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Reproductive biology of the scalloped hammerhead (*Sphyrna lewini*) in the central-eastern Pacific Ocean

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Abstract

There are limited data regarding the reproductive biology of the scalloped hammerhead (*Sphyrna lewini*) in Ecuadorian waters, which limits the development of appropriate management measures of its populations. A total of 1664 *S. lewini* specimens were recorded in Manta, Ecuador in 2003–2009. Specimens were caught by local commercial fisheries and measured between 50–310 cm total length (TL). Females were more frequently caught, with a sex ratio of 1M:1.8F. The median size at maturity was 178.1 cm TL for males and 219.4 cm TL for females, which was larger compared with other localities. Gravid females, which measured 246–298 cm TL, contained 16–22 embryos. Embryos, which were observed from October–July, measured between 11.1–54.6 cm TL and the available data agreed with a gestation period of 10–11 months that starts in September and ends in June/July. Size at birth was 47–55 cm TL. Sampling data indicated that most fishing activity occurred in nearshore and around seamounts in the central-eastern Pacific Ocean, with much of the landed catch comprising immature individuals. This study documents the reproductive biology of *S. lewini* in the central-eastern Pacific Ocean and provides additional information to improve management and conservation measures for this species.

Introduction

The scalloped hammerhead (*Sphyrna lewini*) is a coastal-oceanic species distributed throughout tropical and warm temperate oceans around the world (Compagno, 1984). It occupies a wide range of habitats; the young typically inhabit shallow bays and estuaries, while adults live in continental shelves and adjacent waters, occurring at depths to 1043 m (Moore & Gates, 2015). In the eastern tropical Pacific, *S. lewini* migrate during the summer to the Gulf of California to reproduce (Klimley, 1987). This shark is a placental viviparous species with a gestation period of 11 months (Torres-Huerta *et al.*, 2008). They give birth to 14–41 pups (Bass *et al.*, 1975; Branstetter, 1987; Hazin *et al.*, 2001*a*; White *et al.*, 2008; Bejarano-Álvarez *et al.*, 2011; Chodrijah & Setyadji, 2015; Gallagher & Klimley, 2018) in which the size at birth has been reported to be between 40–53 cm total length (TL) (Clarke, 1971; Bass *et al.*, 1975; Branstetter, 1987; Chen *et al.*, 1990; Torres-Huerta *et al.*, 2008; Bejarano-Álvarez *et al.*, 2011). In the Pacific Ocean, male *S. lewini* reach sexual maturity between 170 and 177 cm TL (Klimley, 1987; Torres-Huerta *et al.*, 2008), while females reach maturity between 207 and 212 cm TL (Compagno, 1984; Torres-Huerta *et al.*, 2008).

Given the large size at maturity and low fecundity, this species may be vulnerable to overexploitation (Chapman *et al.*, 2005; Simpfendorfer & Heupel, 2012). Internationally, a large number of *S. lewini* are subject to direct fishing and bycatch by a variety of fishing gears (e.g. gillnets, long-lines, trammel nets, trawls, static demersal) in both inshore and offshore areas (Maguire *et al.*, 2006; Martínez-Ortíz *et al.*, 2015; Rigby *et al.*, 2019*a*). For instance, in the north-west and central-west Atlantic Ocean (USA), it was estimated that Sphyrnidae (*S. lewini*, *S. mokarran* and *S. zygaena*) abundance decreased 89% during 1986–2005 (Rigby *et al.*, 2019*a*), whereas in the north-eastern Pacific Ocean, countries such as Costa Rica and Mexico demonstrated a 60% decrease in the relative abundance of *S. lewini* (e.g. Arauz *et al.*, 2004; Soriano-Velásquez *et al.*, 2006). Conversely, in Ecuador's central-eastern Pacific Ocean, the landings of *S. lewini* decreased by 50% from 2003–2006 (Martínez *et al.*, 2007) and 45.4% between 2008–2010 (Ministerial Agreement No. 116 in 2013). In accordance, *S. lewini* is categorized as Critically Endangered by the IUCN Red List (Rigby *et al.*, 2019*b*), and it is included in CITES Appendix II in order to verify that such trade is not prejudicial to the survival of this species in the wild (CITES, 2013).

