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ARTICLE

Size, Age, and Spatial–Temporal Distribution of Shortfin Mako in the Mexican Pacific Ocean

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Abstract

Basic population parameters such as age, size, and distribution have been poorly evaluated for the Shortfin Mako *Isurus oxyrinchus* in the Mexican Pacific Ocean. According to data collected by scientific observers on board medium-size fishing vessels during the period of 2006–2013, size as TL was obtained for 5,740 individual sharks. The range of TL was 70–362 cm for females and 71–296 cm for males. Weight (W), measured randomly from 1,409 individuals, ranged from 2 to 90 kg for females and from 2 to 80 kg for males. The weight-to-TL ratio was best fitted by the equation $W = 4 \times 10^{-5}(\mathrm{TL})^{2.59}$ ($r^2 = 0.6532$). No sex-specific difference was found in the weight-to-TL relationship between males and females, nor in W or TL separately. By using the inverse von Bertalanffy equation and parameters described by other authors for the same study area, we determined the age range for individuals captured on the basis of their TL. The age ranged from 0 to 39 years in females and from 0 to 21 years in males. Using a logistic model, the mean length at sexual maturity was obtained for 2,532 males (TL = 190 cm). The quarterly distribution of young of the year and 1-year-old juveniles showed that there is a tendency for these sharks to move

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northward as sea surface temperature increases. Our findings shed new light on how Shortfin Mako juveniles use a habitat that has been proposed by other authors as a nursery area for this species, information that is valuable for the sustainability of the Mexican Pacific fisheries.

The Shortfin Mako *Isurus oxyrinchus* is a highly migratory and epipelagic predatory shark (UNOLOS 2013). It is distributed worldwide in temperate and tropical seas (Compagno 2001) and is rarely found in waters with temperatures below 13–17°C (Stevens 2008). The Shortfin Mako is an ovoviviparous species that shows oophagy. It has late sexual maturity, a gestation period of 15 to 18 months, and a 3-year reproductive cycle (Cailliet et al. 2009). Female Shortfin Makos have litters of 10–18 pups. In the Pacific Ocean, the size at birth for Shortfin Makos has been assessed by several studies; for example, Mollet et al. (2000) established size at birth at 70 cm TL; Joung and Hsu (2005) found a young of the year (age 0) individual of 74 cm TL; Cerna and Licandeo (2009) recorded the minimum TL at 75–76 cm; and Cortés et al. (2010) measured age-0 at 70 cm TL. These characteristics make Shortfin Mako nonresilient and susceptible to fishing pressure. Unlike other shark species, for which only the fins fetch a high price in the market, there is a high demand for Shortfin Mako meat, especially in the European Union (Mejuto et al. 2010). Also, because of its speed and physical strength, the Shortfin Mako is highly prized in sportfishing (French et al. 2015). This shark is captured directly and incidentally by Mexican Pacific fisheries, and it is one of the most exploited species by the medium-size fleet (Castillo-Geniz et al. 2014). Notwithstanding, there are few studies on age and growth of this species in the Mexican Pacific Ocean, such as those by Ribot-Carballal et al. (2005) and Vélez-Marín and Márquez-Farías (2009).

Maia et al. (2007), Semba et al. (2011), and Bustamante and Bennett (2013) determined that male Shortfin Makos mature at 185–217 cm TL. In southern California, Wells et al. (2013) determined length at maturity at 190 cm TL for males and 303 cm TL for females. More recently, Groeneveld et al. (2014) measured length at sexual-maturity at 206 cm TL for males and 271 cm TL for females from the southwestern Indian Ocean.

Age determination is important for population assessment and management of shark fisheries, since it is a necessary element for calculating growth rates, longevity, mortality rates, and age at sexual maturity (Goldman et al. 2012). Mollet et al. (2000) noted that the global average size at sexual maturity for the Shortfin Mako is 270–300 cm TL for females and 200–220 cm TL for males. In a more recent study carried out in the eastern and northern Pacific Ocean, Semba et al. (2011) found that males reached sexual maturity at 156 cm TL, while females did so at 256 cm. In the southeastern Pacific, Cerna and Licandeo (2009) obtained size-at-age ranges of 75–330 cm TL for females and 76–285 cm TL for males. On the other hand, in the Mexican Pacific, Vélez-Marín and Márquez-Farías (2009), reported length ranges of 61–238 cm TL in males and 76–286 cm TL in females.

