

Research Article

Reproductive cycles of the southern banded guitarfish *Zapteryx xyster* and the Velez ray *Raja velezi* caught as bycatch in a bottom-trawl fishery

Juan Carlos Azofoifa-Solano¹, Tayler M. Clarke², Mario Espinoza^{1,3} & Ingo S. Wehrmann^{1,3}

¹Unidad de Investigación Pesquera y Acuicultura, Centro de Investigación en Ciencias del Mar y Limnología
Universidad de Costa Rica, San José, Costa Rica

²Changing Ocean Research Unit, Institute for the Oceans and Fisheries, University of British Columbia
Vancouver, Canada

³Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica

Corresponding author: Ingo S. Wehrmann (ingowehrmann@gmx.de)

ABSTRACT. The southern banded guitarfish, *Zapteryx xyster*, and the Velez ray, *Raja velezi*, are two endemic elasmobranchs in the eastern Tropical Pacific that are commonly caught by the bottom-trawl fishery. Reproductive cycles of these batoids were inferred from the hepatosomatic and gonadosomatic indexes (males and females) and the oviductal gland width and the yolk follicle diameter (females) of mature specimens collected along the Pacific of Costa Rica between 2010 and 2011. *Z. xyster* females have a partially defined annual cycle with one reproductive peak in June and July, with most neonates and gravid females occurring during December and January (beginning of the dry season). The gestation period of *Z. xyster* can range between four and six months; males are probably capable of mating continuously throughout the year. Females and males of *R. velezi* have a continuous reproductive cycle with no clear peaks. Management and conservation measures of these batoids should consider their reproductive ecology, which may be linked to the degree of vulnerability to fishing. Based on our findings, we recommend reducing fishing pressure when mating (June-July) and pupping (December-January) of *Z. xyster* occur. In contrast, a reduction of fishing pressure on previously identified nursery grounds of *R. velezi* in the southern Pacific of Costa Rica may benefit their population.

Keywords: *Zapteryx xyster*; *Raja velezi*; Batoidea; reproductive cycle; bottom-dwelling elasmobranchs; eastern Tropical Pacific

INTRODUCTION

Life history information can help identify vulnerable elasmobranch species and develop effective conservation and management measures (Hoenig & Gruber 1990, Morgan & Hoenig 1997, Goldman et al. 2012, Awruch 2013, Rigby et al. 2016). Given that a quarter of all chondrichthyans species are currently threatened with extinction, conservation measures for this group have become a top priority (Dulvy et al. 2014, Davidson et al. 2015). Some of the main threats affecting elasmobranchs, such as overfishing and habitat degradation, are concentrated in coastal areas (Ferretti et al. 2010, Graham et al. 2010, Ward-Paige et al. 2010, Costello et al. 2012, Worm et al. 2013, Davidson et al. 2015, Spaet et al. 2016). Consequently, elasmobranchs that inhabit these coastal areas, remar-

kably large and slow-moving species like stingrays and guitarfishes, are among the most threatened (Dulvy et al. 2014), whether it is during their entire life cycle or vulnerable stages (Heupel et al. 2007, Jirik & Lowe 2012, Tobin et al. 2014, Chapman et al. 2015). Knowledge of their reproductive cycle can provide useful information to minimize their populations' impacts during vulnerable phases like mating or pupping (Hoenig & Gruber 1990, Awruch 2013).

Fisheries in the eastern Tropical Pacific (ETP) have been poorly managed, in part due to a lack of ecological and biological information and unreliable or non-existent catch and landing data. However, the weak fisheries management framework also plays a significant role (Clarke et al. 2016, 2018, Espinoza et al. 2018). The Costa Rican Pacific is home to 93 elasmobranch species, of which 15% are threatened, and

41% are data deficient (Espinoza et al. 2018). Like other regions, most elasmobranchs in Costa Rica have a high degree of overlap with coastal and pelagic fisheries, some of which operate at unsustainable fishing levels (Whoriskey et al. 2011, Dapp et al. 2013, Davidson et al. 2015, Clarke et al. 2018). Over 35% of the elasmobranch species caught along the Costa Rican Pacific correspond to bycatch of the commercial bottom-trawl fishery (Bussing & López 2009, Clarke et al. 2016, 2018). Two of the most common bycatch species are the southern banded guitarfish, *Zapteryx xyster* Jordan & Everman 1896, and the Velez ray or rasptail skate, *Raja velezi* Chirichigno 1973, account for 10.9 and 20.9% of the total elasmobranch bycatch, respectively (Clarke et al. 2016). There is, however, no published information available of their reproductive cycles throughout their geographic distributions.