In Ecuador, *S. lewini* is one of the main species caught by artisanal and industrial fisheries. However, few efforts have been carried out to gather information on the reproductive biology of the species, despite the importance of generating information for stock assessments and developing management for conservation plans in the region. Currently, there are no studies

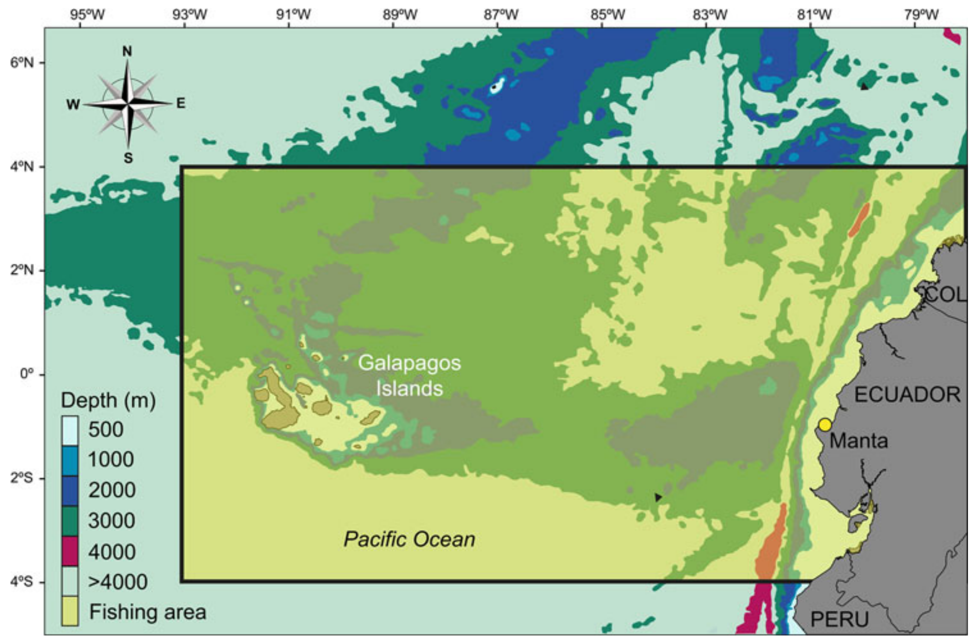

Fig. 1. Study area showing the port of Manta, Ecuador, where specimens of *Sphyrna lewini* were collected from commercial landings (2003–2009, except 2007), with the fishing grounds (crossed area) and bathymetry indicated.

regarding the reproduction of *S. lewini* in Ecuadorian waters, which would permit the generation of adequate management measures (i.e. minimum size for capture, closed fishing seasons, identification of nursery areas, etc.). However, the Ministry of Agriculture, Livestock, Aquaculture, and Fishing (MAGAP) has promulgated precautionary regulations for the management of hammerhead shark stocks. The MAGAP has restricted the captures of *S. lewini* to a maximum of five individuals per each small artisanal boat ('fibres' from 7–9 m of length), in which the caught individuals must not be smaller that 150 cm TL. Additionally, there should be no gravid females on board; if they are captured, they should be returned to the sea immediately. Furthermore, the capture of hammerhead sharks (*S. lewini* and *S. zygaena*) is prohibited for industrial fishing vessels (Ministerial Agreement No. 116 in 2013). In Ecuador, few efforts have been developed for the regulation of *S. lewini* fisheries; therefore, there is a need to increase the knowledge of Ecuador's shark species to appropriately manage their populations. This study aims to provide baseline data on the reproductive biology of *S. lewini* to inform fisheries management plans in the central-eastern Pacific Ocean.

