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Age and growth of the banded guitarfish *Zapteryx exasperata* (Chondrichthyes: Trygonorrhinidae)

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Abstract. The banded guitarfish (*Zapteryx exasperata*) is the third most abundant ray species in the artisanal elasmobranch fishery of Baja California Sur, Mexico. However, there is no biological information about its age and growth parameters, limiting the application of some quantitative population assessment methods, such as demographic models. The aim of the present study was to estimate, for the first time, age and individual growth of *Z. exasperata*. Biometric data from 244 individuals and 236 vertebrae were analysed. The largest number of banded guitarfish in fishery landings was observed during April and August, with a female : male sex ratio of 1 : 1.8. The size range was 56.4–103-cm total length (TL) for females and 51.6–92 cm TL for males, with females being significantly larger than males ($P < 0.05$). The periodicity of the vertebral edge suggests that growth band pairs form annually. The estimated age structure was 5–22.6 years for females and 4–19.6 years for males, with significant differences between sexes ($P < 0.01$). The goodness-of-fit of three models was evaluated. For the von Bertalanffy growth model, the parameters were as follows. For females: theoretical maximum length, $L_\infty = 100.71$ cm TL; growth coefficient, $k = 0.144$ year^{-1}; and theoretical age at length zero, $t_0 = -0.39$ years. For males: $L_\infty = 89.78$ cm TL; $k = 0.174$ year^{-1}; and $t_0 = -0.65$ years.

Additional keywords: age structure, elasmobranchs, fisheries management.

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Introduction

Cartilaginous fish are an important component of fishery landings around the world, but their biological characteristics make them particularly sensitive to overfishing (Holden 1977; Stevens *et al.* 2000; Dulvy and Reynolds 2002). Nearly 50 species of elasmobranchs are regularly caught with gill-nets by artisanal vessels off the west coast of Baja California Sur, Mexico. Of these, *Rhinobatos productus* (now *Pseudobatos productus* (Farrugia *et al.* 2016); 28.6%), *Myliobatis californica* (11%) and *Zapteryx exasperata* (8.3%) are the most abundant ray species, comprising almost half (47.9%) the total catch of elasmobranchs by number of individuals (Ramírez-Amaro *et al.* 2013).

The banded guitarfish *Z. exasperata* (Jordan and Gilbert, 1880) is a benthic species, a member of the Order Rhinopristiformes and Family Trygonorrhinidae. This species inhabits shallow rocky reefs and sandy coastal lagoons from the intertidal zone to a depth of 200 m, although it is primarily found at depths between 2.5 and 10 m. Its distribution in the Eastern Pacific Ocean ranges from Newport Beach (CA, USA) to Peru, including the Gulf of California (Michael 1993; Bizzarro and Kyne 2015; Last *et al.* 2016).

Despite its commercial importance, few studies regarding the biology and fisheries of *Z. exasperata* have been undertaken to date, with those studies that have been performed examining its reproductive biology off the west coast of Baja California Sur (Villavicencio-Garayzar 1995) and in the Gulf of California (Blanco-Parra *et al.* 2009), the fisheries and diet of *Z. exasperata* in the Gulf of California (Blanco-Parra *et al.* 2009*a*, 2012) and its reproduction in Bahía Tortugas, Baja California Sur (Meza-Castillo 2014). However, some aspects of its basic biology, including age and growth, remain unknown. Age and growth studies allow estimation of important parameters, such as age at maturity, the population growth rate and longevity, which are necessary to accurately assess species vulnerability to fisheries. Such information is also necessary for the development of quantitative assessment methods commonly used for elasmobranch populations, such as demographic models.

Z. exasperata is categorised as a data-deficient species by the International Union for Conservation of Nature (Bizzarro and Kyne 2015). Thus, additional biological data are necessary to develop and implement effective fisheries management and species conservation programs. The aim of the present study

