Online ISSN: 0718-1957
RBMO
Revista de Biología Marina y Oceanografía
Vol. 57, N° especial: 68-79, 2022
<https://doi.org/10.22370/rbmo.2022.57.Especial.3333>

ARTICLE

Reproductive biology of the Gorgona guitarfish, *Pseudobatos prahli*, in the central-eastern Pacific Ocean

Biología reproductiva de la raya guitarra punteada, *Pseudobatos prahli,* en el océano Pacífico centro-oriental

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Resumen.- *Pseudobatos prahli* es considerada una especie de importancia pesquera baja-media en Ecuador, capturada comúnmente de manera dirigida e incidental tanto en pesquerías artesanales como industriales. A pesar de su importancia, algunos aspectos básicos de su biología son aún desconocidos, siendo su estudio prioritario. El objetivo del presente trabajo fue describir por primera vez la biología reproductiva de *P. prahli* a partir de individuos desembarcados en el puerto de Santa Rosa, provincia de Santa Elena, Ecuador. Desde enero 2013 a enero 2014 se analizaron 96 hembras y 165 machos. Las tallas observadas para las hembras fueron mayores (51-86 cm de longitud total, LT) que para los machos (51-78 cm de LT), pero no se encontraron diferencias significativas entre las tallas promedio de ambos sexos. La proporción sexual de los individuos desembarcados (0,6H:1M) sugirió la segregación sexual de los individuos de vida libre, sin embargo, la proporción sexual en los embriones fue igual a 1H:1M. Se registraron más individuos maduros (64%) que inmaduros (36%) en las capturas. La talla media de madurez sexual (L_{50}) de las hembras (65,9 cm de LT) fue ligeramente mayor que la de los machos (61,8 cm de LT). La talla de nacimiento estimada fue de 22,5 cm de LT. La fecundidad ovárica fluctuó entre 1 y 10 y, la uterina entre 1 y 6, encontrándose una relación lineal positiva pero baja entre ambas estimaciones de fecundidad y la talla materna. Basado en la comparación de algunos parámetros reproductivos como la talla media de madurez, el periodo de gestación y la fecundidad, se puede concluir que *P. prahli* es una de las especies con productividad biológica más baja entre las especies del mismo género.

Palabras clave: Elasmobranquio, condrictios, longitud de madurez, estadios de madurez, desarrollo embrionario

Abstract.- *Pseudobatos prahli* is considered a low-medium fishing importance species in Ecuador, caught as target species and bycatch in both artisanal and industrial fisheries. Despite its importance, some basic aspects of its biology remain unknown, turning its study a priority. The aim of the present research was to describe for the first time the reproductive biology of *P. prahli* based on the analysis of individuals landed in the port of Santa Rosa, Province of Santa Elena, Ecuador. A total of 96 females and 165 males were sampled from January 2013 to January 2014. Females presented larger sizes (51-86 cm total length, TL) than males (51-78 cm TL), but no significant differences were found between the mean sizes of both sexes. The sexual proportion of landed individuals (0.6F:1M) suggested that free-living individuals segregate by sex, however, sex proportion of embryos was similar to the proportion 1F:1M. The number of mature individuals (64%) in the landings was larger than the immature ones (36%). Mean size at maturity (L_{50}) of females (65.9 cm TL) was also slightly larger than that for males (61.8 cm TL). Size at birth was estimated at 22.5 cm TL. Ovarian fecundity ranged from 1 to10 and uterine fecundity from 1 to 6, and a positive but low linear relationship was found between both fecundity estimates and maternal size. Based on the comparison of some reproductive parameters, such as mean size at maturity, gestation period and fecundity, it can be concluded that *P. prahli* is one of the species with lowest biological productivity among the species of the same genus.

Key words: Elasmobranch, chondrichthyans, length at maturity, maturity stages, embryonic development

INTRODUCTION

The Gorgona guitarfish, *Pseudobatos prahli* (Acero & Franke, 1995), is a coastal-demersal species that inhabits sandy and rocky bottoms near coral reefs in the eastern Pacific, from southern Mexico to Peru, mainly at 18-24 m of depth and up to 70 m in the Colombian Pacific Ocean (Acero & Franke 1995, Payán *et al*. 2010). The species is matrotrophic viviparous, whose embryos feed initially on the yolk for nourishment and then receive nutrients from the mother through indirect absorption of uterine fluids, rich in proteins and fats, secreted by specialized structures (Dulvy & Reynolds 1997).

Pseudobatos prahli is a bycatch of large-scale and small-scale shrimp trawl fisheries and small-scale gillnet and longline fisheries (Kyne *et al.* 2020). In Ecuador, *P. prahli* is categorized as a species of low-medium commercial importance, being commonly found in the landings of Santa Rosa and Anconcito fishing ports, in the province of Santa Elena (Martínez-Ortiz & García-Domínguez 2013). In this region, the species is caught as bycatch, and is occasionally targeted due to their great acceptance for local consumption, by the industrial shrimp fishing and artisanal fisheries targeting flounders (Family Paralichtyidae) and Chilean angel shark (*Squatina armata*). Artisanal vessels are made of fiberglass and wood, whereas industrial vessels are industrial steel bottom trawlers. Both fleets catch the species in this region using diverse fishing gears, including bottom gillnets, trawl nets, shrimp trammel nets, as well as bottom gillnets. Once landed, the species is locally traded for human consumption, either fresh or frozen (Martínez-Ortiz & García-Domínguez 2013), though it can be used for the production of fish flour (Jiménez-Prado & Béarez 2004).

Fisheries operate in most of the distribution range of *P. prahli* with inadequate management or enforcement, but the species is associated with rocky habitat that would provide some refuge from trawling. Overall, given the intensity of fishing pressure throughout its range (particularly in Ecuador which appears to be its core range) and its susceptibility to capture, it is suspected that this species has undergone a population reduction of 30-49% over the last three generation lengths (15 years) due to levels of exploitation, and it is assessed as vulnerable (Kyne *et al.* 2020).

