BIOLOGICAL OBSERVATIONS OF SHORTFIN MAKO SHARK (*Isurus oxyrinchus*) ON SPANISH SURFACE LONGLINE FISHERY TARGETING SWORDFISH

B. García-Cortés, A. Ramos-Cartelle, J. Mejuto, A. Carroceda and J. Fernández-Costa [1]

SUMMARY

Reproductive data of 92 pregnant females were observed in 19,905 females across the Atlantic, Indian and Pacific oceans. Overall sex-ratio showed a slight but not significant predominance of females in the Atlantic and a slight but significant predominance of males in the Indian and Pacific. Litter-size varied from 3 to 17 (mean 11.6 embryos). The sizes of the females with embryos were ≥ 250cm FL. The SST range in which specimens were distributed was 12.7º-31.5ºC but 16.5º-28.5ºC for females with embryos. The results show that the lower the SST the greater the mean size of the embryos. Several areas for parturition are described but no restrictive seasonality was identified in any of the hemispheres neither within any ocean, suggesting diverse periods with a peak in the boreal autumn (33.3%) and in the southern spring (48.6%). The data confirms low availability of pregnant females in all areas observed and low occurrence of gestation and parturition suggesting either that these phases are more likely occur in other areas, or that these pregnant females are not easily accessible to this oceanic fishing gear.

RÉSUMÉ

Les données de reproduction de 92 femelles gravides ont été observées chez 19.905 femelles dans les océans Atlantique, Indien et Pacifique. Le sex-ratio global montre une prédominance légère mais non significative des femelles dans l'Atlantique et une prédominance légère mais significative des mâles dans l'océan Indien et l'océan Pacifique. La taille des portées variait de 3 à 17 (moyenne de 11,6 embryons). Les tailles des femelles avec des embryons étaient ≥ 250cm FL. La gamme de SST dans laquelle les spécimens ont été distribués était de 12,7º-31,5ºC mais de 16,5º-28,5ºC pour les femelles avec embryons. Les résultats montrent que plus la SST est faible, plus la taille moyenne des embryons est grande. Plusieurs zones de parturition sont décrites mais aucune saisonnalité restrictive n'a été identifiée dans aucun des hémisphères ni dans aucun océan, suggérant des périodes diverses avec un pic à l'automne boréal (33,3%) et au printemps austral (48,6%). Les données confirment la faible disponibilité des femelles gravides dans toutes les zones observées et la faible occurrence de la gestation et de la parturition, ce qui suggère soit que ces phases sont plus susceptibles de se produire dans d'autres zones, soit que ces femelles gravides ne sont pas facilement accessibles à cet engin de pêche océanique

RESUMEN

Los datos reproductivos de 92 hembras preñadas se observaron en 19.905 hembras en todos el Atlántico, Índico y Pacífico. En general, la ratio de sexos presentaba una ligera predominancia, aunque no significativa, de hembras en el Atlántico y una ligera predominancia, pero significativa, de machos en el Índico y Pacífico. El tamaño de la camada variaba entre 3 y 17 (media de 11,6 embriones). Las tallas de las hembras con embriones eran ≥ 250cm FL. El rango de SST en el que se distribuían los ejemplares era de 12,7º-31,5ºC, pero 16.5º-28.5ºC para las hembras con embriones. Los resultados demuestran que cuanto menor la SST, mayor la talla media de los embriones. Se describen varias áreas para partos, pero no se identificó una estacionalidad restrictiva en ninguno de los hemisferios ni en ningún océano, lo que sugiere diversos periodos con un pico en el otoño boreal (33,3 %) y en la primavera meridional (48,6 %). Los datos confirman la baja disponibilidad de hembras preñadas en todas

[1] Instituto Español de Oceanografía. Consejo Superior de Investigaciones Científicas. P.O. Box 130, 15080 A Coruña. Spain.
tunidos.corunha@ieo.es
http://www.co.ieo.es/tunidos/

las áreas observadas y la escasa ocurrencia de gestación y parto sugiere bien que estas fases es más probable que se produzcan en otras zonas o bien que estas hembras preñadas no son fácilmente accesibles para este arte pesquero oceánico.

1. Introduction

Analysis of space-time variables in a geographic information system indicated that 71% of the commercially important shark species concentrate in coastal zones, mainly in bays, coastal lagoons, estuaries and wetlands. Shark mating and nursery grounds are thus considered as critical habitats of the utmost importance to maintain continuity of recruitment (Heupel *et al.* 2007). Nursery grounds are regularly geographically discrete locations in the spatial distribution range of a species, where gravid females expend their young or lay their eggs, and where juveniles spend their first weeks, months or years of life (Castro 1993). So, identifying sharks breeding areas is essential to be able to protect them from possible overfishing (Camhi *et al.* 1998, Anislado and Robinson 2001).