Z. xyster is distributed southeast from the Gulf of California to Peru (Compagno 1999), from shallow waters to 150 m deep (Bussing & López 1993). It reaches a maximum total length (TL) of 78.3 cm, with females maturing at 47.0-52.0 cm TL and males at 42.0-47.0 cm TL (Clarke et al. 2014). Casper et al. (2009) reported *Z. xyster* to be viviparous. The geographic distribution of *R. velezi* ranges from the Gulf of California to Peru (Ruiz-Campos et al. 2010), and it is commonly found at depths from 35-300 m (Grove & Lavenberg 1997). The species attains a maximum size of 80 cm TL, with females maturing at 53.0-58.0 cm TL and males at 57.5-60.5 cm TL (Navia et al. 2007, Clarke et al. 2014). Dulvy & Reynolds (1997) reported this species to be oviparous.

Both *Z. xyster* and *R. velezi* are endemic to the ETP (Compagno 1999, Ruiz-Campos et al. 2010) and listed as data deficient by the International Union of Conservation of Nature (IUCN) (Casper et al. 2009, Valenti & Kyne 2009). Previous studies have shown that commercial trawling grounds in the ETP overlap with habitats of *Z. xyster* and *R. velezi* (Clarke et al. 2016, 2018), and therefore, these batoids are vulnerable to fishing pressure. Information on their reproductive cycles is essential to define appropriate conservation and management strategies (Rojas 2006, Clarke et al. 2014, Zanella & López-Garro 2015, Espinoza et al. 2018). We studied the reproductive cycles of *Z. xyster* and *R. velezi*, two tropical endemic batoids in the ETP, according to the classification of Wourms (1977), and discussed how the available life-history information for these species could be used in developing effective management policies.

MATERIALS AND METHODS

Sampling

Specimens of *Zapteryx xyster* and *Raja velezi* were collected by commercial shrimp bottom-trawl vessels

along the Pacific continental shelf of Costa Rica (Fig. 1). Samples were obtained at depths ranging from 25-350 m between February 2010 and September 2011 using two epibenthic nets (20.5 m length, 5.35×0.85 m opening, 4.45 cm mesh size, 3.0 cm cod-end mesh size). Specimens were sexed, measured (total length, from the point of the snout to the end of the tail; disc width, distance between wing tip to wing tip; cm), and weighed (total weight; kg). All the specimens were frozen and transported to the laboratory for further analysis.

Reproductive biology

Maturity was assessed according to macroscopic characteristics, following the criteria used by Clarke et al. (2014). Females were classified as 1) neonates, when the reproductive tract was not developed, and the umbilical scar was open (this just in the case of *Z. xyster*); 2) juveniles, when small, translucent oocytes were present in the ovary, the oviductal gland was undeveloped, and uteri were thin, with no venation; 3) mature adults, when well-developed yolky oocytes were present in the ovary, the oviductal gland was similar in size to the largest oocyte, and uteri were highly developed. Additionally, for *Z. xyster*, females with developing embryo present were classified as gravid, while for *R. velezi*, females with ova capsules present were classified as a bearing. Males were classified as 1) neonates, when the claspers were not calcified, and tips did not reach the distal end of the pelvic fins, and the umbilical scar was open (just in the case of *Z. xyster*); 2) juveniles, when claspers were not calcified, but tips surpassed the distal margin of the pelvic fins; 3) mature adults, when claspers were calcified.

The hepatosomatic index (HSI) and gonadosomatic index (GSI) were estimated for mature females and males of both species, according to Sulikowski et al. (2005). The HSI was calculated as the percentage of the body weight occupied by the liver ($HSI = \frac{\text{liver}_{\text{wet weight}}}{\text{total body}_{\text{wet weight}}} \times 100$). Temporal trends of this index are used to describe the reproductive cycle, based on the assumption that lipids stored in the liver are used for reproduction (Rossouw 1987). The GSI was calculated as the percentage of the body occupied by the gonads ($GSI = \frac{\text{gonads}_{\text{wet weight}}}{\text{total body}_{\text{wet weight}}} \times 100$). The GSI has been used extensively to determine variations in gonad development across time (Hamlett 1999). The reproductive cycle in mature females was also evaluated by measuring the oviductal gland width (OG_w ; mm) and the oocyte (yolk follicle) diameter (YF_D ; mean of the three largest follicles in each right and left ovary; mm), since both measurements are related to females ovarian dynamics (Sulikowski et al. 2005).