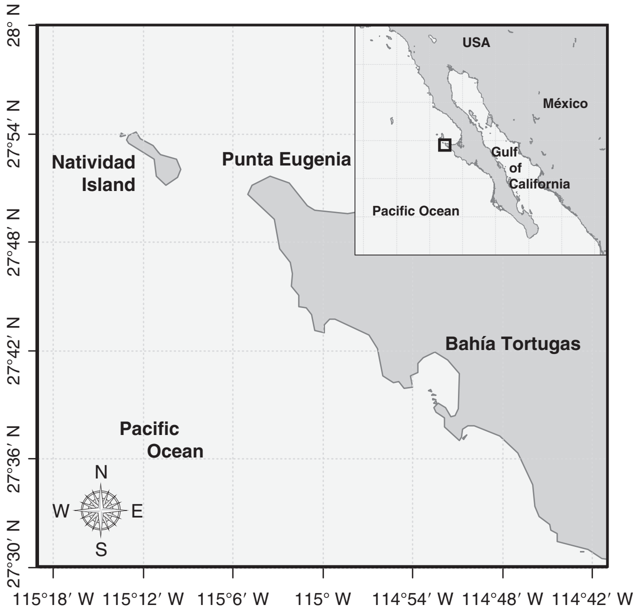

Fig. 1. Location of the study area, close to Bahía Tortugas, Baja California Sur, Mexico.

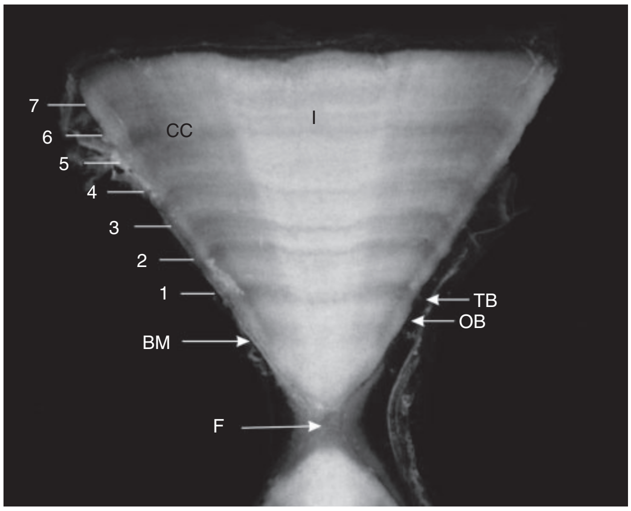

Fig. 2. Sagittal section of a vertebral centrum from a 7-year-old *Zapteryx exasperata* showing the banding pattern. Numbers, annual bands (years); F, focus; BM, birth mark; OB, opaque band; TB, translucent band; CC, corpus calcareum; I, intermedialia.

was to provide information about the age and growth of this species in the north-west of Mexico. The data generated can provide life history information about this species, which can be used together with reproduction parameters to apply demographic models.

Materials and methods

Sample collection

Samples were obtained from August 2013 to August 2015 from artisanal fishery landings along the north-west coast of Baja California Sur, Mexico (27°41′30″N, 114°53′45″W; Fig. 1). The individuals were caught with gill-nets on the continental shelf at depths between 70 and 90 m. The rays were measured to obtain total length (TL) to the nearest centimetre. Sex was determined by the presence or absence of claspers. A section of ~10 vertebrae was taken from the abdominal (precaudal) region of each individual, labelled individually with place and date of sampling, species name, sex, and TL, and kept on ice for transport to the Fish Ecology Laboratory at the Centro Interdisciplinario de Ciencias Marinas (CICIMAR), where samples were processed.

Age and growth

In the laboratory, the vertebrae were cleaned by removing excess of tissue. The samples were then completely dehydrated using a solution of 70% alcohol and then dried at room temperature; no deformation or shrinkage of vertebrae was observed. Once the samples had dried, the largest vertebra was selected (usually the seventh or eighth vertebra from the cephalic region) and sectioned sagittally close to the vertebral focus using a low-speed saw (IsoMet; Buehler, Lake Bluff, IL, USA) with a diamond blade (10.2 cm in diameter, 0.3 mm thick). The thickness of the sections obtained was ~0.4 mm, and sections were stored dry in Eppendorf tubes. Sections were digitised using a digital microscopy camera (AxioCam ICc 1-60N-C 2/3′ 0.63x; Zeiss, Jena, Germany) fitted to a stereoscopic microscope. All sections were digitised using reflected light and a black background at 12× magnification.

Two readers (J. Tovar-Ávila and F. Cervantes-Gutiérrez) estimated the age of each individual by independently counting the growth bands along the corpus calcareum of the vertebrae. Each growth band was confirmed on both sides and, where visible, in the intermedialia. Counts were based on pairs of bands composed of an opaque band followed by a translucent band. Age was determined as the total number of translucent bands completely formed minus the translucent band that forms at birth (birth mark), which was identified as the translucent band closest to the vertebral focus. The birth mark was generally a thicker translucent band with an angle change visible on the interior surface of the corpus calcareum of the vertebra (Fig. 2).