Materials and methods

This study was based on 1664 *Sphyrna lewini* specimens (595 males and 1069 females) collected from various commercial fisheries (e.g. pelagic longline, surface gillnets, purse seines, 'mother-ship' [barco nodiriza in Spanish]) operating in the central-eastern Pacific Ocean (between 4°N and 4°S and from the coast to 93°W; Figure 1) and landed in Manta, Ecuador during 2003–2009.

Once landed at the port, the TL for each specimen was recorded, and the gonads of a subsample (57 males and 92 females) were examined in detail for the evaluation of their reproductive state. Reproductive organs were removed and stored in a solution of 10% formalin prior to transportation to the laboratory. Data collected from males included length and width of the testes, and the outer length and calcification state of the claspers (Pratt, 1979; Hazin *et al.*, 2001*a*, 2001*b*). In the case of females, the oviducal gland width, the maximum ovarian follicle diameter (MOFD), uterine width and, if present, the number of embryos and length and sex of the pups were recorded (Pratt, 1979; Hazin *et al.*, 2001*a*, 2001*b*).

Inferences on stages of maturation were made according to definitions provided in previous studies (Pratt, 1979; Hazin *et al.*, 2001*a*, 2001*b*; ICES, 2013). Male maturation was evaluated based on the development of the testes and the calcification of the claspers; thus, males were classified in three stages. Individuals with relatively short, flexible and non-calcified claspers that did not extend beyond the posterior edge of the pelvic fins and had small and undeveloped testes were considered immature. Males with claspers that were flexible, partially calcified and as long as or longer than the pelvic fins, as well as with developing and commenced segmented testes, were classified as developing males. Mature males were characterized by elongated and calcified claspers (ICES, 2013). Females were separated into four stages based on the development of the oviducal gland, uteri, MOFD and ovary. Specimens were considered immature if they had undeveloped sexual organs, filiform uteri and no vitellogenic activity in their ovaries (Pratt, 1979; Hazin *et al.*, 2001*a*, 2001*b*; ICES, 2013). Developing females had distinguishable and developing oviducal glands, follicles of different stages of development, some small and median sized follicles with yolk, and enlarging uteri (ICES, 2013). Mature females had large follicles ready to be ovulated, as well as fully developed oviducal glands and uteri (ICES, 2013). Finally, females with fully formed embryos and reduced or absent yolk sacs were classified as in late pregnancy (ICES, 2013).

A Chi-squared goodness-of-fit test was used to examine the hypothesis of an equal sex ratio (1:1) among the total number of *S. lewini* landed specimens between 2003–2009. The relationship between TL and the different reproductive structures (e.g. clasper length, testes length and width, oviducal gland width and uterine width) were plotted to indicate the onset of sexual maturity (Natanson & Caillet, 1986). Size at maturity (TL_{50}), which was defined as the length at which 50% of the population is mature, was estimated for males and females by fitting a logistic regression model to the binomial maturity data based on their condition (0 = immature and developing, 1 = mature) (Mollet *et al.*, 2000). The length at which 50% of the individuals had reached sexual maturity was modelled using the maximum likelihood as follows: $TL_{50} = 1/1 + e^{a+b(TL)}$, where TL_{50} is the proportion of mature individuals, a and b are model parameters, and TL is the total length of each specimen. The goodness of fit of the model logistic was examined using the Hosmer–Lemeshow test.