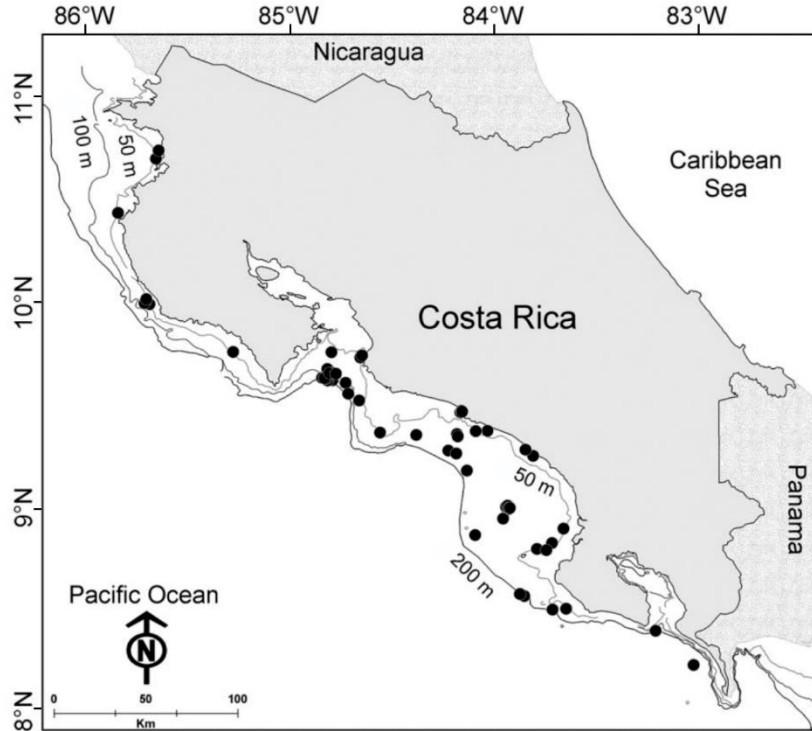


Figure 1. Sampling locations of *Zapteryx xyster* and *Raja velezi* caught as bycatch in the shrimp bottom-trawl fishery between 2010 and 2011 along the Pacific coast of Costa Rica.

Data analysis

The estimated values of HSI and GSI of both males and females, and OG_w and YF_D of females, of *Z. xyster* and *R. velezi*, were grouped in bimonthly periods for further analyses: December-January and February-March (dry season), April-May (transition from dry to the rainy season), June-July, August-September, October-November (rainy season), according to Amador et al. (2006). A bootstrapped ANOVA ($\alpha = 0.05$, 10,000 replicates) was used to detect possible temporal differences in HSI, GSI, OG_w , and YF_D (Ter Braak 1992, Archer et al. 1997). All the analyses were performed using the boot library (Davison & Hinkley 1997, Canty & Ripley 2016) in R (RStudio Team 2015). We classified the reproductive cycles, according to Wourms (1977).

RESULTS

Reproductive cycle of *Zapteryx xyster*

A total of 208 specimens of *Z. xyster* (15.1-78.3 cm total length; 7.1-41.2 cm disc width; 14.8-2635 g total weight) were collected, of which 128 (62%) were immature, and 80 (38%) were mature. Of these, 24 (11%) were males, and 56 (27%) were females. The HSI of female *Z. xyster* did not present significant

bimonthly variations ($F_{6,86} = 2.32$; $P > 0.05$, Fig. 2b); neither did the average YF_D ($F_{3,80} = 2.33$; $P > 0.05$; Fig. 3a) nor average OG_w ($F_{5,84} = 2.33$; $P > 0.05$; Fig. 3b). The GSI for females, however, did vary significantly ($F_{6,85} = 2.73$; $P < 0.05$), presenting a conspicuous peak in June-July 2010 (beginning of the rainy season) followed by a marked decrease during October-November 2010 (mid rainy season) (Fig. 2a). The GSI remained low until February-March 2011 (dry season), followed by another increase during April-May (transition from dry to rainy season), reaching the highest peak during June-July 2011 (beginning of the rainy season) (Fig. 2a). Gravid females were only recorded between December 2010 and March 2011 (dry season) (Fig. 4a). A total of 64 neonates of *Z. xyster* were collected during the study period (Fig. 4a). The highest proportion of neonates (79%) was recorded at the beginning of the dry season (December 2010-January 2011, Fig. 4a). Otherwise, males of *Z. xyster* showed no differences in HSI ($F_{3,29} = 3.47$; $P > 0.05$) nor GSI ($F_{3,29} = 3.47$; $P > 0.05$) during the study period (Fig. 2a-b).