The lack of biological information is one of the main problems for chondrichthyan species conservation, particularly for those species caught as bycatch or with low to medium economic importance (Walker 2005). Among the previous studies of *P. prahli* are the description and taxonomic classification, and distribution of the species in the Colombian (Acero & Franke 1995, Payán *et al.* 2010) and Southern Mexican Pacific (Carrera-Fernández *et al.* 2012, Díaz & Gutiérrez 2012). Martínez-Ortiz & García-Domínguez (2013) reported pregnant females in the landings of Santa Rosa and Anconcito, Ecuador, with 2-5 embryos of 22-25 cm of total length (TL), whereas Romero-Caicedo *et al.* (2015) estimated the relationship between total weight (W) and TL ($W= 0.00408 \cdot TL^{2.99}$).

The aim of the present study was to describe for the first time the reproductive biology of *P. prahli*, based on the macroscopic analysis of the reproductive system of individuals landed in Santa Rosa, Ecuador. The proportion of sexes and maturity stages were also estimated, as well as some key reproductive parameters for population assessments, such as mean size at maturity (L_{50}) and fecundity. Such information could be used in the future to develop effective fisheries management measures in the region, to ensure the sustainable use of the species.

Materials and methods

The fishing port of Santa Rosa (02º20´31"S; 80º 94´79"W) is located in the city of Salinas, in the province of Santa Elena, Ecuador, in the Central-Eastern Pacific Ocean. From January 2013 to January 2014, individuals of *P. prahli* caught in nearby regions such as Chocolatera and Manteca were sampled twice a month at the landing's sites of the artisanal fishery (Table 1). Total length was measured for each individual to the nearest cm, from the tip of the nose to the end of the tail. Clasper length (CL) was measured for males. To obtain the reproductive system, a sagittal section was made from the cloaca to the upper part of the abdominal cavity. All the reproductive system was removed and preserved in hermetic containers closed with ice and transported to the laboratory for analysis.

The size composition of landings was analyzed through histograms of frequency with size intervals of 5 cm (modified from Holden & Raitt 1975). Size composition was compared by sex and seasons of the year (rainy and dry seasons, from December to May and June to November, respectively). Kolmogorov-Smirnov test proved absence of normal distribution for both sexes size and the rainy season of the year data (P < 0.01 in all cases), whereas the Levene test showed heterogeneity of variances between the data of both sexes (P < 0.001). Thus, a Mann-Whitney test (W) was used to test for significant differences between the size of females and males and between rainy and dry seasons using Minitab® v. 18.1 software (Minitab Inc., State College, Pennsylvania, USA, 2017).

The proportion of sexes in the landings was estimated by dividing the number of females by the number of males. Then, a χ^2 test was used to determine the existence of significant differences to a proportion of 1:1 (Daniel 2012).

The macroscopic morphology of the reproductive system of both sexes was described. The condition of the gonads was determined based on their size, form and colour. The maturity stage was determined based on the degree of development of the reproductive system, using as a reference the scale proposed for chondrichthyans by Grijalba-Bendeck *et al.* (2008).

For females, the length (UL) and width (UW) of the uterus were measured, as well as the maximum width of the ovaries (OW) and the oviducal glands (OGW). For males, the testis length (TestL) and width (TestW) were measured. The relationship between TL-UL, TL-UW, TL-OD and TL-OGD was determined for females, and TL-CL, TL-TestL, and TL-TestW for males (Conrath 2005).

The follicles were classified as previtellogenic (whitish colour with 0.1-1.0 cm diameter), vitellogenic (yellowish colour with 1.1-3.5 cm diameter) or preovulatory (yellow or orange colour with 3.6-5.0 cm diameter) (modified from Tresierra *et al*. 2002). The presence of embryos was recorded, including their sex, TL and development stage (Conrath 2005).

Table 1. Number of individuals (n), size interval, mean (x̄), standard deviation (±) of *Pseudobatos prahli* by sex and for each month from January 2013 to January 2014 in Santa Rosa, Ecuador, Central Eastern Pacific Ocean / Número de individuos (n), intervalo de tallas, promedios (x̄), desviación estándar (±) de *Pseudobatos prahli* por sexos y para cada mes desde enero de 2013 hasta enero de 2014 en Santa Rosa, Ecuador, océano Pacífico centro-oriental

Month	Females				Males			
	n	Size interval (cm)	x̄	±	n	Size interval (cm)	x̄	±
2013								
January	11	52-80	65.9	11.4	22	54-71	65.6	4.5
February	5	77-86	80.8	4.0	8	66-72	69.8	2.1
March	7	53-79	62.7	8.6	7	55-65	58.3	3.5
April	1	62	62	-	4	51-69	62.5	8.1
May	2	51-69	60	12.7	7	53-69	62.1	5.5
June	0	-	-	-	0	-	-	-
July	4	57-77	66.5	9.5	3	58-66	63.0	4.4
August	1	68	68	-	4	59-71	65.8	5.4
September	1	77	77	-	1	71	71	-
October	0	-	-	-	4	66-71	68.8	2.2
November	5	62-82	70.4	10.6	18	57-75	67.7	5.5
December	27	54-86	69.1	8.8	59	57-78	67.4	4.2
2014								
January	32	56-82	67.3	7.3	28	56-73	66.1	4.2

Mean size at maturity (L_{50}), determined as the size at which 50% of the individual of a population are mature (Chen *et al.* 1997, Flammang *et al.* 2008), was estimated for each sex through the logistic model (King 1995):

$$P = \frac{1}{1+\exp\left[-r\left(TL-L_{50}\right)\right]}$$

where, P is the proportion of mature individuals at length (TL) and r is the steepness of the curve that describes the change rate from 0 (immature individuals: maturity stages I and II) to 1 (mature). The model was adjusted with minimum squares using the Solver tool of Microsoft Excel® (V. 2016).

To determine the ovulation period, the maximum size of follicles was compared through the year, whereas the gestation period was determined by analyzing the monthly variation of average size and degree of development of the embryos, as well as the presence of eggs in the uterus. The size at birth was estimated based on the maximum size of the embryos, but comparison with the minimum size of free-living individuals was not possible as no new-borns were found in the landings (Conrath 2005). Additionally, the embryos were classified in four development stages according to their morphology and size: (1) early stage, (2) medium stage, (3) late stage, and (4) advanced stage (modified from Liu *et al.* 1999, Mollet *et al.* 1999, Grijalba-Bendeck *et al.* 2008).

Fecundity was estimated by two methods: first, by counting the number of preovulatory follicles (ovarian fecundity) and second, by counting the number of eggs or embryos found in the uterus (uterine fecundity). The relationship between maternal length and both fecundity estimates was determined with a simple linear regression analysis (Conrath 2005).