The distribution of age-0 fish has been used to identify shark nurseries, which are defined as those sites where there is a greater abundance of sharks, where juveniles remain (or return to) for prolonged periods, and which are used in the same way for several years (Heupel et al. 2007). To date, there are few studies on nursery areas for pelagic sharks in the eastern Pacific Ocean. Weng et al. (2007) demonstrated that the U.S. coast of California and Baja California in Mexico are part of the nursery zone of the White Shark *Carcharodon carcharias*. Cartamil et al. (2016) used a combination of satellite tag data, tag-recapture data, and fisheries data to determine habitat use, movements, and geographic distribution of juveniles of the Common Thresher Shark *Alopias vulpinus* in Pacific coastal waters from Morro Bay, California, to Punta Eugenia, Mexico. Vélez-Marín and Márquez-Farías (2009) suggested that the southern California Bay area, which extends in an ocean polygon to the Marías and Revillagigedo islands, is a nursery area for the Shortfin Mako. This was determined by analyzing data from scientific observers on board commercial longline vessels in the Mexican Pacific.

Studies that help understand the population dynamics of the Shortfin Makoand its habitat use are important to develop and update management systems that guarantee the sustainability of this fishery. Therefore, our objectives were to update essential population parameters, specifically the age, growth, and size of this species and to continue with previous work done using historical data obtained by observers in this same area in order to contribute to the knowledge on habitat use by juvenile Shortfin Makos in the Mexican Pacific Ocean.

METHODS

Study site.— Mexico's Pacific Exclusive Economic Zone (EEZ) and territorial sea covers an area of 2,320,380 km^2 (INEGI 2010) (Figure 1A). The Mexican Pacific Ocean extends from the entrance of the Gulf of California (25°C isotherm) to the southern border with Guatemala. At the

