those predicted with the VBGF (Table 1), which were considerably higher than the actual maximum lengths observed for the golden cownose ray and seemed to be overestimated.



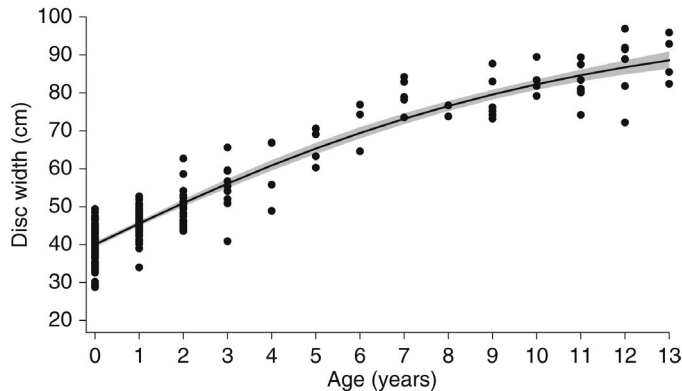
### Discussion

Our results indicate that the golden cownose ray lives up to 13 years, an age that is similar to the ages reported for the cownose ray (*R. bonasus*) in the Chesapeake Bay (13 years for females and 8 years for males; Smith and Merriner, 1987). However, the maximum reported age for the

**Table 1**

Comparison of the Gompertz and von Bertalanffy growth models fit to length-at-age data for golden cownose rays (*Rhinoptera steindachneri*) sampled between 2008 and 2014 in the southern Gulf of California in Mexico. Posterior values and 95% credible intervals (lower quartile: 2.5%; upper quartile: 97.5%) are provided from the fit of the growth models with a Markov chain Monte Carlo algorithm to data pooled for both sexes of golden cownose rays. The model parameters are disc width (DW) at birth ( $DW_0$ , in centimeters), theoretical maximum length ( $DW_\infty$ , in centimeters), the completion growth parameter ( $g$ , year<sup>-1</sup>), and the growth coefficient ( $k$ , year<sup>-1</sup>). The standard deviations (SDs) and median values are given in addition to mean values. The Watanabe–Akaike information criterion (WAIC) was used in model selection.

| Model           | Parameter   | Mean   | SD   | 2.5%   | Median | 97.5%  | WAIC    |
|-----------------|-------------|--------|------|--------|--------|--------|---------|
| Gompertz        |             |        |      |        |        |        | 1459.82 |
|                 | $DW_0$      | 40.00  | 0.36 | 39.29  | 40.00  | 40.71  |         |
|                 | $DW_\infty$ | 101.10 | 4.15 | 94.19  | 100.67 | 110.43 |         |
|                 | $g$         | 0.15   | 0.01 | 0.12   | 0.15   | 0.18   |         |
|                 | SD          | 4.5    | 0.2  | 4.12   | 4.49   | 4.92   |         |
| von Bertalanffy |             |        |      |        |        |        | 1462.26 |
|                 | $DW_0$      | 39.93  | 0.37 | 39.20  | 39.93  | 40.65  |         |
|                 | $DW_\infty$ | 118.78 | 9.35 | 104.06 | 117.41 | 140.85 |         |
|                 | $k$         | 0.08   | 0.01 | 0.05   | 0.08   | 0.10   |         |
|                 | SD          | 4.52   | 0.21 | 4.15   | 4.51   | 4.95   |         |

**Figure 6**

Estimated growth curve for golden cownose rays (*Rhinoptera steindachneri*) in the southern Gulf of California in Mexico, from use of the Gompertz growth model for sexes combined. The black circles represent observed lengths at age for rays sampled during 2008–2014, and the gray shaded area indicates 95% credible intervals of estimates.

cownose ray is 21 years (Fisher et al., 2013). Vertebrae are considered a valid structure for aging the golden cownose ray, as indicated by the proportional growth of the vertebrae to body size observed in our study. Also, values of IAPE and CV for band counts among readers were within the standard threshold for age determination in elasmobranchs (Campana, 2001).