Reproductive cycle of *Raja velezi*

A total of 629 specimens of *R. velezi* were collected (13.2-85.6 cm total length; 8.5-62.8 cm disc width, 7.8-2460 g total weight), of which 290 (46%) were imma-

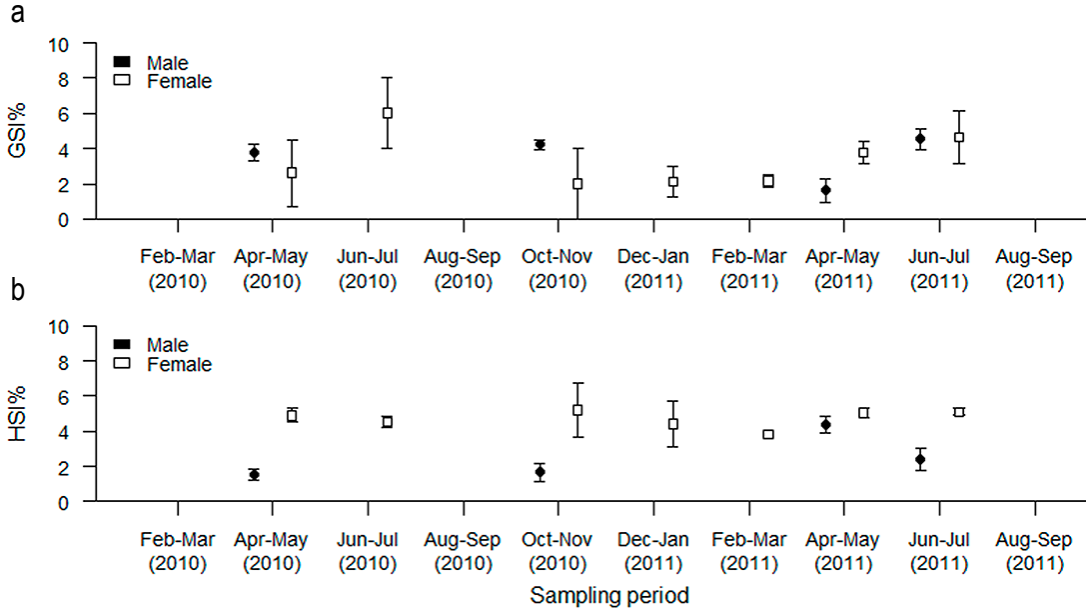


Figure 2. Bimestrial average and standard deviation of a) gonadosomatic index (GSI) and b) hepatosomatic index (HSI) in males (black) and females (white) of *Zapteryx xyster* from the Costa Rican Pacific coast (2010-2011).

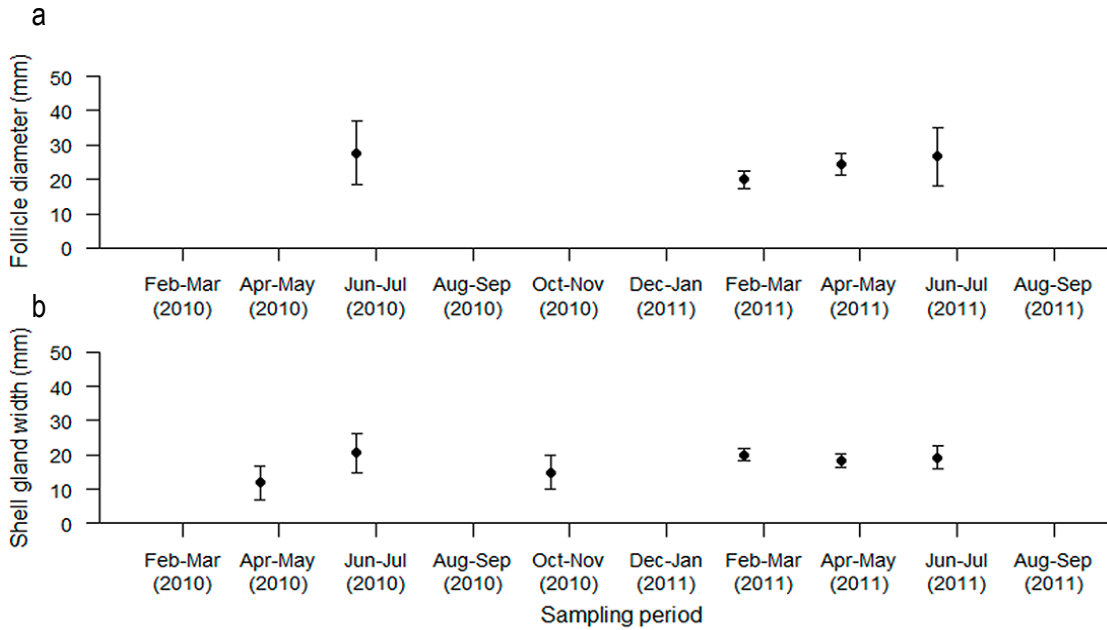


Figure 3. Bimestrial average and standard deviation of a) follicle diameter (mm), and b) oviductal gland width (mm) in females of *Zapteryx xyster* from the Costa Rican Pacific coast (2010-2011).