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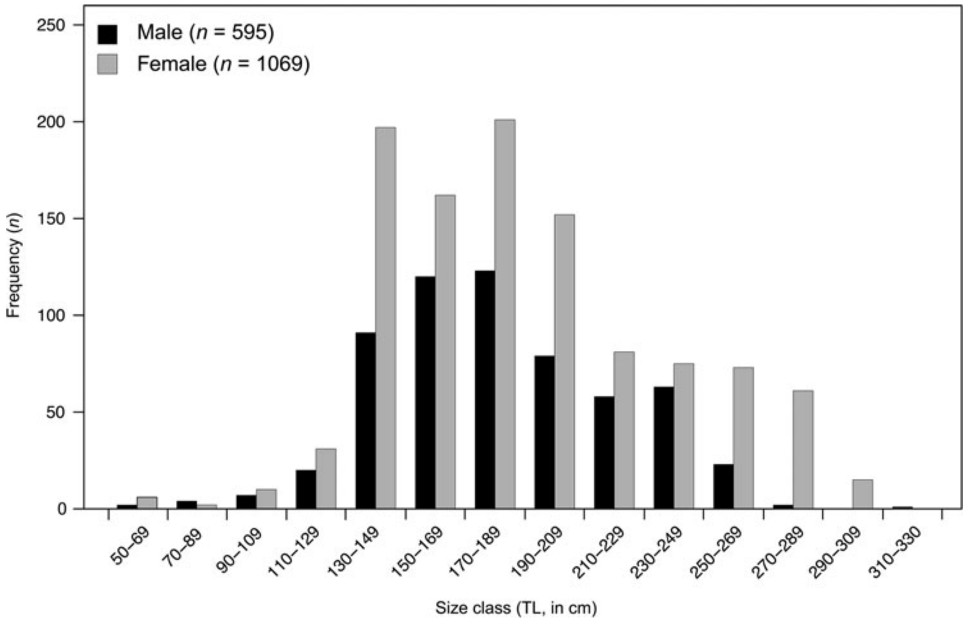

Fig. 2. Length frequency distribution of males and females of *Sphyrna lewini* landed in the port of Manta, Ecuador, between 2003–2009 (except 2007).

Table 1. Number of individuals of scalloped hammerhead (*Sphyrna lewini*) in the central-eastern Pacific Ocean landed in the artisanal port of Manta (Ecuador), between 2003–2009 (except 2007), expressed in the number of individuals (N), total length (TL, in Interval and mean ± SD) and sex ratio.

	Males			Females					
Year	N	Interval TL (cm)	Mean ± SD	N	Interval TL (cm)	Mean ± SD	Total (N)	M:F	Statistics
2003	70	127.0–272.0	175.3 ± 28.2	67	91.0–300.0	172.0 ± 37.6	137	1:0.96	$\chi^2 = 0.07$; $P = 0.80$
2004	185	77.0–316.0	181.7 ± 37.9	351	98.0–291.0	187.8 ± 42.6	536	1:1.9	$\chi^2 = 51.41$; $P = 7.49 \times 10^{-13}$
2005	84	132.0–264.0	189.8 ± 36.3	114	114.0–298.0	209.5 ± 46.1	198	1:1.4	$\chi^2 = 4.54$; $P = 0.03$
2006	146	65.0–266.0	179.5 ± 45.1	291	50.0–292.0	181.9 ± 51.2	437	1:1.9	48.11; $P = 4.02 \times 10^{-12}$
2008	84	113.0–256.0	178.8 ± 36.0	199	117.0–291.2	188.5 ± 44.4	283	1:2.4	$\chi^2 = 46.73$; $P = 8.14 \times 10^{-12}$
2009	26	118.0–288.0	192.5 ± 44.8	47	127.8–286.0	197.2 ± 48.9	73	1:1.81	$\chi^2 = 6.04$; $P = 0.01$
Total	595	65.0–316.0	181.6 ± 38.8	1069	50.0–300.0	188.1 ± 46.6	1664	1:1.80	$\chi^2 = 135.02$; $P < 2.2 \times ^{-16}$

Fecundity was estimated by counting the total number of embryos and plotted as mean embryo size against time (months) to estimate the length and timing of the gestation period. To construct the gestation period graph, the quartiles were used with 95% confidence intervals. Size at birth ranged from the measurement of the largest embryo to that of the smallest neonate. All analyses were conducted with the significance level set at $\alpha = 0.05$.