Results

A total of 261 individuals of *P. prahli* (96 females and 165 males) in different stage of maturity were analyzed. Females size ranged from 51 to 86 cm of TL ($\bar{x}$= 68 ± 6.8), being more frequent in the interval size of 60-64 cm of TL (24 individuals, representing 25% of the total females). Meanwhile, males size ranged 51-78 cm of TL ($\bar{x}$= 66.1 ± 6.8), being more frequent in the interval size of 65-69 cm of TL (70 individuals, representing 42% of the total males). Despite females reaching a larger size than males, no significant differences were found between the average size of both sexes (W= 13,309.5; P > 0.21) (Fig. 1).

A larger number of individuals of *P. prahli* were sampled during the rainy season (220 individuals) in comparison to the dry season (41 individuals). December was the month with the largest number of samples (86 individuals, representing 39% of the total sampled), whereas no samples were obtained in June. No significant differences were found between the average size of both seasons of the year (W= 28,285.5; P > 0.23).

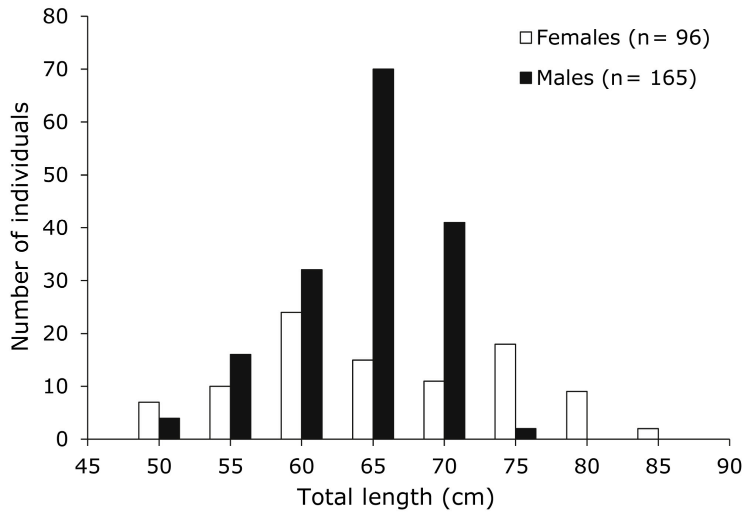

Figure 1. Size composition of *Pseudobatos prahli* recorded in the artisanal fishery in Santa Rosa during January 2013-January 2014 / Composición de tallas de *Pseudobatos prahli* registradas en la pesca artesanal en Santa Rosa durante enero 2013-enero 2014

Sex ratio of *P. prahli* in the landings (0.6H:1M) was significantly different to the proportion 1:1 (χ^2= 18.2; $P <$ 0.05) being caught with almost two males for every female, suggesting a sexual segregation in the fishing area. However, sex ratio of embryos (1.2H:1M) was not significantly different from the proportion 1:1 (χ^2= 0.4; $P >$ 0.05), proving the incorporation to the population of individuals of both sexes in the same degree.

Both ovaries of *P. prahli* were functional. Immature females (stage I, representing 18% of the analyzed females) had no differentiated ovaries, elongated, smooth and of pink colour; fully embedded in the upper region of the epigonal organ. Previtellogenic follicles were small (0.1-1.0 cm diameter) and of whitish or light yellowish colour. Oviducal glands and uteri were undifferentiated from the oviducts (Fig. 2a). Maturing females (stage II, representing 35% of the females) had elongated ovaries, but still embedded in the epigonal organ; some medium size, soft and yellowish vitellogenic follicles (1.1-3.5 cm diameter) were already visible. Oviducal glands started to be differentiated from the oviducts, being reddish and measuring up to 1.5 cm length and 1.5 cm width. Uteri of cream or pink colour started to be wider (Fig. 2b). Non-pregnant mature females (stage IIIa, accounting for 5% of females) presented two types of follicles: (1) a great deal of large very dense, yellowish preovulatory follicles (3.6-5.0 cm of diameter), and (2) a small number of vitellogenic follicles, oviducal glands that are reddish colour in the anterior part and yellowish in the posterior part, well differentiated from the oviduct, with an oval shape, up to 3 cm of length and 2.5 cm of width; also, the uterus was well differentiated from the oviduct, there were no uterine eggs or embryos (Fig. 2c). Pregnant females (stage IIIb, representing 39% of the females) had preovulatory follicles; oviducal glands were well differentiated and the uteri were widened, with uterine eggs or embryos at different stages of development (Fig. 2d). Post-partum females (stage IV, representing 3% of females) had both preovulatory and vitellogenic follicles; oviducal glands were well differentiated and the uteri presented stretch marks and vascularized walls (Fig. 2e).

Immature males (stage I, representing 10% of the analyzed individuals) had undifferentiated genital ducts and testicles, which were fully embedded in the epigonal organ (Fig. 3a). Maturing males (stage II, representing 17% of males) had cream to pink and elongated testicles with small lobes, still embedded in the epigonal organ. Genital ducts started to differentiate, forming small lobes in the anterior region, while the posterior region had a spiral form (Fig. 3b). Mature males (stage III, representing 73% of males) had fully white or pink lobulated testicles; genital ducts well differentiated (Fig. 3c).