The age at the moment of capture was determined using the following formula:

$$Age = B + \frac{[(M \times 30) + D]}{365}$$

where B is the number of pairs of bands (without the birth mark), M is the number of complete months and D is the number of days from the incomplete months between the formation of the last translucent band, which appeared to form in winter (arbitrarily established as 1 January), and the day of capture (Tovar-Ávila *et al.* 2014).

To assess the accuracy of the growth band counts of the different readers (inter-reader accuracy) and the counts of the same reader (intra-reader accuracy), the average percentage error (APE) was calculated using the following formula (Beamish and Fournier 1981):

$$APE = \frac{1}{R}\left[\frac{\sum_{i=1}^{R}|X_{ij} - X_j|}{X_j}\right]$$

where R is the number of times the structure was read (i.e. number of readers), X_{ij} is the age i determined for individual j, and X_j is the mean age calculated for individual j.

In addition, the CV was calculated using the following formula (Chang 1982):

$$CV = \frac{100}{N}\left(\frac{\sum_{i=1}^{R}\sqrt{\frac{(X_{ij}-X_j)^2}{R-1}}}{X_j}\right)$$

where N is the total number of individuals for which age was estimated and R, X_{ij} and X_j are as defined above.

Once the CV was estimated, the index of precision (D) could be estimated using the following formula (Chang 1982):

$$D = \frac{CV}{\sqrt{R}}$$

Frequency histograms were used to analyse the size and age structure for each sex. For the size structure, an interval width of 5 cm TL was used. To assess whether there were significant differences between the sexes, a Kolmogorov–Smirnov test was used with the confidence level set at 95% (Sokal and Rohlf 1981).

The vertebral radius (VR) was measured on the corpus calcareum from the focus to the distal portion of the vertebra using Sigma Scan Pro, ver. 4.0 (SYSTAT, San Jose, CA, USA). Linear regression analysis of VR *v*. TL was used to assess the relationship between vertebrae and somatic growth.

Marginal increment analysis and the percentage of vertebrae with opaque and translucent edges were used to infer the periodicity of growth band pair formation (Hayashi 1976; Ishiyama 1978, cited in Yudin and Cailliet 1990; Tanaka and Mizue 1979).

Models

The von Bertalanffy growth model (VBGM) was used to estimate the individual growth of *Z. exasperata* based on the length-at-age data using the following equation:

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

where L_t is the total length at age t (cm), L_∞ is the asymptotic length, k is the growth coefficient, t is the age in years and t_0 is the theoretical age at length zero (years).

The inverse of the VBGM was used to determine age at size of maturity:

$$t(L) = \frac{t_0 - 1}{k}\cdot\ln\left(\frac{1 - TL}{L_\infty}\right)$$

where $t(L)$ is the age at size of maturity (years).

In addition, individual growth was estimated using the two-parameter VBGM, in which L_0 is fixed, because this model is more common in studies of shark age and growth (Cailliet *et al.* 2006):

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

where L_0 is the length at birth. Birth size has been estimated between 16.3 and 19.5 cm TL based on the largest embryos reported by Villavicencio-Garayzar (1995) and Meza-Castillo (2014) respectively. For the present study, 19.5 cm TL was used as the size at birth because this is the maximum embryo size reported for this species (Meza-Castillo 2014).

The Gompertz model (Ricker 1975) was used to explore an alternative model and to evaluate which of the three models best fit the observed growth of the banded guitarfish:

$$L_t = L_0 \cdot e^{\left(-(\ln(L_0/L_\infty))\cdot(1-e^{-kt})\right)}$$

The parameters in all models were estimated using StatSoft STATISTICA, ver.10 (Tulsa, OK, USA), whereas calculations were performed and graphics drawn using Microsoft Excel 2013 (Armonk, NY, USA).

Model comparisons

For all models, residual sum of squares (RSS) analysis was used to assess significant differences between sexes (Chen *et al.* 1992) in Microsoft Excel 2013. The fit of the growth models was compared with the Akaike information criterion (AIC):

$$\mathrm{AIC} = -2(\ln(RSS/n)) + 2(k)$$

where n is the number of samples and k is the number of parameters in each model.

The Akaike difference (Δ_i) was calculated using the following formula:

$$\Delta_i = \mathrm{AIC}_i - \mathrm{AIC}_{\min}$$

where AIC_i is the Akaike criterion value for each model and $\mathrm{AIC}_{\min}$ is the smallest Akaike criterion value for all models.

The Akaike weight for each model (W_i) was calculated using the following equation:

$$W_i = \frac{e(-0.5\cdot\Delta_i)}{\sum_{k=1}^{K} e(-0.5\cdot\Delta_k)}$$

where Δ_k is the sum of all the Akaike difference values.