The protection of recruitment areas (critical habitats) during peak breeding periods could be an essential part of management plans. Many sharks could be susceptible to overfishing because of their generally low reproductive potential in many species, small number of offspring, long gestation period, slow growth and late sexual maturity in many species (Castro 1993, Salomon-Aguilar *et al.* 2009). However, some large pelagic sharks can be very abundant in oceanic areas, and widely distributed where important levels of biomass are available. A better understanding of habitats or regions that serve as nurseries should improve shark conservation and management actions (NMFS 2006). Moreover, factors such as the increase in fishing effort and the degradation of important nursery grounds in coastal, estuaries, and fresh-water habitats contribute to a decrease in populations (Camhi *et al.* 1998, Stone *et al.* 1998).

The shortfin mako *Isurus oxyrinchus* (SMA) is a large pelagic and highly migratory shark species with a tendency to follow the poleward movements of warm water during the summer seasons in the extreme northern and southern parts of its range. This species is distributed circumglobally in tropical, subtropical and temperate seas (Compagno 1984) with a preference range described between 17º-22ºC. Horizontal migrations of Atlantic SMA have been described from conventional tagging-recapture information recorded since the 1960s (Kolher *et al.* 2002, Anon. 2017). However, most of the tagging programs have been developed in relatively restricted geographical areas. These sharks are solitary and can move at high speed and are extremely active. They are distributed mainly from the surface to depths of 450m, although dives down to 888m have been noted. No clear pattern in horizontal movements has been observed so far among all fish tracked with electronic devices with the exception of an inshore trend around the beginning of the austral winter (Abascal *et al.* 2011). This species is frequently taken and reported by commercial fisheries mainly as bycatch of tunas and swordfish longlining, but coastal gillnets and many other coastal-artisanal fisheries can be relatively important in some countries. This species is also a very important targeted species in game-fishing and recreational fisheries in coastal areas of some countries (Casey and Kohler 1992, Pepperell 1992).

Aplacental viviparity with oophagy was described (a form of intrauterine cannibalism whereby the embryos in the uterus feed on other eggs produced by the mother) (Snelson *et al.* 2008). A seasonal analysis of the index of the expansion of the uterus and of the gonado-somatic index of pregnant and postpartum females indicated a gestation period of 15 to 18 months (Mollet *et al.* 2000, 2002). Parturitions were previously described from the end of the winter to spring in both hemispheres, and could extend up to summer. The assumed reproductive cycle so far is three years (Duffy and Francis 2001, Mollet *et al.* 2000, Anon. 2017) but high uncertainty exists regarding a likely shorter period (Anon. 2018) considering the reproductive strategy of other neighboring species of the same family, such as the porbeagle, which is less reproductive, geographically restricted to cold waters and in lower abundance.

For the stock assessment of shortfin mako, sex-specific maturity size is necessary to estimate the maturity at size and later at age of each sex and furthermore, the productivity of this population. Taking into consideration the scientific recommendations of ICCAT and other tRFMO, this study aims to provide new biological information and documents surrounding the reproductive biology of female shortfin mako based on the observations carried out in the Spanish longline fishery, targeting swordfish across oceans.

2. Material and methods

Biological observations of shortfin mako *Isurus oxyrinchus* (SMA) were conducted with standardized criteria on board commercial surface longliners targeting swordfish (*Xiphias gladius*) in different zones of the Atlantic, Pacific and Indian oceans where the Spanish surface longline fleet fished over the 1993-2019 period. The records were obtained and provided in the framework of a research activity kept over a long period of time. Many of the observations are from areas where commercial fishing activity is unusual or minor and the data was obtained during prospecting surveys in those particular cases. The records were initially grouped into of 5°x5° areas (years combined) by ocean. The months in which these observations were made in each hemisphere have also been considered. Capture dates for fish were combined on a single time scale basis in respective seasons. Seasons were divided into four periods of equal length (North Hemisphere= winter: January, February, March; spring: April, May, June; summer: July, August, September; autumn: October, November, December. South Hemisphere: the opposite). The sea surface temperature (SST) of observations has also been taken in °C.

The length of SMA individuals and of the embryos found in pregnant females was measured in a straight line to the nearest centimeter from the furthermost part of the head to the fork in the caudal fin -fork length (FL cm)- which is generally accepted and recommended as the standard size. The FL of the individuals observed was subsequently grouped into 5cm classes. The FL of the embryos was analyzed using 1cm length classes. In both cases, the length classes were defined by using their respective lower limits.