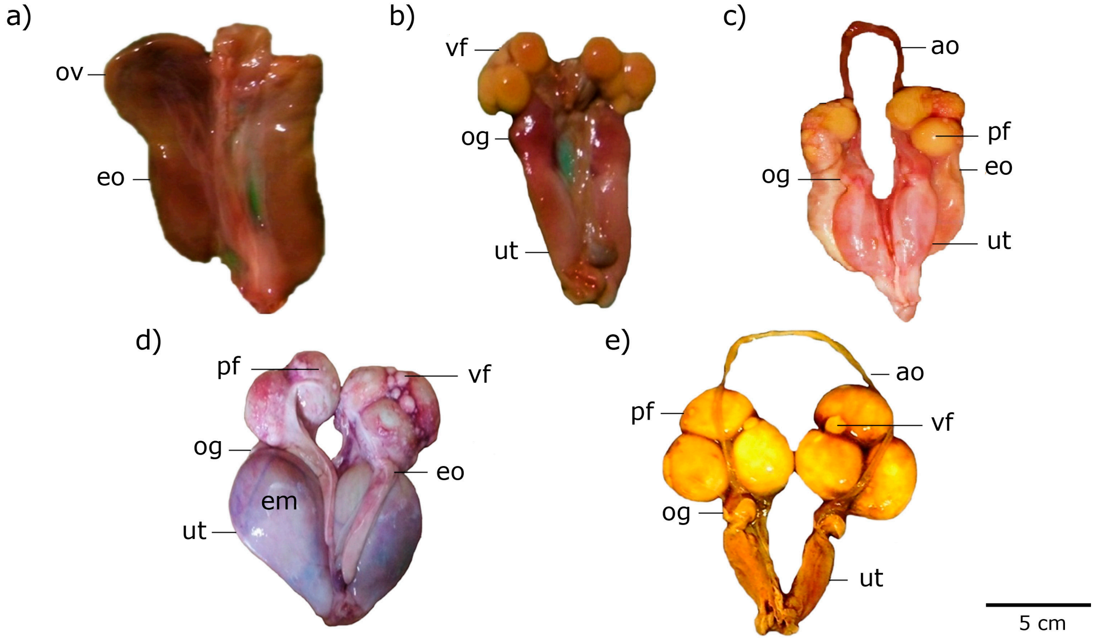

Figure 2. Stages of sexual maturity in females of *Pseudobatos prahli* in Santa Rosa, Ecuador, Pacific Ocean: a) Stage I, immature; b) stage II, maturing; c) stage IIIa, mature non pregnant; d) stage IIIb, pregnant and e) stage IV, post-partum. ao= anterior oviduct, em= embryo, eo= epigonal organ, og= oviducal gland, ov= ovary, pf= preovulatory follicle, ut= uteri, vf= vitellogenic follicle / Estadios de madurez sexual en hembras de *Pseudobatos prahli* en Santa Rosa, Ecuador, océano Pacífico*:* a) estadio I, inmadura; b) estadio II, en maduración; c) estadio IIIa, madura no grávida; d) estadio IIIb, grávida y e) estadio IV, postparto. ao= oviducto anterior, em= embrión, eo= órgano epigonal, og= glándula oviducal, ov= ovario, pf= folículo preovulatorio, ut= útero, vf= folículo vitelogénico

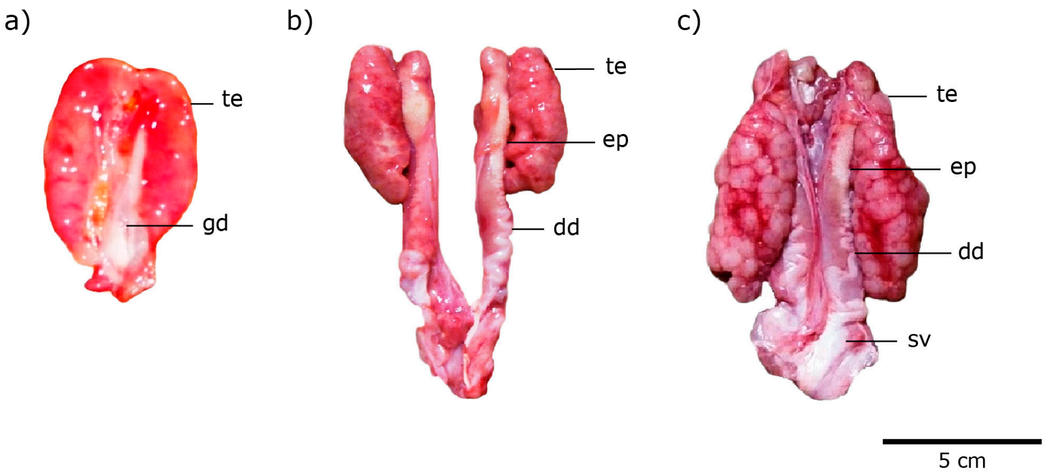

Figure 3. Stages of sexual maturity in males of *Pseudobatos prahli* in Santa Rosa, Ecuador, Pacific Ocean: a) Stage I, immature; b) stage II, maturing and c) stage III, mature. dd= ductus deferens, ep= epididymis, gd= genital ducts, te= testes, sv= seminal vesicle / Estadios de madurez sexual en machos de *Pseudobatos prahli* en Santa Rosa, Ecuador, océano Pacífico: a) estadio I, inmaduro; b) estadio II, en maduración y c) estadio III, maduro. dd= conductos deferentes, ep= epidídimo, gd= conductos genitales, te= testículos, sv= vesícula seminal

Only two of the relationships between total length and reproductive organ size showed a high correlation, for females it was TL-OGW (r^2= 0.81) and for males TL-CL (r^2= 0.75) (Fig. 4). In the case of females, the relationships were medium for TL-UL (r^2= 0.67), TL-UW (r^2= 0.55) and TL-OW (r^2= 0.42). For males, there was not a relationship for TL-TestL (r^2= 0.02) and it was of low correlation for TL-TestW (r^2= 0.33).

The number of mature individuals of both sexes (64%) in the landings was larger than the immature ones (36%). The largest immature female measured 67 cm TL, whereas the smallest mature female was 68 cm TL. The smallest and largest gravid females measured 72 and 86 cm TL, respectively. On the other hand, the largest immature male measured 66 cm TL, whereas the smallest mature male was 60 cm of TL. The mean size at maturity (L_{50}) estimated for females (65.9 cm TL) was larger than that estimated for males (61.8 cm TL) (Fig. 5). According to the L_{50}, *P. prahli* females reached sexual maturity at 73% of their maximum length whereas males at 69%.