Results

In total, 35.8% (N = 595) of the 1664 specimens were males, and 64.2% (N = 1069) were females. Males ranged from 65–310 cm TL, with a modal TL class between 130–209 cm (Mean ± SD = 181.6 ± 38.8 cm TL), whereas females ranged from 50–300 cm TL, with a modal TL class between 130–209 cm TL (188.3 ± 46.5 cm TL) (Figure 2). More females were landed, with an overall sex ratio of 1M:1.8F ($\chi^2 = 135.02$; $P < 2.2 \times 10^{-16}$); this trend was observed in all years except 2003, when the sex ratio was not significantly different from 1:1 (Table 1).

In the males that measured between 65–195 cm TL, non-calcified claspers were present (varying in length from 2–17 cm) and clasper length increased rapidly with TL. Males between 151–316 cm TL had calcified claspers that measured 15–24 cm; thus, 285 individuals were mature, 32 were developing and 278 were mature specimens (Figure 3). Of the total male specimens landed (N = 595), only 57 of them were examined in detail: 25 were immature, 8 were developing and 24 were mature specimens (Table 2). The TL_{50} at maturity of the males was estimated to be 178.1 cm (95% CI: 175.5–180.6, $TL_{50} = 1/1 + e^{-19.211 + (0.108 \times TL)}$; Hosmer–Lemeshow test, $\chi^2 = 3.47$, $P = 0$ 0.90) (Figure 4A). According to the estimated TL_{50}, the percentage of immature and mature males caught between 2003–2009 (except 2007) was 54.3 and 45.7%, respectively.

Of the total number of female specimens recorded (N = 1069), only 92 were examined in detail: 49 were immature, 27 were developing, 4 were mature and 12 were in late pregnancy (Table 3). From this sample, the TL_{50} for females was estimated at 219.4 cm TL (95% CI: 208.89–229.9, $TL_{50} = 1/1 + e^{-15.516 + (0.071 \times TL)}$; Hosmer–Lemeshow test, $\chi^2 = 1.06$, $P = 0$ 0.98) (Figure 4B). On this basis, few mature females (17.3%) were recorded between 2003 and 2009, as compared with immature females (82.7%).

A total of 12 gravid females were analysed in detail; a total of 127 embryos were counted, with an estimated fecundity of 16–22 embryos. Smaller embryos were observed during October and measured between 11.1–14.2 cm TL (13.1 ± 0.74 cm TL). Larger embryos were recorded in June and measured 43.6–54.6 cm TL (50.2 ± 3.31 cm TL) (Figure 5). Size at birth was estimated as

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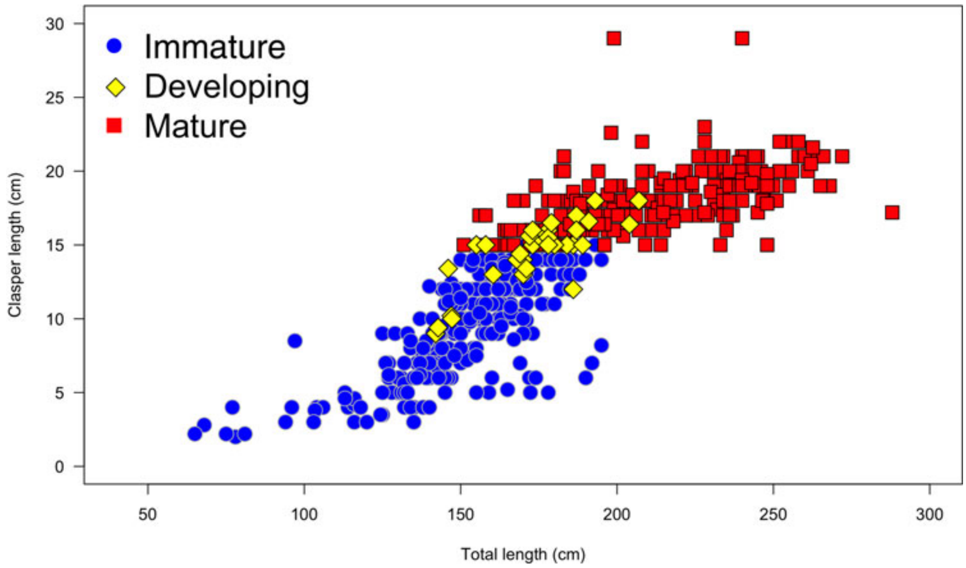