The sex of the individuals was visually identified according to the presence (M: males) or absence (F: females) of claspers in the pelvic fin. Special care was taken when observing juveniles and embryos, since at first sight young males may be erroneously identified as females as their claspers may not go beyond the further edge of the pelvic fin. When the sex was not identified it was then catalogued as unknown (Unk).

Most identified females could be specifically analyzed in order to detect the presence or absence of internal fertilization signs (females in very early pregnancy with blastodisc and nutritive eggs were not taken into consideration). The internal fertilization signs in females were defined in this case by the internal detection of fetuses (so-called "embryos") in the uteri, in which case they were classified as pregnant females (*F_Pre*). When embryos were found, the litter size was counted and/or measured in order to estimate their degree of development. The average values of the number of embryos per female (litter size) were calculated, as well as the average length (FL cm) of the embryos found per female when possible. The embryos were sexed and counted by uterus on some occasions and their development categorized as early (E), mid (M) and near-term (T) litters as having embryo sizes between 0 to 39cm, 40 to 54cm and 55+cm FL, respectively.

Overall sex-ratios of individuals observed were calculated as the percentage of females present with regard to the total number sexed. Sex-ratios were obtained for all sizes combined -overall sex ratio (SRo)- as well as by length classes -sex ratio at size (SRs)- including in the last case their respective confidence intervals (Restrepo 1999).

Catches per unit of nominal effort (CPUE) were calculated per thousand hooks, by sex and by sexes combined (M+F+Unk), both in kg dressed weight -DW- (CPUEw) and in number of fish (CPUE#) as well as for size-FL categories: 60-115cm, 120-175cm, 180-245cm and large adults 250+cm.

3. Results

Observations of SMA took place in the Atlantic, Indian and Pacific oceans within a broad geographical range during the period 1993-2019 (**Figure 1**). Zones with the highest number of observations did not match the regular commercial fishing areas of this fishery especially in the Indian and Pacific oceans cases because many observations were recovered from prospective fishing activities.

3.1. Whole oceans

The total number of SMA observed in the whole oceans was 42,961 individuals -19,905 females; 22,152 males and 904 unidentified (Unk)- (**Table 1**). The broad range of SST observed was from 12.7° to 31.5°C.

The FL range for all SMA sampled was from 60-360cm for years and oceans combined (**Figure 2**). The frequency by size class observed per year for all the oceans as a whole is presented (**Table 2**). A total of 708 individuals considered neonates (FL≤75cm) were recorded (N= 140, 164 and 404 individuals in the Atlantic,

Indian and Pacific oceans, respectively). No conclusions about trends over time in each ocean should be drawn given that most size data from some years pertain only to specific ocean/s. The length range (FL) by sex went from 60-360cm for females and 60-320cm for males (**Figure 2**). The cumulative-relative length frequency for all the combined years and oceans by sex and combined sexes is also shown (**Figure 3**). Roughly 50% of the overall individuals recorded FL measured, ≤150cm, ≤145cm and ≤160cm for the sex combined, females and males, respectively. In general, the captured specimens (males and females) in the oceans mentioned proved to be predominantly immature (pre-reproductive).

The overall SRo obtained for all the oceans was 47.3% of females (**Table 3**). The SRo by square and ocean is shown in **Figure 4**. The SRs pattern for all of the oceans combined shows similar proportions between sexes at least for sizes smaller than 180cm FL. But a lowered percentage of females is observed from 180cm FL to 265cm FL, whereas from 265cm FL upwards females outnumber males with males rarely being encountered in this size range (**Figure 5**). These SRs patterns are affected by the temporal variability of SRs and were not assessed in the present analysis.

A total of 19,905 females were specifically observed to identify their internal signs of fertilization. The results showed that 99.5% of the females observed exhibited no embryos and in only 0.5% of those females (92 observations of *F_Pre*) were embryos identified (**Table 3**). The minimum, maximum and average FL observed of the pregnant females was 250cm, 340cm and 294.0cm (CI90%:±4.18), respectively. Due to the low number of pregnant females, it was not possible to make an estimation of the size of first sexual maturity in the populations by means of traditional methods. Nonetheless, the cumulative percentage of *F_Pre* for all the oceans combined indicates that approximately 50% of them measured less than 290cm FL (**Figure 6**). Taking into consideration that females with embryos are observed from 250cm FL upwards, it can be deduced that the percentage of potentially reproductive females only represented 3.1% of all females specifically analyzed.

Reproductive parameters of sharks are regularly taken as the age at first breeding or as the age at maturity. Conventionally, age at first breeding is obtained at maturity by adding one year to the age in order to calculate an approximation for the gestation period (Cortés 2016). However, a shorter time period should be considered in this species between size at maturity and size at first breeding. The description between size and reproduction has been established in the present paper based on the presence or absence of litters in different stages of development, including the highly developed pups. Therefore, the size at maturity and size at first breeding should be understood as very close concepts in the present paper.