There is an inverse proportional relationship between Δ_i and W_i; if the difference is zero, the weight will be greater (Burnham and Anderson 2002).

Results

Sample collection

Biometric data were collected from 244 individuals (87 females, 157 males) during the 3 years of the study (2013, $n = 70$; 2014, $n = 130$; 2015, $n = 44$). The largest number of samples was collected in August ($n = 150$). The Kolmogorov–Smirnov test indicated that the ratio of females : males (1 : 1.8) was significantly different ($P < 0.01$) from a 1 : 1 ratio. The smallest differences in the proportion of females and males were seen in April and November (1 : 1.27 and 1 : 1.2 respectively), whereas in March, August and September the largest differences were observed (1 : 2.1, 1 : 1.7 and 1 : 5 respectively).

The size range of females was 56.4–103 cm TL (mean ± s.d., 85.71 ± 13.19 cm); however, one female measuring 22 cm TL was found as prey in the stomach of a swellshark (*Cephaloscyllium ventriosum*). Although the internal organs of this small ray were missing, its identification was possible based on its morphological characteristics. In addition, we were able to sample the vertebrae and observed the birthmark of this individual. For males, the size range was 51.6–92 cm TL (mean ± s.d., 79.52 ± 7.73 cm). The Kolmogorov–Smirnov test indicated significant differences between the mean TL of males and females ($P < 0.05$; Fig. 3). Significant differences were also found between females and males in terms of the VR–TL relationship ($P < 0.05$), which, in both cases, was linear ($r^2 = 0.87$ and 0.77 respectively; Fig. 4).

Despite not being able to collect samples from all months, a lower percentage of opaque vertebral edges was observed during March and April, with a larger percentage observed in August, September and November (Fig. 5). This pattern allowed us to assume that growth bands in the vertebrae of this species are formed annually, with the opaque bands being associated with warmer months and the translucent bands being associated with cooler months. Marginal increment analysis (MIA) revealed a statistically significant ($P < 0.05$, $r^2 = 0.8123$) tendency to annual formation as well (Fig. 6).

Age and growth

The vertebrae of 236 individuals were used for age and growth estimations: 83 females (56.4–103 cm TL) and 153 males (51.6–92 cm TL). For females, the predominant age was 18 years (4.24% of individuals), whereas for males it was 14 years (4.24% of individuals). Based on previously reported size at maturity (69 cm TL for males, 77 cm TL for females; Villavicencio-Garayzar 1995), 12% of the individuals in the present study were juveniles. According to the inverse VBGM equation, maturity is reached at 9 years in females and at 7 years in males. Juvenile individuals are not targeted by the fishery and were landed

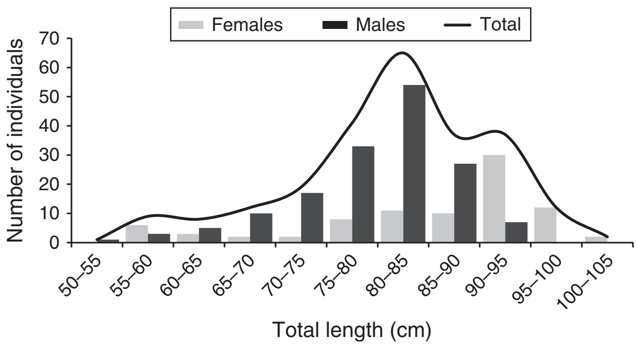

Fig. 3. Size structure for *Zapteryx exasperata* in the Bahía Tortugas area in Baja California Sur, Mexico ($n = 244$).

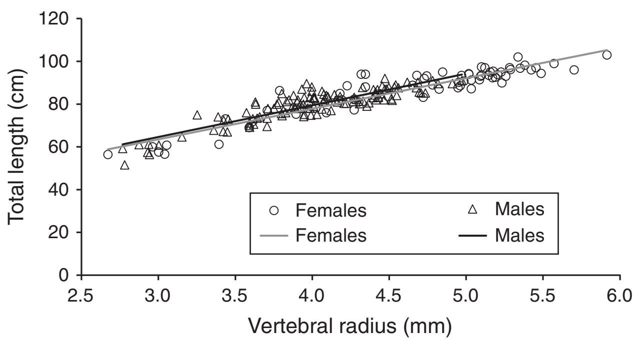

Fig. 4. Relationship between vertebral radius and total length for male and female of *Zapteryx exasperata* in the area of Bahía Tortugas, Baja California Sur, Mexico. Symbols show values for individual *Z. exasperata*, with the regression lines also shown.