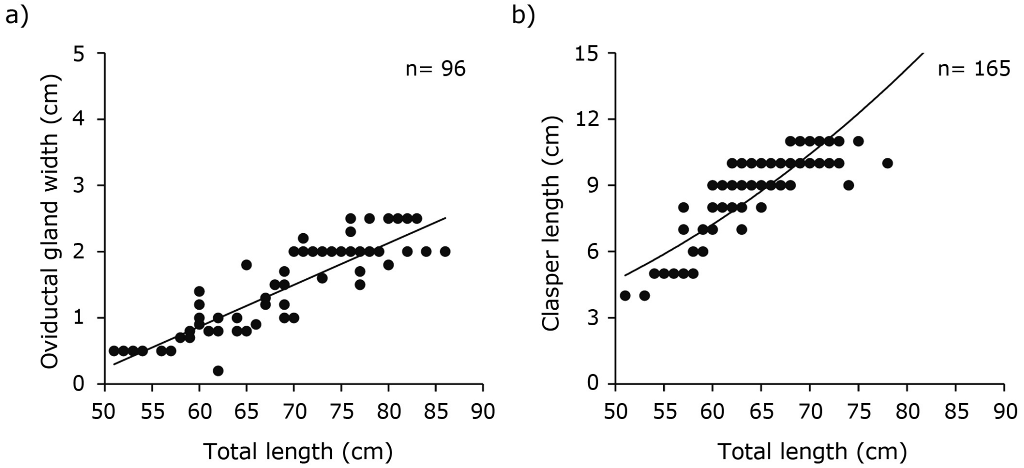

Figure 4. Relationships between (a) *Pseudobatos prahli* female's total length and oviducal gland width (OGW= 0.063 TL − 2.917; r²= 0.81) and (b) male's total length and clasper length (CL= 0.278 TL− 9.183; r²= 0.75) in Santa Rosa, Ecuador, Pacific Ocean / Relaciones entre (a) la longitud total y el ancho de la glándula oviducal de hembras de *Pseudobatos prahli* (OGW= 0,063 LT − 2.917; r²= 0,81) y (b) la longitud total y el largo del gonopterigio (CL= 0,278 LT − 9,183; r²= 0,75) para machos en Santa Rosa, Ecuador, océano Pacífico

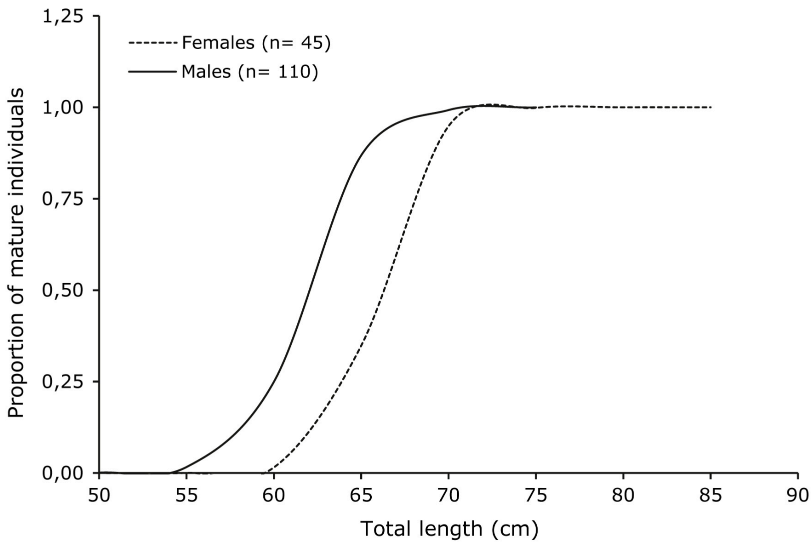

Figure 5. Mean size of sexual maturity in females (65.9 cm TL) and males (61.8 cm TL) of *Pseudobatos prahli* in Santa Rosa, Ecuador, Pacific Ocean / Talla media de madurez sexual para hembras (65,9 cm LT) y machos (61,8 cm LT) de *Pseudobatos prahli* en Santa Rosa, Ecuador, océano Pacífico

The follicles diameter observed during the whole study ranged 0.1-5.0 cm ($\bar{x}$= 2.9 ± 1.1 cm). The largest follicles diameters were found during January (1.9-5.0 cm; $\bar{x}$= 3.8 ± 0.9) and February 2013 (4.0-5.0 cm; $\bar{x}$= 4.2 ± 0.4). A steady size of follicles was observed from March to October of 2013 (1-1.2 cm), except in August, when a single female had larger follicles (1.3-3.8 cm). This female also had eggs in the uterus. A marked increase in follicles diameter was observed again in November (1.5-1.7 cm; $\bar{x}$= 1.6 ± 0.1) and December 2013 (1.5-5 cm; $\bar{x}$= 3.1 ± 0.8), as well as January 2014 (1.1-4.0 cm; $\bar{x}$= 2.6 ± 1.0). Based on the development of the follicles, an annual ovarian cycle was estimated, with a period of increase of size of the follicles from November to February (Fig. 6a).

A total of 65 embryos (35 females and 30 males) were observed, with size ranging 8.5-22.5 cm of TL (n= 65; $\bar{x}$= 17.3 ± 3.7). Embryos were found only during four months of the study: January, February and December 2013, and January 2014. Besides the embryos, 42 eggs of different size were observed in the uterus during most of the months of the study, except April, May, June and October, when no gravid females were found in the landings (Fig. 6b).

Embryos in early stage of development (I) ranged 8-11 cm of TL (n= 7; $\bar{x}$= 9.9 ± 1.1) and presented soft body and jelly consistency; the dorsal area was pink colour with big rounded brown spots all around, whereas the ventral area lacked a black spot around the nose; the vitelline sac was large, soft and yellow; the candle was incomplete and of brown to yellow color (Fig. 7a-c). Embryos at medium stage (II) ranged 12-15 cm of TL (n= 12; $\bar{x}$= 13.5 ± 0.9) and still had soft body; the dorsal area was pink with rounded brown spots scattered over the entire surface and the ventral area already had a black spot around the nose; the vitelline sac was small, almost half of the size of the previous stage, yellow to orange colour; the candle was smaller (Fig. 7d). Embryos at late stage (II) ranged 16-19 cm of TL (n= 24; $\bar{x}$= 18.4 ± 1.0) and presented hardened bodies; the dorsal area was brown with white spots all around; the vitelline sac was small and yellow as well as the candle (Fig. 7e). Finally, embryos at advanced stage (IV) ranged 20-23 cm of TL (n= 22; $\bar{x}$= 20.6 ± 0.8) and had a hard consistency; the dorsal area had white spots all around; the vitelline sac is absent and only remains of the candle persisted (Fig. 7f).