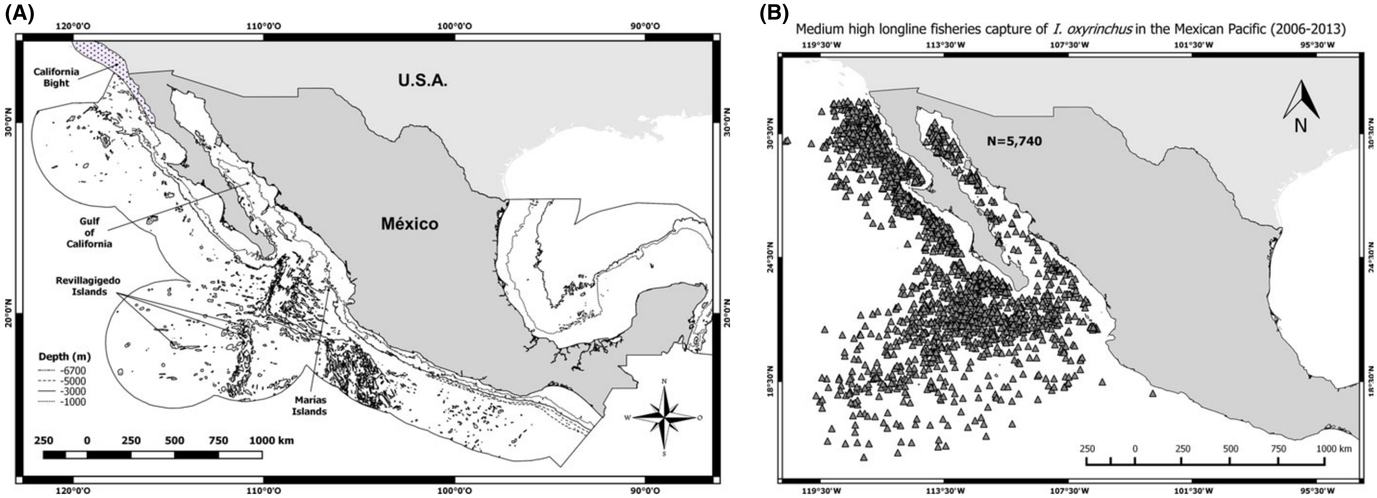

FIGURE 1. **(A)** Mexican Pacific Exclusive Economic Zone and **(B)** zone within where the commercial longline shark fleet registered captures of Shortfin Makos from 2006 to 2013.

northern boundary, the subarctic waters of the California Current and the equatorial, high-salinity waters of the Gulf of California meet the tropical waters that come from the south. Towards the equator, the Mexican Pacific Ocean borders the central American seas, where the Equatorial Countercurrent seasonally reaches the coast, covering the surface with high-salinity, low-nutrient waters (Trasviña et al. 2004).

Data collection.— We analyzed data collected during 8 years (2006–2013) by scientific observers on board medium-sized vessels of the shark longline fleet of the Mexican Pacific (Figure 1B). Due to the difficulty of performing dissections on board, sexual maturity of males was assessed on the basis of the calcified claspers (Castro 1993). Total length (TL) and fork length (FL) were taken. Since TL was taken more regularly than FL, the analyses were carried out using TL to take advantage of as much of the available data as possible. When possible, captured sharks were selected at random and weighed.

Data analyses.— Regression analysis techniques were used to determine the relationships between the TL and FL and between TL and weight (W) in both sexes. The equations were $\mathrm{TL} = a{\cdot}\mathrm{FL} + b$ and $W = a{\cdot}\mathrm{TL}^b$, where a and b are the parameters describing the regression lines. After linearizing the data and corroborating homogeneity of slopes, an ANCOVA was applied to detect statistical differences between males and females. For the length–weight relationship, the data were log transformed before testing the homogeneity of slopes. Using the inverse von Bertalanffy function, sizes (TL) were converted to age by using the growth parameters ($L_\infty = 411$ cm, $k = 0.05$ cm/year, $t_0 = -4.7$ years) described by Ribot-Carballal et al. (2005) for Shortfin Mako from the northwestern Mexican Pacific. All aforementioned analyses were performed with the statistics package IBM SPSS Statistics (version 20).

Maturity ogive for males was constructed by grouping individuals in size-classes of 4 cm TL. The logistic model, from the family of generalized linear models in R (R Development Core Team 2016) was fitted to binomial data in order to estimate the size at maturity. Likewise, we constructed distribution maps of age-0 and 1-year-old juveniles (1-year juveniles). Age-0 juveniles were considered those sharks with TL $\leq$ 100 cm (Lyons et al. 2013). Additionally, longevity was calculated with the equation proposed by Taylor (1958): $\text{Longevity} = \left(\frac{1}{k}\right)\ln\frac{(L_\infty - L_0)}{L_\infty(1-x)}$ where $x = L_t/L_\infty = 0.95$, k is the von Bertalanffy growth parameter, L_t is length at time t, L_∞ is the mean maximum length, and L_0 is the mean length at birth.

RESULTS

Of the 5,740 Shortfin Makos that were captured during the 8 years of study 56.27% were females and 43.73% were males. Total length ranged from 70 to 362 cm: the largest female was 362 cm and largest male was 296 cm; the smallest female was 70 cm and smallest male was 71 cm. Since TL of males did not trend towards normality (Kolmogorov–Smirnov test: $P < 0.5$), the frequency distributions of both sexes are shown separately (Figure 2). There was no significant difference in mean TL between males and females (ANOVA: $F = 0.325$, $P = 0.713$). The correlation between TL and FL was strongly supported by the coefficient of determination ($r^2 = 0.961$) (Table 1).