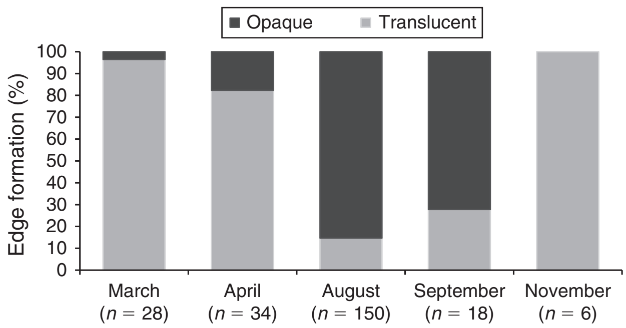

Fig. 5. Monthly vertebral edge formation in *Zapteryx exasperata*.

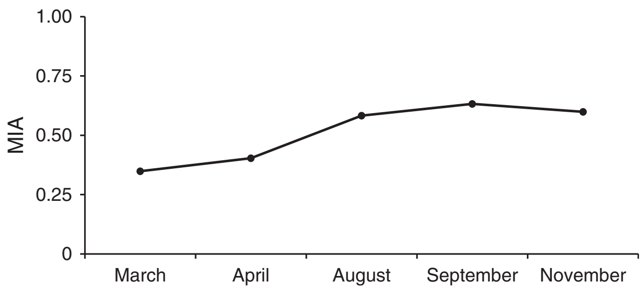

Fig. 6. Monthly marginal increment analysis (MIA) of *Zapteryx exasperata* vertebrae.

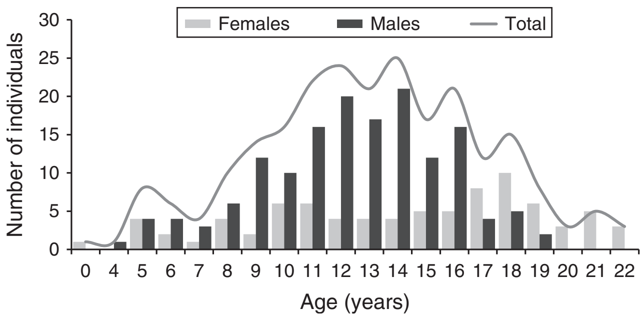

Fig. 7. Age structure of *Zapteryx exasperata* caught in Bahía Tortugas, Baja California Sur, Mexico ($n = 236$).

exclusively for scientific purposes in order to obtain a wider size range.

The estimated maximum age for females was 22.6 years (Fig. 7), for two individuals measuring 95 and 96.8 cm TL, whereas the maximum age for males was 19.6 years, for individuals measuring 87.8 and 90.2 cm TL. The inter-reader *APE* was 6.71 (CV = 9.65; *D* = 6.82), whereas the intra-reader APE was 3.77 (CV = 5.34; *D* = 3.77).

Individual growth models

Estimates of VBGM parameters were as follows. For females: $L_\infty = 100.71$ cm, $k = 0.14$ year^{-1} and $t_0 = -0.39$ years; for males: $L_\infty = 89.78$ cm, $k = 0.17$ year^{-1} and $t_0 = -0.65$ years (Fig. 8). Estimates of parameters for the two-parameter VBGM were $L_\infty = 103.86$ cm and $k = 0.12$ year^{-1} for females and $L_\infty = 91.52$ cm and $k = 0.15$ year^{-1} for males (Fig. 9). For the Gompertz model, the parameters were $L_\infty = 98.26$ cm and $k = 0.19$ year^{-1} for females, and $L_\infty = 87.75$ cm and $k = 0.23$ year^{-1} for males. Significant differences were found between the curves for females and males ($P < 0.05$) for all growth models.

Model comparisons

Based on the AIC (Table 1), both VBGM and the two-parameter VBGM adequately fit the length-at-age data for both males and females.

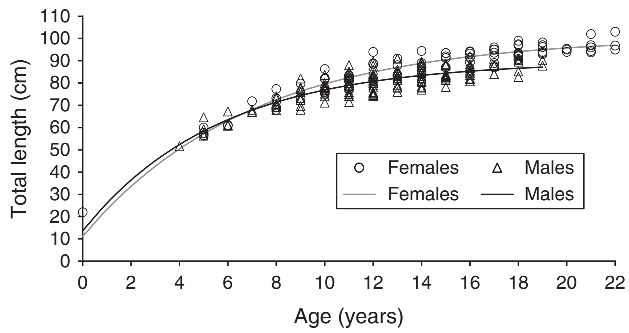

Fig. 8. Traditional von Bertalanffy growth model (VBGM) curves for male and female *Zapteryx exasperata* ($n = 236$ in total).