ture, 339 (54%) were mature, of which 189 (30%) were males and 150 (24%) were females. The females of *R. velezi* exhibited no bimonthly variations in HSI ($F_{7,114} = 2.09$; $P > 0.05$, Fig. 5b), GSI ($F_{7,107} = 2.10$; $P > 0.05$, Fig. 5a), average YF_D ($F_{7,102} = 2.60$; $P > 0.05$, Fig. 6a) nor average OG_W ($F_{7,104} = 2.59$; $P > 0.05$, Fig. 6b). Egg-bearing females were collected several times throughout the study period: February-May 2010,

December-May 2010, and October-November 2011 (Fig. 4b). Additionally, neonate's *R. velezi* were only captured between October 2010 and March 2011 (from the rainy season to the dry season) (Fig. 4b). Males of *R. velezi* showed no difference in HSI ($F_{7,117} = 2.09$; $P > 0.05$, Fig. 5b) or GSI ($F_{7,121} = 2.08$; $P > 0.05$, Fig. 5a) between sampling periods.

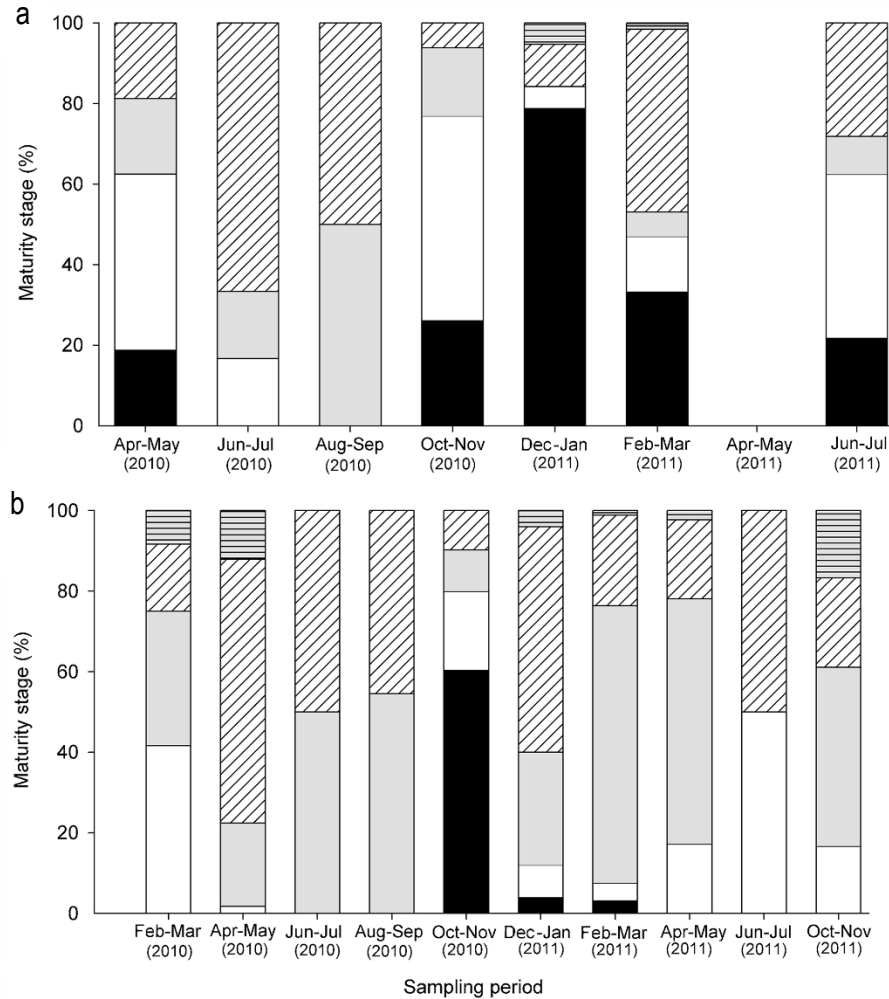


Figure 4. Bimestrial percentage of individuals per maturity stage of a) *Zapteryx xyster* and b) *Raja velezi* from the Costa Rican Pacific coast (2010-2011). Black: neonates; white: juveniles; gray: mature males; diagonal line over white: adult females; horizontal lines over gray: gravid (*Z. xyster*)/egg-bearing (*R. velezi*) females.

DISCUSSION

Reproductive cycle of *Zapteryx xyster*

Our study results suggest that *Z. xyster* has a partially defined annual reproductive cycle with a single peak occurring between June and July. Up to 79% of *Z. xyster* neonates were observed during the dry season (December-January), with the remaining 21% collected during the rainy season. These findings suggest that some females mate and give birth outside the main reproductive peak. A partially defined reproductive cycle has also been reported for *Zapteryx exasperata* (Jordan & Gilbert 1880) from the west coast of Baja California and the Gulf of California (Table 1) (Villavicencio-Garayzar 1995, Blanco-Parra et al. 2009). On the other hand, a three-year reproductive cycle was

reported for *Zapteryx brevirostris* (Müller & Henle 1841) in the southwestern Atlantic Ocean (Table 1) (Colonello et al. 2011).