Weight ranged from 2 to 90 kg; the highest recorded weight was 90 kg for a female, while that for a male was

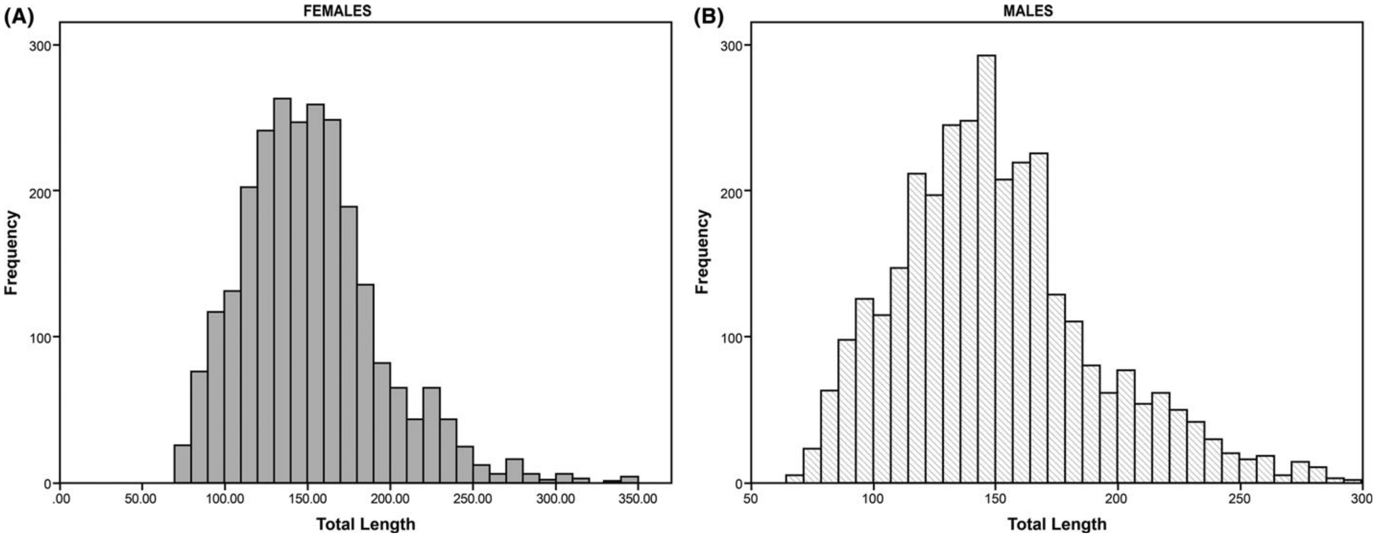

FIGURE 2. Length frequency histograms of **(A)** 3,225 female and **(B)** 2,515 male Shortfin Makos captured during 2006–2013 by the medium-sized commercial longline fleet in the Mexican Pacific Ocean.

TABLE 1. Comparison of the regression lines (ANCOVA) for the biometric relationships: TL versus FL and TL versus weight (*W*).

Biometric relationship	Equation	*N*	*a*	*b*	r^2
TL versus FL	TL = *a*·FL + *b*	4,887	0.088	1.119	0.961
TL versus *W*	$W = a \cdot \mathrm{TL}^b$	1,409	4×10^{-5}	2.590	0.653

80 kg. The lowest weight recorded for both sexes was 2 kg. There was no significant difference in mean weight between males and females (ANOVA: $F = 3.662$, $P = 0.056$).

The coefficient of determination indicated a moderate correlation between length and weight ($r^2 = 0.6532$) and parameter *b* indicated an allometric negative growth; values of the parameters of best fit are shown in Table 1. This type of relationship was compared between males and females; weight was associated with TL, and sexes