Fig. 3. Relationship between clasper length and total length according to the degree of calcification of the clasper in males of *Sphyrna lewini* landed in the port of Manta, Ecuador, between 2003–2009 (except 2007).

Table 2. Characteristics of maturation stages, size range (total length) and number of males of *Sphyrna lewini*

Characteristics	Immature	Developing	Mature
Number of specimens	25	8	24
Size range	48.0–177.0	154.0–207.0	175.0–264.0
Testis length	0.50–22.24	15.15–23.80	16.50–31.80
Testis width	0.29–1.88	1.54–3.39	1.09–4.80

All lengths are in cm.

the interval between the largest embryo and the smallest neonate, which ranged from 47 (smallest neonate) to 55 (largest embryo) cm TL.

Discussion

This is the first study to estimate the length-at-maturity (males = 178.1 cm TL, females = 219.4 cm TL) and the size at birth (47–55 cm TL) of *Sphyrna lewini* in Ecuadorian waters. Although the results were based on limited data, fecundity was observed as 16–22 pups, and the gestation period was likely to be <12 months, although the reproductive cycle may be longer.

Over the study period, there were proportionally more females caught, with the mean annual sex composition over the years 2003–2009 comprising 62.2% females and 37.8% males, and the sex ratio significantly favouring females in five of the six years. These results contrast with previous studies in the Gulf of California (Mexico), where males dominated in the catches (Torres-Huerta *et al.*, 2008). This may be due to: (1) the location of the sampling areas; (2) the individuals that are most likely caught by different fishing gear and methods (e.g. long-lines, gill-net, purse seines); (3) the use of different habitats, possibly in deeper waters beyond the continental shelf (Stevens & Lyle, 1989); and (4) tendencies for sexual segregation in different areas (Wearmouth & Sims, 2008; Harry *et al.*, 2011); whereby females may spend more time in oceanic areas, whilst males exhibit a preference for coastal environments (Estupiñán-Montaño *et al.*, in press). The potential for a high fishing pressure on females of the stock could affect recruitment, which could indicate that further management measures may be required.

The length range recorded in this study is consistent with those reported by Torres-Huerta *et al.* (2008) in the Gulf of California, Mexico (males = 42–290 cm TL; females = 41–363 cm TL) which included neonates, juveniles and adults. However, the most frequent measurements for males and females in this study ranged between 140–186 cm TL and 118–208 cm TL, respectively ($N \geq 100$; Figure 2). The results of the length–frequency distribution produced by the study according to the LT_{50}, showed that more juveniles of both sexes were captured. This information suggests that fishing activity in the Pacific Ocean is mainly carried out near the coast and around seamounts (Estupiñán-Montaño *et al.*, in press). In such habitats, there may be access to nursery areas and other aggregation zones, which increases the likelihood of capturing immature organisms. Therefore, if significant numbers of immature and gravid