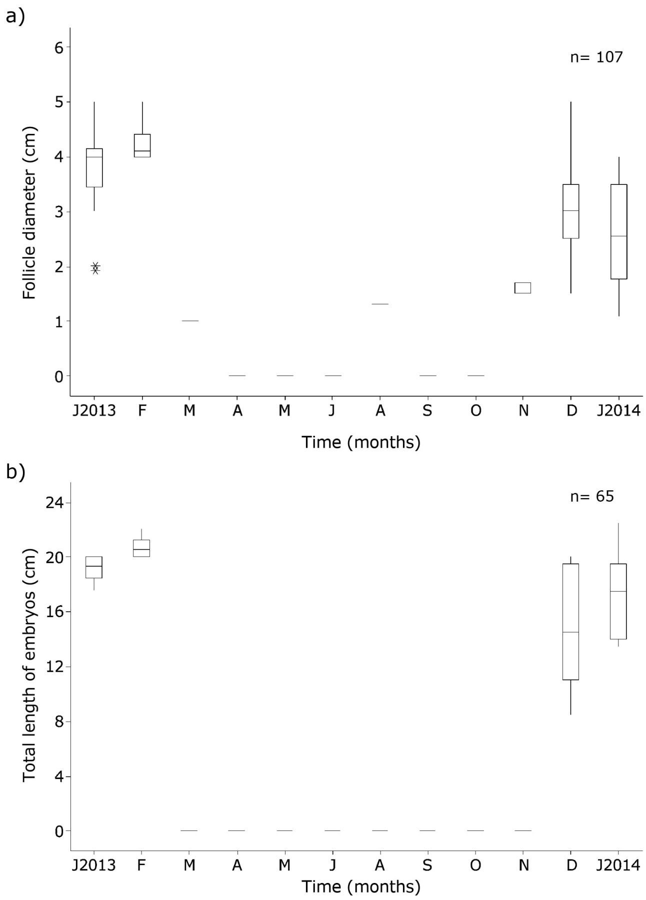

Figure 6. Monthly variation of (a) follicles diameter and (b) embryos size of *Pseudobatos prahli* in Santa Rosa, Ecuador, Pacific Ocean (whiskers= maximum and minimum values; boxes= quartiles; lines= median; asterisks= outliers) in Santa Rosa, Ecuador, Pacific Ocean / Variación mensual del (a) diámetro de los folículos y (b) talla de los embriones de *Pseudobatos prahli* (bigotes= valores máximos y mínimos; cajas= cuartiles; líneas= medianas; asteriscos= valores atípicos) en Santa Rosa, Ecuador, océano Pacífico

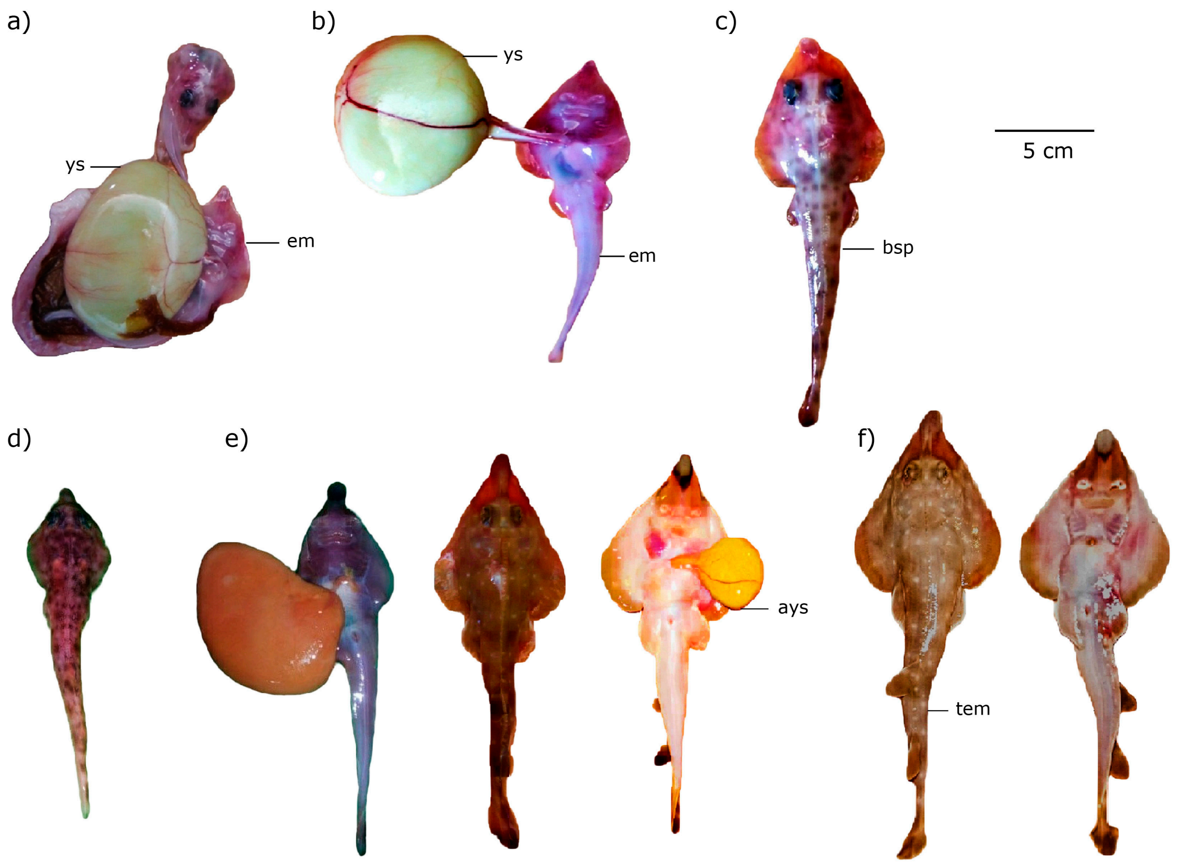

Figure 7. Embryos of *Pseudobatos prahli* in different stages of development in Santa Rosa, Ecuador, Pacific Ocean: a-c) early stage (8-11 cm TL); d) medium stage (12-15 cm TL); e) late stage (16-19 cm TL); f) advanced stage (20-23 cm TL). ays= absorption of the yolk sac, bsp= beginning of skin pigmentation, em= embryos, tem= terminal embryos, ys= yolk sac / Embriones de *Pseudobatos prahli* en diferentes estadios de desarrollo en Santa Rosa, Ecuador, océano Pacífico: a-c) estadio temprano (8-11 cm LT); d) estadio medio (12-15 cm LT); e) estadio tardío (16-19 cm LT); f) estadio avanzado (20-23 cm LT). ays= absorción del saco vitelino, bsp= inicio de la pigmentación de la piel, em= embriones, tem= embriones en etapa terminal, ys= saco vitelino

Based on the embryos size increment and its development stage, it was estimated that the gestation period of *P. prahli* lasts 12 months. Size at birth could be around 22.5 cm of TL (representing 25% of the maximum length of the species), being the size when embryos had all morphological characteristics of free-living individuals. Nevertheless, individuals with a size lower than 51 cm of TL were not observed in the landings preventing the comparison with the minimum size of newborns. It was estimated that parturition might occur in March, when embryos were not found any more in the uterus and after reaching their maximum size in February.