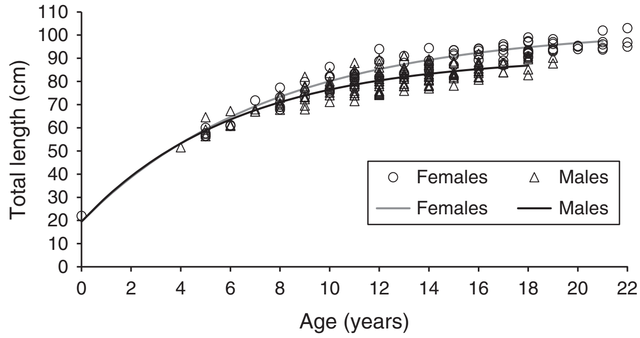

Fig. 9. Two-parameter von Bertalanffy growth model curves, in which L_0 is fixed, for male and female *Zapteryx exasperata*.

For females, Δ_i and W_i values were slightly better for goodness of fit in the VBGM ($\Delta_i = 0$, $W = 0.686$), although they were almost equally good in the two-parameter VBGM ($\Delta_i = 1.57$, $W = 0.313$). The Gompertz model had the largest Δ_i (236.86) and lowest W (2.53×10^{-52}) values. For males, the Δ_i and W values were slightly better for goodness of fit in the two-parameter VBGM ($\Delta_i = 0$, $W = 0.608$), although they were almost equally good in the VBGM ($\Delta_i = 0.88$, $W = 0.391$). As for females, the Gompertz model of males had the largest Δ_i (436.39) and the lowest W (1.05×10^{-95}) values (Table 1).

Discussion

During the present study, a high proportion of male *Z. exasperata* was found in the fishery landings from the north-west coast of Baja California Sur, in contrast with the report of Villavicencio-Garayzar (1995) in Bahía Almejas, Baja California Sur, Mexico, where a higher proportion of females was found. This difference can be attributed to the catches coming from different fishing zones (in the same study area). Females may prefer more protected areas than males because, according to Álvarez-Borrego *et al.* (1975), Bahía Almejas is part of the Bahía Magdalena lagoon complex and is probably less exposed to currents than Bahía Tortugas. Another possible explanation could be depth; however, Villavicencio-Garayzar (1995) did not report their sampling depth.

The largest differences in the sex ratio found during March, August and September may be related to the breeding season. Meza-Castillo (2014) noted that in August 2009, 2011 and 2012 the sex ratio was equal in Bahía Tortugas, but in August 2010 males dominated the landings. Similarly, in the present study, the sex ratio was 1 : 1 in August 2013, but in August 2014 and August 2015 the landings were dominated by males; this could be due to different sampling sites or interannual variations in weather conditions.

As in the present study, sexual segregation for *Z. exasperata* was reported by Villavicencio-Garayzar (1995) and Meza-Castillo (2014). However, Blanco-Parra *et al.* (2009) found no significant difference in the sex ratio of this species in the eastern Gulf of California, reporting a ratio of 1 : 1 during samplings, suggesting that *Z. exasperata* has no sexual segregation.

The size range in the present study (51.6–103 cm TL) was slightly larger than that reported by Villavicencio-Garayzar (1995) in Bahía Almejas (55.5–97 cm TL), but smaller than that reported by Blanco-Parra *et al.* (2009; 41–90 cm TL) and Meza-Castillo

Table 1. Akaike information criteria (AIC) for three growth models of *Zapteryx exasperata* according to sex

VBGM, von Bertalanffy growth model; 2-VBGM, two-parameter von Bertalanffy growth model, in which L_0 is fixed; Δ_i, Akaike difference; *W*, Akaike weight

	Females			Males		
	AIC	Δ_i	*W*	AIC	Δ_i	*W*
VBGM	195.56	0	0.686	405.87	0.88	0.391
2-VBGM	197.13	1.57	0.313	404.99	0	0.608
Gompertz	434.42	236.86	2.53×10^{-52}	841.38	436.39	1.05×10^{-95}

(2014; 55–124 cm TL). Moreover, we observed maximum sizes larger than those reported previously by Villavicencio-Garayzar (1995) for both females and males (by 6 and 7.2 cm respectively); however, these maximum sizes were smaller than those reported by Meza-Castillo (2014), who found females up to 124 cm TL, 27 cm larger than the largest female reported by Villavicencio-Garayzar (1995) and 21 cm larger than the largest female in the present study. This may be due to the method of capture, the sampling sites, season or effort. For example, in the study of Villavicencio-Garayzar (1995), the sampling interval was 3–5 days, whereas in the study of Meza-Castillo (2014) and the present study the sampling frequency was 15 days–1 month with daily sampling. Although Blanco-Parra *et al.* (2009) reported sample collection over 3 years (July 1998–May 2000 and November 2004–July 2005), they did not report sampling frequency.