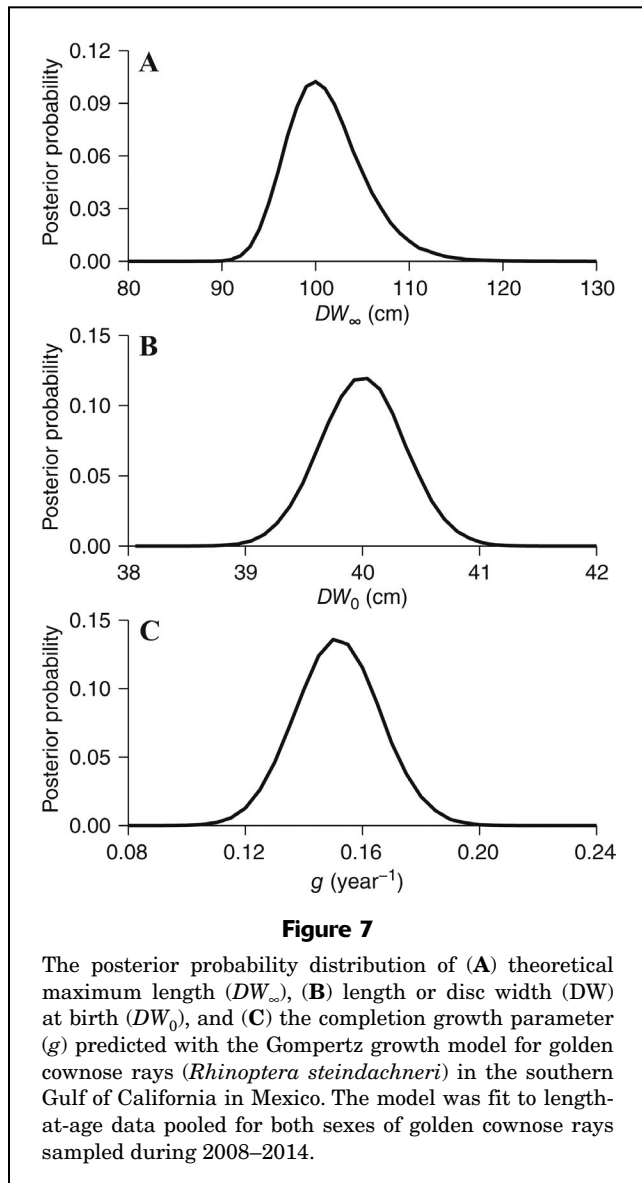
The assumption of an annual pair of bands in the vertebrae is supported by the results of MI and edge percentage analyses and has been validated for the golden cownose

ray by using biomarkers (Osuna-Soto, 2016). In addition, the same pattern of band formation has been observed for other species of the same genus (Neer and Thompson, 2005; Fisher et al., 2013). An annual pattern of band pairs has also been described for other batoids in the tropical and subtropical Pacific Ocean (Davis et al., 2007; Hale and Lowe, 2008; Mejía-Falla et al., 2014). Although there are more precise methods for validation of periodicity of band formation for aquatic organisms (e.g., biomarkers and mark and recapture), MI and edge percentage analyses provide the advantage of producing cost-effective and comparable results (Campana, 2001).

We found that the GM best described the growth of the golden cownose ray in the GOC for sexes combined, as indicated by the WAIC. Such a model includes an inflection point that represents a change in growth rate (Joung et al., 2011); this change in growth rate is assumed to be associated with a difference in ontogenetic feeding patterns between juveniles and adults. The GM may be a better option when the volume of an

organism greatly expands with age, as has been observed for myliobatiform rays (Cailliet and Goldman, 2004; Neer and Thompson, 2005) and for elasmobranchs that have a change in growth rate after age 0 (Smart et al., 2016).

Results of several studies indicate that the conventional VBGF does not always satisfactorily describe the growth of chondrichthyans (Cailliet et al., 2006), and the authors of some studies have emphasized the need to explore different nonlinear models to describe growth (Bishop et al., 2006; Natanson et al., 2007). In our study, an exhaustive



test of other growth models was not done because the versions of both models tested (VBGF and GM) conveniently include length at birth, an appropriate inclusion for viviparous species (Cailliet et al., 2006).