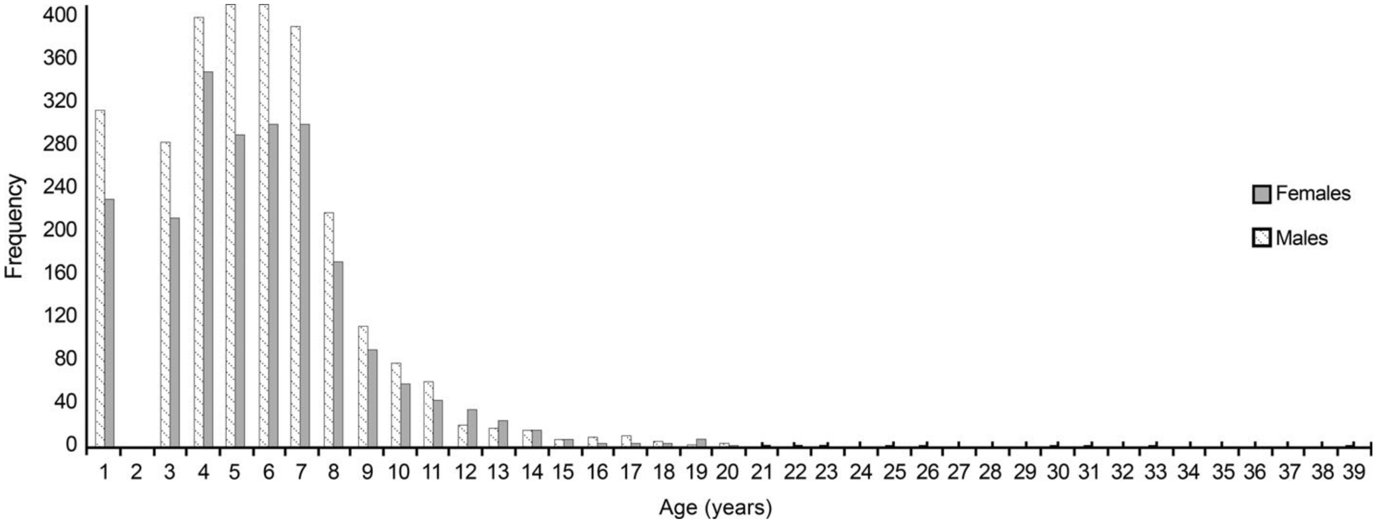

FIGURE 3. Age frequency distribution of 2,762 female and 2,132 male Shortfin Makos captured by the medium-sized commercial longline fleet in the Mexican Pacific Ocean during 2006–2013.

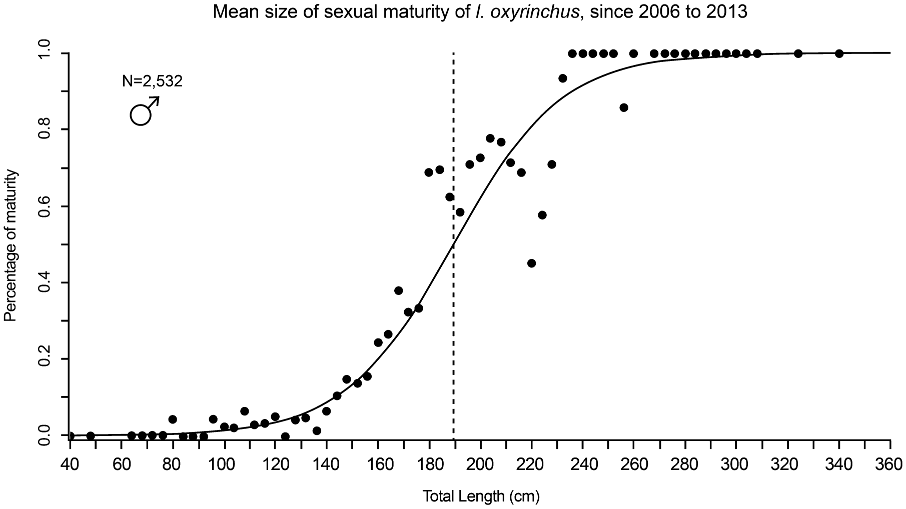

FIGURE 4. Mean size at sexual maturity of male Shortfin Makos captured during the 2006–2013 study period by the commercial longline fleet in the Mexican Pacific Ocean.

TABLE 2. Abundance of age-0 and 1-year-old juvenile Shortfin Makos during each quarter of the 2006–2013 study period. The range and mean sea surface temperature (SST) at which they were captured are shown.