Mating and fertilization of female *Z. xyster* probably occur between June and July, as suggested by the GSI peak, whereas pupping occurred between December and January when many neonates were found. These results suggest that this species may have gestation periods lasting between four and six months, following the definition of the gestation period for sharks as the period from fertilization to birth (Mejía-Falla et al. 2012). The gestation period of *Z. xyster* is relatively short compared to the one-year gestation period of *Z. brevirostris* (Colonello et al. 2011), but similar to the 3-5 months gestation period of *Z. exasperata* (Villavicencio-Garayzar 1995, Blanco-Parra et al. 2009) (see details in Table 1).

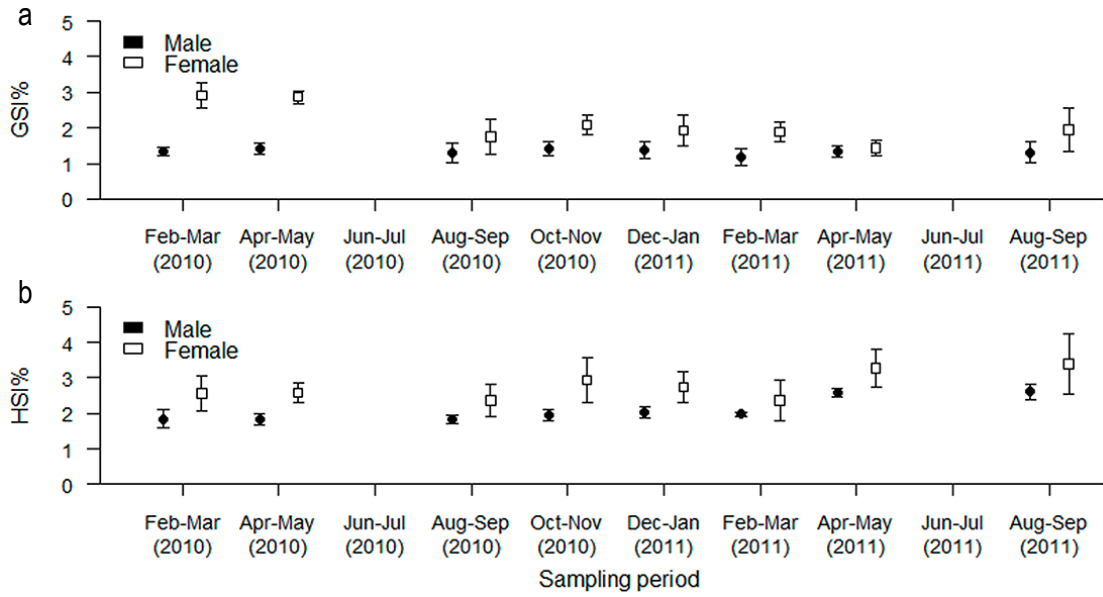


Figure 5. Bimестrial average and standard deviation of a) gonadosomatic index (GSI), and b) hepatosomatic index (HSI) in males (black) and females (white) of *Raja velezi* from the Costa Rican Pacific coast (2010-2011).