Villavicencio-Garayzar (1995) reported that *Z. exasperata* males and females reach maturity at 69 and 77 cm TL respectively. Based on these criteria, only 12% of our sample corresponded to juvenile individuals, indicating that the fishery primarily captures adults. Demographic studies including elasticity analyses are necessary to determine the effect of the survival of newborns, juveniles and adults on the population growth rates (Cortés 2007).

Age and growth

The differences observed between sexes in the VR–TL relationship are similar to those reported by Carrasco-Bautista (2011) for *Zapteryx xyster* and Downton-Hoffmann (2007) for *Rhinobatos productus*, which implies sexual dimorphism in size. Cortés (2000) reported that for elasmobranchs, the maximum size of males is usually 10% smaller than that of females, and females tend to live longer than males. In addition, Bigelow and Schroeder (1948) reported that among carcharhinids, it is commonly observed that females are bigger than males.

No other study has addressed the age or growth of *Z. exasperata* along the western coast of Baja California Sur or other regions of its distribution. In their study, Carrasco-Bautista (2011) noted that *Z. xyster* ranged in age from 0 to 3 years for both sexes, and sexually mature individuals were observed in their sample. In the Atlantic Ocean, Do-Carmo (2015) noted that the *Zapteryx brevirostris* sampled presented a size structure of 0–10 years. In Bahía Almejas, Downton-Hoffmann (2007) reported a maximum age of 16 years for females and 11 years for males of *R. productus* (*P. productus*), whereas Timmons and Bray (1997) reported a maximum age of 11 years for both females and males of the same species in waters between the Seal and Redondo beaches in California. Enajjar *et al.* (2012) reported a maximum age of 14 years for females and 10 years for males of *Rhinobatos cemiculus* (*Glaucostegus cemiculus*) in the central Mediterranean. Finally, Başusta *et al.* (2008) reported a maximum age of 15 and 24 years for male and female *Rhinobatos rhinobatos* in the north-eastern Mediterranean, Turkey. All these species are members of the Order Rhinopristiformes (Families Rhinobatidae, Glaucostegidae and Trygonorrhinidae) and the longevity of almost all these species is lower than that estimated for *Z. exasperata*, which means that *Z. exasperata* may be more sensitive to fishing mortality. It also be can inferred that within the order Rhinopristiformes, and even within the genus *Zapteryx*, species exhibit marked differences in age and growth.

Because a non-fishing season has been established in Mexico (Diario Oficial de la Federación 2013) from May to July each year, was not possible to obtain samples during these months in the present study. However, we observed an apparent annual trend in the formation of opaque bands, which formed primarily in the warmer months (August, September and November), whereas the translucent bands formed during colder months (March and April). Timmons and Bray (1997) reported opaque edges for *R. productus* (*P. productus*) in August, October and December, concluding that the opaque bands form from August to November, as in the present study, whereas the translucent bands form in January. Although January samples were not obtained in the present study, the predominance of translucent edges was observed during the following months. The annual periodicity of growth bands estimated in the present study is also consistent with the report of Carrasco-Bautista (2011) for *Z. xyster* in the southern Mexican Pacific.

The inter-reader APE and CV values in the present study (6.7 and 9.65 respectively) were higher than those reported by Carrasco-Bautista (2011) for *Z. xyster* (3.33 and 4.62 respectively) between two readers, but lower than those reported by Do-Carmo (2015) for *Z. brevirostris* (9.71 and 13.7 respectively). Even though the APE in the present study is higher than that reported by Carrasco-Bautista (2011), it is within an acceptable range ($<10\%$) according to Campana (2001). Therefore, the precision in the present study was considered to be good.

Models

The parameter values estimated using the traditional VBGM and the two-parameter VBGM were similar. Estimated L_∞ with both models was closer to the maximum length observed in the present study (103 cm for females, 92 cm for males), but larger than the maximum size observed by Villavicencio-Garayzar (1995; 97 cm TL for females, 83 cm TL for males) and smaller than that reported by Meza-Castillo (2014; 124 cm TL for both sexes). In both the VBGM and two-parameter VBGM, values of k were larger for males (0.17 and 0.15 respectively) than females (0.14 and 0.12 respectively), indicating that females grow more slowly than males.