Life stage	Quarter	Number of individuals captured	Range of SST (°C)	Mean SST (°C)
Age-0 juveniles	1	1	16.0	16.0
	2	5	19.1–22.8	24.5
	3	43	13.8–26.6	22.7
	4	26	13.0–19.7	16.9
1-year-old juveniles	1	1	26.8	26.8
	2	10	18.9–23.5	21.8
	3	45	16.6–26.6	23.0
	4	76	16.8–21.5	19.0

were not significantly different (ANCOVA: $F_{\text{sex}} = 0.036$, $P_{\text{sex}} = 0.965$). The variance of the weight explained as a function of TL was 62.2%. The mean weight of females (16.76 kg) was slightly lower than that of males (18.22 kg). The equation describing the biometric relationship between TL and FL is shown in Table 1.

The age range of females was 0–39 years and that for males was 0–21 years (Figure 3). The age structure shows that the distribution was dominated by individuals between 1 and 14 years (246–251 cm TL). Longevity, calculated according to the model proposed by Taylor (1958), was 56 years. The mean size of males at sexual maturity was 190 cm TL (n = 2,532) (Figure 4).

The size of age-0 sharks captured during the study period ranged from 78 to 99 cm TL, with a mean of 87.1 cm. The abundance of age-0 and 1-year-old juveniles, with their respective ranges and mean sea surface temperatures (SSTs) at which they were captured, is summarized for the first quarter (January–March), second quarter (April–June), third quarter (July–September), and fourth quarter (October–December) of the year in Table 2.

In the quarterly distribution maps (Figure 5) we observed that the months having the lowest catch of juveniles were January, February, and March and the months with the greatest abundance were from July to December. Our data indicate that these fish could give birth in open water between the Marias Islands and Revillagigedo Islands and then move to more coastal waters during the months of July–September and to northern latitudes during the last quarter of the year.

DISCUSSION

The TL range for Shortfin Makos in this study (70–362 cm) was higher than the one described by Ribot-Carballal et al. (2005), who found a TL range of 77 to 290 cm. However, only 11 sharks (nine females and two males) exceeded the length range found by those authors. It is possible that larger sharks, mainly females, spend more time at greater depths and away from the coast (Casey and Kohler 1992; Mollet et al. 2000). That possibility implies that their horizontal overlap with the area where the fishing fleet operates as well as the vertical overlap with the fishing gear are smaller. This could have been the reason for the lack of Shortfin Makos of sizes close to 300 cm in our study. Another possibility is that individuals of larger sizes are not attracted to the fishes that are used to bait the longlines, such as Atlantic Mackerel *Scomber scombrus* and Pacific Herring *Clupea pallasii*