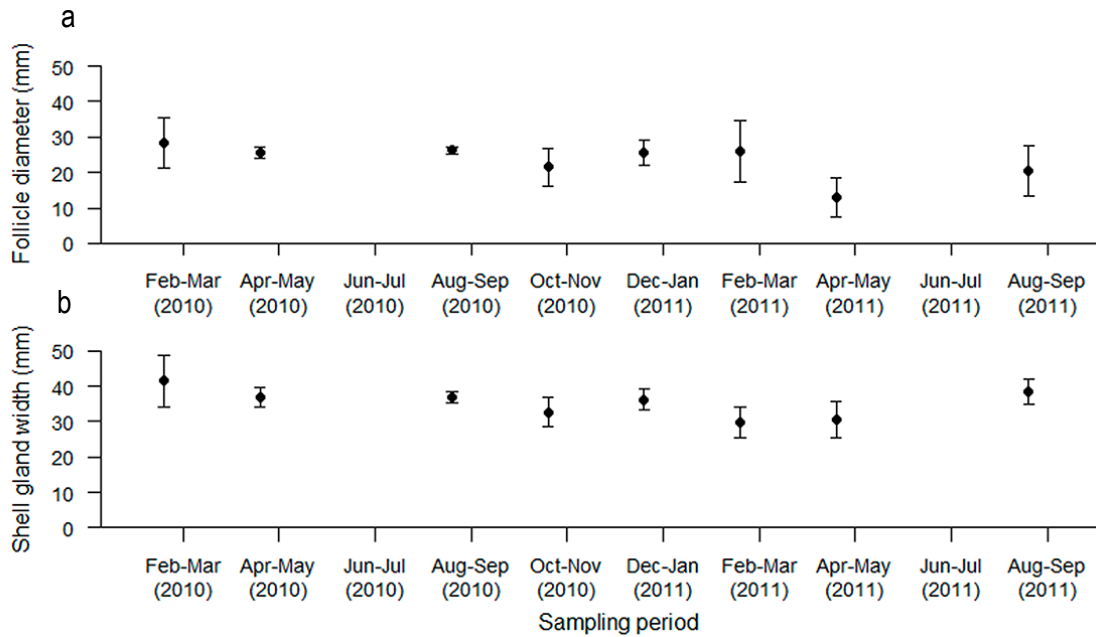


Figure 6. Bimестrial average and standard deviation of a) follicle diameter (mm), and b) shell gland width (mm) in females of *Raja velezi* from the Costa Rican Pacific coast (2010-2011).

Differences in reproductive cycles and gestation periods among *Zapteryx* species could be related, in part, to environmental gradients among their geographic distribution ranges. Specifically, the longer reproductive cycle reported for *Z. brevirostris* could be attributed to lower temperatures in the southwestern Atlantic Ocean. The higher temperatures throughout the distributions of *Z. exasperata* (Mexico) and *Z.*

xyster (Costa Rica) could lead to faster growth rates and smaller adult sizes that would accelerate reproductive rates, including gestation periods. Several studies have demonstrated that variations in reproductive traits related to latitudinal gradients may occur even at the species level (Sulikowski et al. 2007a, Pérez-Jiménez & Sosa-Nishizaki 2008, Driggers & Hoffmayer 2009, Frisk & Miller 2009). For example, differences in repro-

Table 1. Reproductive cycle, gestation period, maximum number of embryos, study site, and reference for three *Zapteryx* species.

Species	Reproductive cycle	Gestation period months	Maximum number of embryos	Study site	Reference
<i>Zapteryx brevirostris</i>	Three years	One year	1-2	Southwestern Atlantic Ocean, off Argentina	Colonello et al. (2011)
<i>Zapteryx exasperata</i>	One year	3-4	-	West coast of Baja California	Villavicencio-Garayzar (1995)
<i>Zapteryx exasperata</i>	One year	5	7	Gulf of California	Blanco-Parra et al. (2009)
<i>Zapteryx xyster</i>	One year	4-6	8	Costa Rica, Central America	Clarke et al. (2014), present study

ductive traits of the bonnethead shark *Sphyrna tiburo* (Linnaeus 1758) were reported among populations at Tampa Bay (warm-temperate conditions) and Florida Bay (tropical conditions), which could be associated with changes in the metabolism influenced by different temperature regimes (Parsons 1993). Although the effect of latitude on elasmobranch reproduction has been poorly studied (Parsons et al. 2008), there is growing evidence in other aquatic taxa that latitudinal clines, such as water temperature, can regulate the differences observed in life-history traits. For example, the Eurasian perch's growth rates and reproductive investment (*Perca fluviatilis*) decrease with latitude, while the life span, size, and age at maturity increase with latitude (Heibo et al. 2005). Similarly, females of several species of caridean and sicyoniid shrimps tend to have shorter periods in broods at lower latitudes than at higher latitudes (Bauer 1992). Both authors argue that latitudinal differences in these aquatic taxa are influenced by temperature, which strongly affects these organisms' growth and reproduction (Bauer 1992, Heibo et al. 2005).

The litter size is positively correlated with the maximum size of females (Frisk 2010), then larger females tend to produce higher numbers of produced offspring. This relation is supported by data from three *Zapteryx* species (Table 1). *Z. brevirostris* produces the lowest number of embryos and has a more extended gestation period; conversely, *Z. exasperata*, and *Z. xyster* carry more embryos but generally have shorter gestation periods (Table 1). *Z. brevirostris* is the smallest species (54.0 cm maximum TL, Bigelow & Schroeder 1953) and has the lowest number of embryos, while both *Z. exasperata* and *Z. xyster* produce more embryos and reach a maximum TL of 90.0 (Blanco-Parra et al. 2009) and 78.3 cm (Clarke et al. 2014), respectively.

The description of elasmobranch reproductive cycles is often based on female gestation periods and ovarian cycles, and consequently, most studies do not include males in the reproductive cycle analysis (Carrier et al. 2004, Castro 2009). Our results revealed

no evidence of reproductive seasonality in male *Z. xyster*. However, since we propose a partially defined annual reproductive cycle with one peak for females, and some females were reproductively active outside their main reproductive peak season, males are likely to mate continuously throughout the year. There are few studies on the male reproductive cycle of other batoid species in the ETP; for example, males of *Z. exasperata* with semen in the seminal vesicle and claspers were found only during the mating months (Blanco-Parra et al. 2009). In *Urotrygon rogersi*, mature males were found year-round; the highest proportion, however, was observed during female ovulation (Mejía-Falla et al. 2012). Additional studies on the male reproductive cycle of batoids are needed to better understand potential reproductive synchronicity in this species.