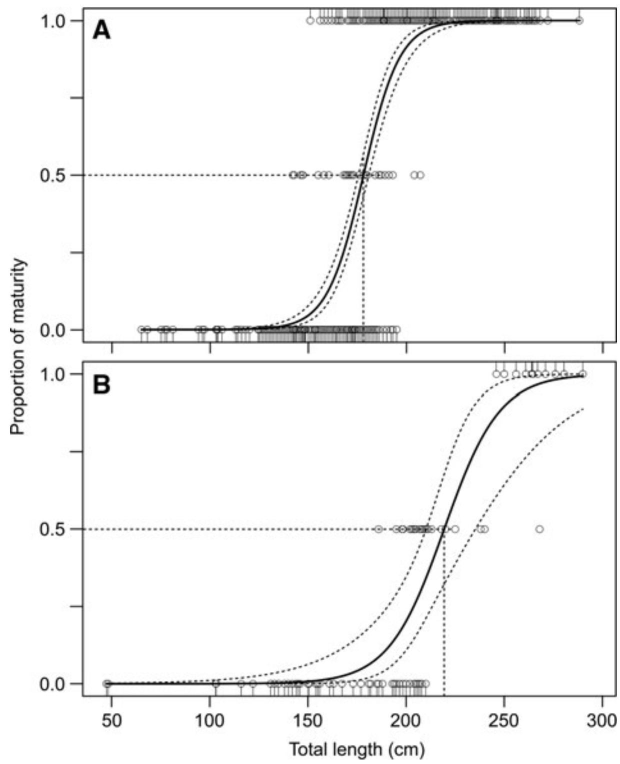

Fig. 4. Maturity ogives for males (A; N = 595 specimens) and females (B; N = 92 specimens) of *Sphyrna lewini* landed in Manta, Ecuador, between 2003–2009 (except 2007), representing the length at which 50% of the population had reached sexual maturity.

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Table 3. Characteristics of maturation stages, size range (total length) and number of females of *Sphyrna lewini*

Characteristics	Immature	Developing	Mature	Late pregnancy
Number of specimens	49	27	4	12
Size range	47.4–210.0	186.0–268.0	261.0–264.0	246.0–290.0
MOFD	0.25–1.28	1.01–1.78	2.77–2.79	1.76–2.79
Oviducal gland width	0.27–2.98	0.73–3.97	3.99–5.20	3.14–4.82
Uterus width	0.14–2.61	0.84–3.15	9.07–12.0	10.32–31.0

MOFD, Maximum ovarian follicle diameter. All lengths are in cm.

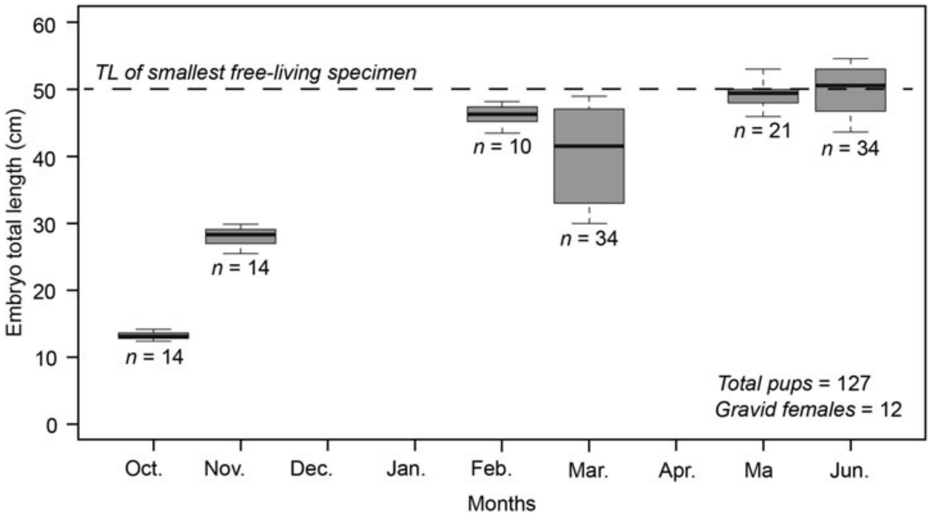

Fig. 5. Length of *Sphyrna lewini* embryos according to the month, with the number of gravid females examined ($N_L = 12$) and the total number of pups ($N_P = 127$) as observed from the landings at Manta, Ecuador, between 2003–2009 (except 2007). The length of the smallest free-living specimen observed (50 cm) is shown as a dashed line.