Fecundity estimated by counting the number of preovulatory follicles of 45 females ranged 1-10 ($\bar{x}$= 3.96 ± 1.76), whereas fecundity estimated by counting the number of embryos of 37 females ranged 1-6 ($\bar{x}$= 2.9 ± 1.0). A positive linear relationship was found between maternal size and the number of preovulatory follicles and embryos, but they presented low correlations in both cases (r^2 = 0.12 and 0.20 respectively).

Discussion

The analyzed individuals of *P. prahli* in the present study showed slightly smaller size than that registered previously for females in Ecuador by Martínez-Ortiz & García-Domínguez (2013) (90 cm of TL) but considerably smaller in the case of males (91 cm of TL registered previously). The sizes were also smaller than those found in Colombia by Acero & Franke (1995) (81 cm of TL for a male) and Payán *et al.* (2010) (90 cm TL for an individual of not registered sex). However, the observed size was greater than those reported by Carrera-Fernández *et al.* (2012) in México (77 and 71 cm TL for females and males respectively), Béarez (2000) in Perú (71 cm TL for a male) and Jiménez-Prado & Béarez (2004) in Ecuador (60-75 cm TL for combined sexes). Nevertheless, the sizes of the observed individuals were within the reported size interval for the species (Martínez-Ortiz & García-Domínguez 2013). The size differences found between the present and previous studies could be related to the fishing gear used and the depth of capture, since *P. prahli* has a wide vertical distribution, from 18 to 70 m deep (Acero & Franke 1995, Payán *et al.* 2010), and can be caught by various types of gear such as bottom gillnets, trawl nets, shrimp trammel nets, and bottom gillnets (Martínez-Ortiz & García-Domínguez 2013).

It has been reported that, despite being commercialized when caught, *P. prahli* is not an abundant species in shark and ray landings of Ecuador (Jiménez-Prado & Beárez 2004), except in Santa Rosa and Anconcito (Martínez-Ortiz & García-Domínguez 2013), where it is commonly caught as either target fishery or bycatch of other commercially important species, such as angel shark, sole fish and shrimps. According to the National Fisheries Institute of Ecuador, during 2008, 6,631.86 t of chondrichthyans were landed in the country, of which only 152 t corresponded to rays (Peralta 2009). The low importance of rays in fishery statistics could be masked by the abundance and large size of sharks, commonly caught as target species in the fisheries in some regions of Ecuador, while rays seem to be only a common resource in the fisheries of the province of Santa Elena. Also, due to its low-medium importance category (Martínez-Ortiz & García-Domínguez 2013), updated and accurate landing statistics of this species caught by the artisanal and industrial fisheries do not exist to date, preventing the quantitative evaluation of their populations in the region.

The sex ratio found in the present study indicated sex segregation in the region, though this could be related in part to the exploited fishing area. The sex proportion of embryos indicated, however, that both sexes recruit to the population in the same way. Sex segregation has been reported for other species of the same genus, such as *P. productus* (Villavicencio 1993, Downton 2007, Márquez-Farías 2007, Juaristi 2016), *P. leucorhynchus* (Payán *et al.* 2011, Romero-Caicedo & Carrera-Fernández 2015, Carrasco 2016) and *P. percellens* (Acevedo *et al.* 2007, Rocha & Gadig 2013, Tagliafico *et al.* 2013), whose females have been found to be more abundant in catches in those cases. On the contrary, for *P. percellens* in the Colombian Atlantic (Grijalba-Bendeck *et al.* 2008, 2012) and *P. horkelii* in Brazil (Martins *et al.* 2018) same sex ratio in the landings has been reported. The tendency of elasmobranchs to segregate by sex and size is relatively common (Holden 1974), though the region, depth and season of capture, as well as the fishing gear selectivity can have an important role in the number of individuals of each sex captured. Therefore, it would be advisable to obtain the population sex ratio based on intrauterine offspring in place of free-living organisms (Pratt & Otake 1990).

The largest number of mature males in the landings, observed in the present study, has also been reported for *P. leucorhynchus* in the Colombian Pacific (Payán *et al.* 2011) and *P. percellens* in Venezuela (Tagliafico *et al.* 2013). This could be related to the selectivity of the fishing gears favoring the capture of large size individuals, as well as most of the individuals (69%) were fished during the reproductive season of *P. prahli* in Ecuador (December-March). Nevertheless, during the present research, immature females were slightly more abundant than mature ones.

Relationships between TL and size of several reproductive structures as an indicator of sexual maturity, like those reported in the present study, have been found for other species, such as the relationship between TL and CL for *P. horkelii* (Martins *et al.* 2018), between TL and UW or TestW for *P. leucorhynchus* (Payán *et al.* 2011, Romero-Caicedo & Carrera-Fernández 2015), between TL and length of the oviducal gland or testicles for *P. productus* (Timmons & Bray 1997, Downton 2007, Juaristi 2016), and between TL and gonad weight for *P. percellens* (Rocha & Gadig 2013). It is important to consider that according to Holden & Raitt (1975), during the reproductive period of a species, the reproductive organs of some individuals can increase with their size and the reproductive activity, after which can enter in a reabsorption (follicles) or contraction (organs) process. Thus, the size of reproductive organs can change along the year, making it necessary to consider it to determine which can be used as an indicator of maturity.