The multi-model approach to estimation of growth parameters allows selection of the model that best fits the data (Katsanevakis, 2006). Although growth models with multiple parameters may be useful for estimating growth of elasmobranchs (Richards, 1959; Chapman, 1961; Schnute, 1981), the multi-model approach suffers from testing models with more parameters, some of which might have no biological meaning as is the case with the theoretical age when length is zero in the VBGF (Cailliet and Goldman, 2004). In addition, researchers may eventually be conditioned to ignore factors that potentially bias the selection of data collected from a fishery when fitting models to that data.

Use of fishery-dependent data can potentially lead to a distorted growth curve through sampling bias due to gear selectivity and migration (Ricker, 1979; Moulton et al., 1992). Such biases can potentially straighten the growth curve and change the magnitude of parameters because of their autocorrelation (Gallucci and Quinn, 1979). Such an effect, known as the *phenomenon of apparent change in growth rate*, is common in studies of age and growth of chondrichthyans (Lee, 1912; Walker et al., 1998). The occurrence of the phenomenon of apparent change in growth rate in our study may have been caused by the susceptibility of fish of certain sizes to be caught by the fishing gears used during our sampling campaign (Moulton et al., 1992).

Distorted growth curves are common for shark species in fisheries that use highly size-selective fishing gear and high fishing intensity (Walker, 1998). In the samples of golden cownose ray taken from the artisanal fishery, small individuals (<55 cm DW) predominated. Individuals older than 4 years could escape from fishing gears because of their large size (>59 cm DW). Their shape means they avoid the proper length selectivity of gill nets and, therefore, are easily captured or entangled. In contrast, length selectivity of fishing gear is more likely to work for thinner guitarfish species with a more pointed shape (Márquez-Farías, 2005). However, the inclusion of golden cownose rays caught incidentally in the shrimp trawl fishery in the GOC allowed an increase in size ranges because it has been reported that trawl nets do not allow their escape (Garcés-García et al., 2020). Another explanation for size classes being misrepresented in our sample could be size-dependent migration, and it should be investigated in the future. We believe bias was minimal in our sample because we included individuals in all classes within the known size range for the golden cownose ray and combined the DW for both sexes.

The Bayesian approach applied in our study was particularly useful for exploring the effect of uncertainty in modeling life history characteristics (Cortés et al., 2015; Doño et al., 2015) and is likely to be useful for examining life history traits of other data-deficient batoid species. For instance, Rolim et al. (2020) implemented a Bayesian approach to assess estimates of life history characteristics derived from a growth model. This approach included more realism in the process of fitting the model to data and accounting for uncertainty in the other growth parameters.

The convergence of the growth parameters  $DW_{\infty}$ ,  $g$ , and  $DW_0$  was satisfactorily achieved, considering the well-defined posterior distribution profile of each parameter. The informative prior distribution for  $DW_0$  favored model fitting because it helped select realistic birth size values and because it represents the  $y$ -axis intercept (Rolim et al., 2020). The size at birth of elasmobranchs is often well-defined and known; therefore, it is easy to judge whether the  $DW_0$  from the fitted model is a reasonable value (Cailliet et al., 2006). However, using prior values and uncertainty seems to be a better alternative than using fixed values for the length at birth and solving only for  $g$  and  $DW_{\infty}$  (Smart et al., 2016).



Low availability of data is a common problem in studies of elasmobranch growth because most of the data on species of low value in fisheries usually come from instances of bycatch; therefore, it becomes difficult to determine the real asymptotic size for such species (White et al., 2014). Nevertheless, our results were similar to those of other studies in which the GM was a better fit to data and yielded more realistic estimates of growth parameters (Mollet and Cailliet, 2002; Carlson and Baremore, 2003; Neer and Thompson, 2005).

Information on the age structure and growth parameters provided from our study is valuable input for further demographic studies. The data are useful for estimating the trajectory of stock productivity and the resilience to fishing of the golden cownose ray.

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