specimens continue to be caught in the future, the rate of recruitment will likely decrease, and recovery could take several years (Chodrijah & Setyadji, 2015). These results show the need to revise and adjust existing regulations, given that the Ministerial Agreement No. 116 of 2013 prohibits the capture of individuals smaller than 150 cm TL and gravid specimens. The present results could be adopted to establish a minimum size for capture (LT_{50}; males: 178.1 cm; females: 219.4 cm), and to implement other potential protective measures (e.g. quotas and/or size limits) with regard to the management of relevant fisheries and the capture of hammerhead shark species (*Sphyrna* spp.).

This study estimated that male and female of *S. lewini* reach sexual maturity at larger sizes in Ecuadorian waters in comparison to other sites of the north-eastern Pacific Ocean (i.e. Gulf of California, Mexico), where smaller sizes for sexual maturity have been recorded (170 cm TL and 207 cm TL for males and females, respectively; Torres-Huerta *et al.*, 2008). This discrepancy may be due to: (1) *S. lewini* from the Gulf of California have been heavily exploited and may have responded by reducing the median size at maturity; (2) methodological differences being used to assess sexual maturity (e.g. statistical analysis, direct observation, or microscopic analysis of gonads); (3) the effects of other fisheries and activities; and (4) latitudinal and/or stock-related differences in life-history parameters which may related to different environmental factors, conditions and food sources (e.g. Conover, 1990; Lombardi-Carlson *et al.*, 2003).

In the present study, the smallest embryos (11.1–14.1 cm TL) were recorded in early (12th) October. This is similar to that observed in the Gulf of California, Mexico, where embryos with an average size of 10.4 cm TL were reported in September (Torres-Huerta *et al.*, 2008), suggesting that ovulation for this species occurs in August/September. The largest embryos observed in the present study (>43 cm TL) were observed in June. This also coincides with the observations reported by Torres-Huerta *et al.* (2008) in the Gulf of California, Mexico, where embryos of 41–59 cm TL were detected in July, suggesting a gestation period of about 11 months in which the birth occurred during the latter month. The high similarity in terms of the period of the gestation and birth may be explained by the genetic relationship among small populations of *S. lewini* along the eastern Pacific Ocean (Nance *et al.*, 2011), as well as the presence of neonates in the Pacific coast of Costa Rica during July–August (Zanella & López-Garro, 2015) and in Panama during March–June (Robles *et al.*, 2015). In spite of the similarities between our results and those from other studies, our results should be interpreted with caution due to the low number of gravid females analysed (N = 12); hence, more studies are needed to support these findings.

Furthermore, this study suggests that the size at birth of *S. lewini* in Ecuadorian waters is estimated between 47–55 cm TL, considering the largest embryos and the smallest neonates observed. Although few neonates were registered in this study, our approach to the size at birth for this species is consistent with the approach taken by Torres-Huerta *et al.* (2008) whose estimation was between 41–53 cm TL.

In conclusion, based on the similarities with other studies in the eastern Pacific Ocean which have focused on the reproductive biology of *S. lewini*, this work suggests that for the central-eastern Pacific Ocean: (1) the fishing activity is in nearshore areas and oceanic islands (i.e. seamounts), from where mostly immature individuals are landed; (2) the size at maturity in this area is larger than in other localities; and (3) the gestation period starts in September and ends between June–July (10–11 months), with sizes at birth between 47–55 cm TL. Additionally, this work highlights the need to increase the basic knowledge of *S. lewini* in Ecuadorian waters and the central-eastern Pacific Ocean, which along with other research (e.g. demography and genetics) can

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support the development and implementation of appropriate management and conservation measures for the species.

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