The Gompertz model estimated higher k values and thus slightly lower L_∞ than the VBGM and two-parameter VBGM. Nonetheless, the same relationship was seen with the Gompertz model between the sexes (i.e. higher k and smaller L_∞ for males than females).

All k values estimated for both sexes with all three models were greater than 0.10, which indicates that the growth rate of this species is moderate among the elasmobranchs (Cailliet and Goldman 2004). According to Cailliet and Goldman (2004), Do-Carmo (2015) and the present study, guitarfish species (*P. productus*, *Z. brevirostris and Z. exasperata*) have k values between 0.02 and 0.25, thus exhibiting a wide range of growth rates. However, Cailliet and Goldman (2004) noted that differences in the growth coefficient, k, can be related to the sample size, the methods used for age estimation, verification and validation, and the growth model used.

Table 2. Comparison of von Bertalanffy growth parameters in different species of Rhinobatidae
L_∞, theoretical maximum length; k, growth coefficient; t_0, theoretical age at $L = 0$, where L is length

Species	Reference	Females			Males		
		L_∞ (cm)	k (year^{-1})	t_0 (years)	L_∞ (cm)	k (year^{-1})	t_0 (years)
Rhinobatos productus	Timmons and Bray (1997)	594	0.016	−3.8	142	0.095	−3.942
Rhinobatos productus	Downton-Hoffmann (2007)	136.69	0.16	−0.83	100.5	0.24	−0.83
Rhinobatos rhinobatos	Başusta *et al.* (2008)	154.88	0.134	−1.264	121.65	0.31	−0.131
Rhinobatos cemiculus	Enajjar *et al.* (2012)	198.7	0.202	−0.81	179	0.272	−0.71
Zapteryx brevirostris	Do-Carmo (2015)	59.5	0.11	−3.42	54.9	0.13	−3.07
Zapteryx exasperata	Present study	100.71	0.14	−0.39	89.78	0.17	−0.65

Downton-Hoffmann (2007) reported k values of 0.16 and 0.24 for female and male *R. productus* (*P. productus*) respectively, suggesting that the banded guitarfish *Z. exasperata* grows more slowly than *R. productus* (*P. productus*). However, for *R. productus* (*P. productus*) off the coast of California, Timmons and Bray (1997) reported k values of 0.016 for females and 0.095 for males; these values are considerably lower than those reported in the present study, likely because the former study involved only 43 samples (19 females, 24 males). Similarly, Başusta *et al.* (2008) reported k values for female and male *R. rhinobatos* of 0.134 and 0.310 respectively, suggesting that male *R. rhinobatos*, at least, grow faster than the other reported species, followed by *R. cemiculus* with a k value of 0.272 (Enajjar *et al.* 2012). For females, Enajjar *et al.* (2012) reported a k value of 0.202 in *R. cemiculus*, thus exhibiting the fastest growth, followed by female *R. productus* (*P. productus*) with $k = 0.16$ (Downton-Hoffmann 2007) and then *Z. exasperata* (Table 2).

Cailliet *et al.* (2006) proposed that it is better to use the two-parameter VBGM, in which L_0 is fixed, considering the lack of biological meaning of t_0 (Sparre and Venema 1997). Moreover, L_0 as the third parameter allows an easy evaluation of the growth curve (Cailliet and Goldman 2004). However, in the present study, both versions of the VBGM performed adequately, probably due to the asymptotic trend of the length-at-age data estimated.

Conversely, the Gompertz model did not adequately fit the data, because of its sigmoidal form and inflection point. According to Cailliet and Goldman (2004), the Gompertz model may be a better option when the volume of an individual greatly expands with age, as in the case of Myliobatiform rays, skates or stingrays.

The age structure of a population and its growth parameters must be known in order to understand population dynamics (Araya and Cubillos 2006). According to Cailliet and Goldman (2004), species with $k < 0.10$ tend to be particularly vulnerable. Although this does not apply to the species examined in the present study because its growth coefficient values exceeded 0.10, careful management of the population may be recommended because *Z. exasperata* is under fishing pressure during several months of the year in several regions of the Baja California Sur. The age structure and growth parameters reported in the present study offer data on biological aspects of *Z. exasperata* that had not been studied previously in the north-west Mexican Pacific, providing information on longevity, age at maturity and growth, which are important for future research on population dynamics.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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