Reproductive cycle of *Raja velezi*

Our findings suggest that *R. velezi* has a continuous reproductive cycle with no apparent peaks throughout the year. All of the four reproductive parameters used to infer the reproductive cycle of *R. velezi* (HSI, GSI, YF_D, and OG_w) showed no evidence of reproductive seasonality. A continuous reproductive cycle means fertile females can be found throughout most of the year, and potentially the population can produce more offspring. Moreover, egg-bearing females and neonates were observed year-round. These findings are in agreement with similar observations in several other species of the family Rajidae: *Amblyraja radiata* (Donovan 1808) in the Gulf of Maine (Sulikowski et al. 2005), *Atlantoraja cyclophora* (Regan 1903) in Uruguay and Brazil (Oddone & Vooren 2005, Oddone & Velasco 2006, Orlando et al. 2011), *Bathyraja albomaculata* (Norman 1937) in southwestern Atlantic (Henderson et al. 2005, Ruocco et al. 2006), *Leucoraja erinacea* (Mitchill 1825) in Delaware Bay (Fitz & Daiber 1963), *Malacoraja senta* (Garman 1885) in the Gulf of Maine (Sulikowski et al. 2007b), *Beringraja binocularata* (Girard 1855) in Gulf of Alaska (Ebert et al. 2008), *Raja clavata* Linnaeus 1758 in the Black Sea (Saglam & Ak 2012), *Beringraja rhina* (Jordan &

Gilbert 1880) in Gulf of Alaska (Ebert et al. 2008), and *Raja texana* Chandler 1921 in the Gulf of Mexico (Williams et al. 2011). On the other hand, some skates, such as *Rioraja agassizii* (Müller & Henle 1841) in Brazil, have conspicuous reproductive peaks (Oddone et al. 2007, Oddone & Capapé 2011). In our study, the highest catches of neonates of *R. velezi* occurred during October-November 2010; no egg-bearing females, however, were caught during this period, probably related to the oviparous strategy of *R. velezi*, as females release their capsules well before neonates hatch (Dulvy & Reynolds 1997).

Management implications

Both *Z. xyster* and *R. velezi* are commonly caught as bycatch by the semi-industrial trawl fishery in Central (Clarke et al. 2016) and South America (Mejía-Falla et al. 2006, Navia et al. 2007). These two batoids share a similar geographic distribution (Compagno 1999, Ruiz-Campos et al. 2010, Clarke et al. 2014, 2016), bathymetric range (Bussing & López 1993, Grove & Lavenberg 1997), and have high dietary and isotopic niche overlap (Espinoza et al. 2012, 2013, 2015). Nonetheless, *Z. xyster* and *R. velezi* exhibit different reproductive cycles, and thus their vulnerability to fishing vary through time. For example, *Z. xyster* is probably more vulnerable to fishing during reproductive aggregations and recruitment (e.g. mating, gestation, and pupping) (Clarke et al. 2014, 2016), whereas *R. velezi* is not as vulnerable to fishing during reproductive aggregations because of their continuous reproductive cycle. Consequently, management approaches to protect these species cannot assume that they are subject to the trawl fishery's same time pressures. Also, sex segregation in both species has been observed, with males of *R. velezi* primarily occurring at deeper waters, while females of *Z. xyster* are more abundant at intermediate depths (Clarke et al. 2014). In both species, immature stages dominate in shallow waters (Clarke et al. 2014). Therefore, management measures should also consider protection in shallow waters to protect immature specimens.

Based on our results, conservation efforts for *Z. xyster* should focus on reducing the fishing pressure on its populations between June and July and during December and January, when the mating and pupping seasons are likely to occur, respectively. In contrast, conservation measures for *R. velezi* should focus on spatial protections on previously identified nursery grounds along the coast of Costa Rica (Clarke et al. 2014, 2016). These management measures could also help protect the other 23 elasmobranch species accidentally caught by the bottom-trawl fishery (Clarke et al. 2014).

This study provides the first information on the reproductive cycle of two endemic coastal elasmobranchs from the ETP, commonly caught in this region's trawl fisheries. Both species are currently classified as data deficient by the IUCN Red List (Casper et al. 2009, Valenti & Kyne 2009). However, due to their life histories, spatial/temporal overlap with bottom-trawl fisheries, and the poor reporting and management in the ETP, they are considered to be highly vulnerable by more recent assessments (Dulvy et al. 2014, Clarke et al. 2018), indicating the need to update conservation status based on life-history traits.

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