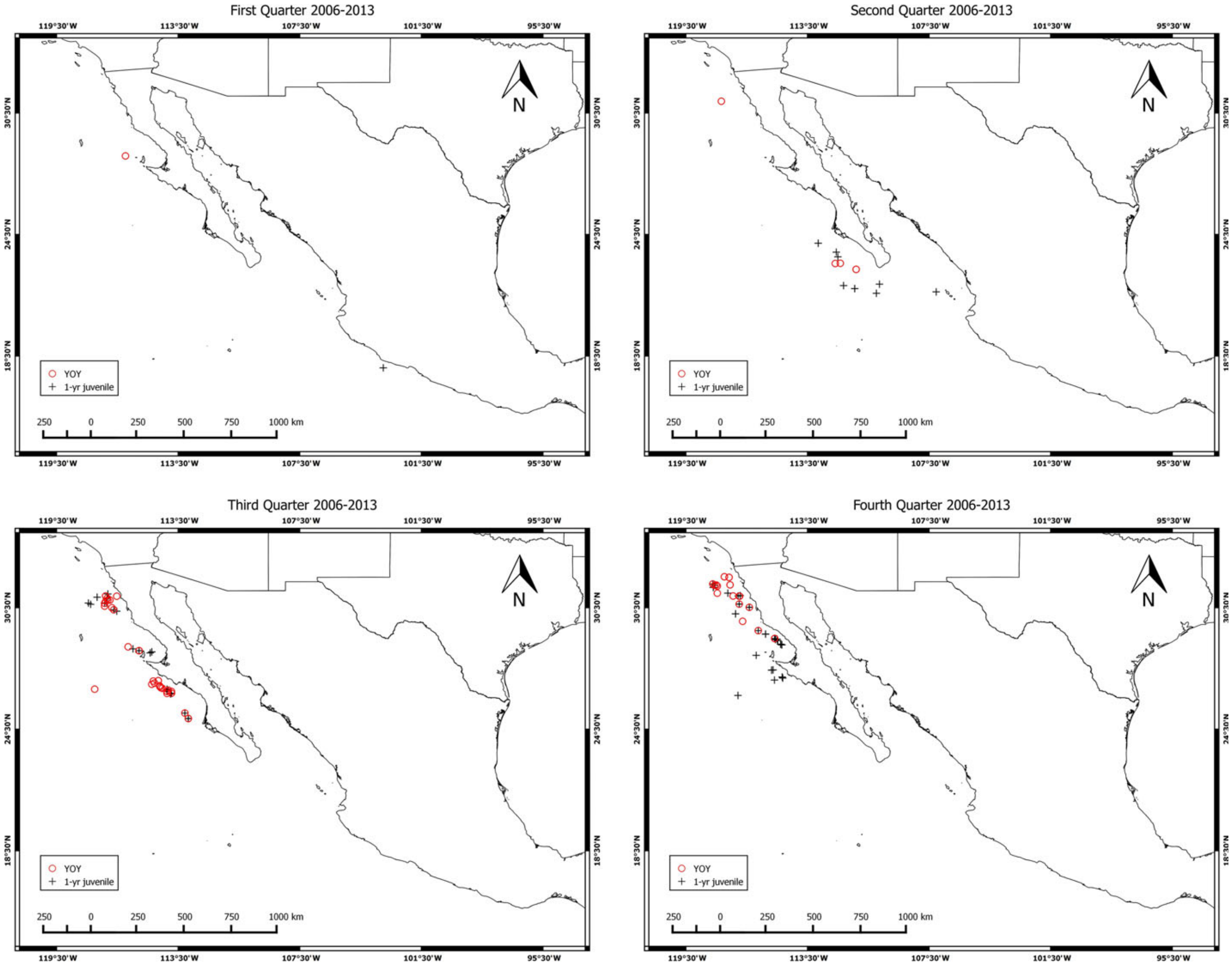

FIGURE 5. Quarterly distribution of age-0 and 1-year-old Shortfin Mako juveniles obtained from the commercial fishery in the Mexican Pacific Ocean during 2006–2013.

(Stillwell and Kohler 1982). It is also necessary to point out that since the NOM-029-PESC-Sharks and Rays “Specifications for their use” was implemented in 2006 (NOM 2007), medium-sized vessels have been prohibited from using any type of fishing nets, limiting them to the use of standardized longlines and hooks. This could imply bias occurred in the sample because the size of the specimens captured is directly related to the type and size of hook used (Pratt and Casey 1983).

Due to the difficulties faced by scientific observers on board fishing vessels when recording the weights, the length–weight relationship was estimated only on the basis of 1,409 individuals. The value of the parameter *b* obtained in the present study was 2.53. Kohler et al. (1996) reported a value of 3.14 for the parameter *b* in a length–weight relationship of Shortfin Makos from the North Atlantic Ocean. Those authors registered more accurate biometric measurements from sport and commercial fishing once they recorded data themselves. Because the scientific observers determined sexual stage data using only external features, which can jeopardize the accuracy of female sexual stage data, this study only assessed the mean size of males at sexual maturity. Our results agree with Maia et al. (2007), Semba et al. (2011), and Bustamante and Bennett (2013), who reported males matured at 185–217 cm TL, and with Wells et al. (2013) who calculated the length at sexual maturity of males at 190 cm TL Shortfin Makos in southern California, a study area near to the Mexican Pacific. Size at sexual maturity may vary according to sample size, length range sampled, and different models for estimations; however, it can also be affected by geography, such as differences between the hemispheres (Mollet et al. 2000).