Pseudobatos prahli females reached their maturity at higher sizes than males, as commonly happens in elasmobranchs, due to the necessity to have bigger body sizes so they carry embryos during the gestation period (Cortés 2000). Maturity in this species appears to be reached at a larger size proportion of maximum length than other species (based on maximum length presented by Séret *et al.* 2016 for each species) such as *P. percellens* (47-58% for females and 50-55% for males; Grijalba-Bendeck *et al.* 2008, Rocha & Gadig 2013, Tagliafico *et al.* 2013), *P. productus* (34-66 and 31-59% for females and males respectively; Villavicencio 1993, Timmons & Bray 1997, Downton 2007, Márquez-Farías 2007, Juaristi 2016) and *P. horkelii* (58-65 and 51-65% for females and males respectively, Lessa *et al.* 1986, Martins *et al.* 2018). However, *P. prahli* maturity of females would be reached at a similar of length than *P. leucorhynchus* (69-83%) and at a lower proportion in the case of males (73-87%) according to Payán *et al.* (2011) and Romero-Caicedo & Carrera-Fernández (2015).

The gestation period of *P. prahli* was similar to those of *P. horkelii* (12 months) which gives birth in March in the Brazilian coasts (Lessa *et al.* 1986); *P. percellens* (10-12 months), which gives birth in February and March in the Colombian Atlantic (Grijalba-Bendeck *et al.* 2008); *P. productus* (10-12 months), which gives birth in June-October in the Mexican Pacific (Villavicencio 1993, Downton 2007, Márquez-Farías 2007, Romo-Curiel 2007, Juaristi 2016). On the other hand, the estimated gestation period of *P. leucorhynchus* in Ecuador´s coast was considerably shorter (5-6 months) and, although the largest embryos were found in November, due to fully developed embryos encountered along the year, it was stated that this species does not have a defined birth season (Romero-Caicedo & Carrera-Fernández 2015).

The birth season of *P. prahli* (February-March 2013) appears to be related to the highest temperatures in the area of study (26 °C; INOCAR 2020), creating a favorable environment for the reproductive event. Simpfendorfer (1992) stated that the embryos of Australian sharpnose shark, *Rhizoprionodon taylori*, are usually born when water temperatures are maximized and conditions for juvenile growth are optimal.

The size-at-birth of *P. prahli* is reached at a larger percentage of the maximum length attained by the species (25%) in comparison to *P. percellens* (17-20%; Grijalba-Bendeck *et al.* 2008, Rocha & Gadig 2013, Tagliafico *et al.* 2013), *P. productus* (9-14%; Villavicencio 1993, Downton 2007, Márquez-Farías 2007, Romo-Curiel 2007, Juaristi 2016), and *P. horkelii* (12-17%; Lessa *et al.* 1986). However, the proportion of maximum size representing the size-at-birth would be lower than that of *P. leucorhynchus* (27-37%; Payán *et al.* 2011, Romero-Caicedo & Carrera-Fernández 2015).

The fecundity estimated through counting the embryos was lower than that estimated by counting the largest follicles, and both estimates were similar to those reported for *P. leucorhynchus* in the Colombian Pacific (1-16 follicles and 1-6 embryos; Payán *et al*. 2011), in Ecuador (1-7 embryos; Romero-Caicedo & Carrera-Fernández 2015) and *R. percellens* in the Colombian Atlantic and Venezuela (2-4 embryos; Acevedo *et al.* 2007, Grijalba-Bendeck *et al.* 2008, 2012; Tagliafico *et al.* 2013). However, the estimated fecundity (through counting the number of embryos) was smaller than that of *R. percellens* (2-13 embryos; Rocha & Gadig 2013) and *P. horkelii* (4-12 embryos; Lessa *et al.* 1986, Martins *et al.* 2018) in Brazil, as well as for *P. productus* in the Mexican Pacific (1-18 embryos; Villavicencio 1993, Timmons & Bray 1997, Downton 2007, Márquez-Farías 2007, Juaristi 2016).

It has been reported that gravid females can abort embryos when they have been caught due to stress, mainly if they are close to the size-at-birth (Villavicencio 1993). Conrath (2005) also points out that in some species the number of pups that survive the full development process can be lower than the number of mature follicles (pre-ovulatory) ovulated, due to failures during the gestation period. Furthermore, some pre-ovulatory follicles could not be ovulated in some cases and were reabsorbed at the end of the reproductive season. Thus, estimating fecundity by counting the number of full-term embryos could lead to an underestimation, whereas counting the number of pre-ovulatory follicles could lead on the other hand to an overestimation. The comparison of both estimates might be then recommended.

Pseudobatos prahli presented a positive relationship between both estimates of fecundity and maternal size, as has been observed in *P. leucorhynchus* (r^2= 0.24 for the number of embryos; Romero-Caicedo & Carrera-Fernández 2015), *P. percellens* (r^2= 0.90 and 0.96 for the number of follicles and embryos, respectively; Rocha & Gadig 2013), *P. productus* (r^2= 0.66 and 0.83 for the number of follicles and embryos, respectively; Downton 2007; and r^2= 0.72 for the number of follicles; Márquez-Farías 2007), *P. horkelii* (r^2= 0.43 and 0.84 for the number of follicles and embryos, respectively, Lessa *et al.* 1986). A relationship between the number of embryos and maternal size has been reported for *P. leucorhynchus* and *P. productus* by other authors (Villavicencio 1993, Romo-Curiel 2007, Payán *et al.* 2011), though the level of correlation was not reported in their studies. On the other hand, no relationship between the number of follicles and embryos with maternal size was observed for *P. percellens* (r^2= 0.01 and 0.02 respectively, Grijalba-Bendeck *et al.* 2008). Though Pratt & Casey (1990) stated that in elasmobranchs larger females tend to produce higher number of offspring, in an opposing way, Conrath (2005) suggest that maternal size is indeed a poor predictor of fecundity, since both parameters tend to present low correlation values.

Pseudobatos prahli is a viviparous aplacental species that presents a similar reproductive strategy to other species of the genus *Pseudobatos*, with an annual reproductive cycle, low fecundity, embryos feed on a yolk sac and most likely are born in March. However, in comparison to related species, *P. prahli* appears to attain maturity and born at a larger proportion of its maximum length, as well as lower fecundity than some species, which might derive in lower biological productivity. Understanding the reproductive biology of a species is of great importance for the evaluation of their populations and adequate fishery management (Walker 2005). This work presents, for the first time, a detailed description of the development of the reproductive system of *P. prahli* in the central-eastern Pacific Ocean, including an estimation of important reproductive parameters. These parameters should be used in further population assessments to ensure its sustainable use in the region.

Acknowledgments

We thank Warren Hair for the review of the English version and the anonymous reviewer that improved the manuscript with his comments.

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Editor: Francisco Concha
Received 21 August 2020
Accepted 1 October 2021