One of the biological variables that has the most influence on population analysis of any species is age, since this is the basis for calculating mortality and productivity rates (Campana 2001). Most studies have reported deposition of one age ring per year for Shortfin Makos (Cailliet and Bedford 1983; Ribot-Carballal et al. 2005; Bishop et al. 2006; Natanson et al. 2006; Semba et al. 2009). We chose the growth parameters reported by Ribot-Carballal et al. (2005) to estimate the age structure of the Shortfin Mako individuals, because those authors conducted their work in the same study area. Also, they presented age-validation data clearly correlated with the water temperature profile. Although Shortfin Makos displayed large displacements in the western North Pacific (Medina Trujillo 2013), another study carried out by Wells et al. (2013) along the California coast (north of the Mexican Pacific coast) reported the deposition of two age rings per year, based on the oxytetracycline (OTC) age-validation technique. The difference in ring deposition (i.e., periodicity), and consequently dissimilar growth patterns in sharks between nearby study areas (northern Mexican Pacific versus California waters), could be a consequence of the low sample size of the OTC-marked vertebrae analyzed ($n = 29$) and the maturity stages that were dominated by juveniles in the study of Wells et al. (2013). Juvenile Shortfin Makos appear to have higher growth rates during the first years of life (Natanson et al. 2006; Barreto et al. 2016). This rapid growth in the early stages of life could explain the high growth rate ($k = 0.17$–0.19 cm/year) reported by Wells et al. (2013), which contrasts with that ($k = 0.05$ cm/year) reported by Ribot-Carballal et al. (2005). In any case, because accuracy in age and growth parameters is important for fishery management and conservation, more age and growth studies covering all size and age ranges of Shortfin Makos will be necessary in the western North Pacific to confirm the periodicity of ring formation in vertebrae.

Comparing the age ranges of the same population of a species subject to fishing pressure in different time intervals allows the evaluation of its response to fishing in order to determine the species' sustainability and to make future projections. There is a lot of controversy about the estimated longevity of the Shortfin Mako because of differences in techniques, interpretations, models, and the lack of validation or verification of them (Cailliet and Goldman 2004). Besides, the longevity of Shortfin Mako has been usually estimated to range between 10 and 25 years. Our results agree with Chang and Liu (2009) for the estimated longevity of this species in the Pacific Ocean at 56 years. Natanson et al. (2006) used data from Ribot-Carballal et al. (2005) and six other studies to confirm their calculations. Those investigators estimated the longevity of the Shortfin Mako in the Mexican Pacific at 55 years, which is very close to our findings and supports an estimated age range for this species in this specific study area.

The migration of age-0 and 1-year-old juveniles observed in our results could be related to the increase in SST during the year, which coincides with the findings reported by Kai et al. (2015) in the North Pacific Ocean and western Pacific Ocean for the Shortfin Mako and which is related to the thermal preferences of this species. Another possibility is that juveniles may be migrating in response to the movement of smaller fish that serve as food and in turn seek the nutrient-rich waters of coastal upwellings, such as the California Current. In their study, Vélez-Marín and Márquez-Farías (2009) did not report these migratory movements of juveniles. Those authors only mentioned their average location for their study period and, accordingly, they proposed the polygon from the southern Bay of California up to the Marías and Revillagigedo islands as a nursery area for the Shortfin Mako. The results of our seasonal analysis complement the information provided by those authors as they allow us to elucidate how Shortfin Mako juveniles are distributed seasonally in the Mexican Pacific. The findings of our study allow us to add to our previous knowledge of the distribution of age-0 and juvenile Shortfin Makos in the Mexican Pacific Ocean so that, in conjunction with future projects, a more specific delineation of nursery areas for this species can be defined, which is a priority for the management of this fishery.

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