A total of 1,071 embryos were observed in those 92 pregnant females. The average litter size was 11.6 embryos per pregnant female (CI90%:±0.43). A minimum number of 3 embryos per litter was observed in a female of 310cm FL and a maximum of 17 embryos per litter in a female of 313cm FL (**Table 4**). The linear fit between corresponding litter size and *F_Pre* length proved to be very weak (y= 0.033x+1.9198, r^2= 0.11) suggesting, based on the present data, a weak or a lack of significant correlation between litter size and the length of each pregnant female, although it would appear to have a seemingly better fit when the relationship between average litter size by size classes of the pregnant females is presented (**Figure 7**).

The size of the embryos was measured in 90 specimens *F_Pre*. The average size of the observed embryos was 51.6cm FL (CI90%:±2.28) for all the oceans combined (**Table 4**). The minimum size of embryo observed was 14cm (in a female of 320cm) and a maximum of 75cm (in females of 318cm and 323cm). **Figure 8** shows the average size of the embryos related to the size classes of pregnant females *F_Pre*. **Table 5** contains a summary of the average number and length of embryos with their respective confidence intervals (CI90%) per length class of the pregnant females.

Taking into consideration all the years analyzed, the females with embryos have appeared in both hemispheres between the months of April and December. No female with embryos was found between the months of January and March. In the Northern Hemisphere, from April to December, 18 pregnant females were found, 8 of which with early-term embryos (April, August and December), 9 with mid-term embryos (April, June, July and August) and one female with near-term embryos (June). In the Southern Hemisphere, between the months of May and December, 72 pregnant females were found, 6 of which with early-term embryos (May, August, September, October and November), 28 with mid-term embryos (July, August, September, October and November) as well as 38 females with near-term embryos (July, August, September, October, November and December) (**Table 6**, **Figure 9**).

Additionally, in 89 specimens *F_Pre*, it was possible to identify the sex of 1,032 embryos analyzed. The average number was 6.1 (CI90%:±0.33%) of male embryos and 5.5 (CI90%:±0.34%) of female embryos. The average number of male and female embryos by size class of *F_Pre,* in all oceans, is shown in **Figure 10**. The overall sex-ratio obtained for the total of embryos sexed was 47.7% for females (540 males and 492 females), representing a similar proportion to the results obtained in the total amount of the population analyzed (**Table 4**).

It was also possible to count a total of 262 and 263 embryos found in the right and left uterus respectively, in a total of 47 *F_Pre*. The range of embryos found per uterus was from 0 to 10 (right uterus) and 1 to 9 (left uterus). The average number of embryos found per uterus in both the right and left was 5.6 pups (CI90%:±0.50% and ±0.39%, respectively) (**Table 7**, **Figure 11**).

The range of sea surface temperatures (SST), where all SMA individuals were observed, was from 12.7° to 31.5°C. Taking into consideration only the adults of the population (the reproductive fraction by sex), the SST ranges from 15.2° to 31.2°C and 12.7° to 31.5°C observed for females ≥250cm FL and for males ≥180cm FL (Francis and Duffy 2005), respectively. A narrower range from 16.5° to 28.5°C was observed when only the pregnant female fraction with embryos was considered.

Only a weak correlation was found between the SST and the pregnant females (y= -0.0403x+33.678, r^2=0.12). Neither was a correlation found between the SST and the distribution of male adults (y= -0.0121x+24.283, r^2=0.0082). Nonetheless, the data suggests a correlation between the SST and the average size of the embryos, which appears to indicate that the lower the SST, the greater the average size of the embryos found (y= -0.1413x+29.235, r^2=0.46). The surface temperature in which the small specimens (≤120cm FL) appear distributed would be similar to that of the rest of population as a whole within each ocean. No correlation was found between the SST and the presence of these small specimens (y= 0.0008x+19.284, r^2=3E^{-05}).

The CPUE in number of fish by square (5°x5°) of small individuals has been plotted for identifying possible areas of concentration of small specimens (**Figure 9**). The resulting CPUE# and CPUEw for all the individuals sampled by sex and total are shown (**Table 8**). Considerably higher values were obtained in the Pacific areas sampled than in other oceans-areas observed. An average yield of 2 specimens (78.9kg DW) per thousand hooks was obtained from all the oceans analyzed, which would support previous descriptions from this surface long-line fishing fleet, which generally fish in open ocean areas, regarding the relatively low prevalence of this species.

3.2. Atlantic Ocean

37% of the total observations recorded during the period 1993-2015 and 2017-2018 were found in the Atlantic Ocean. A total of 15,962 specimens - 8,022 females; 7,786 males and 154 unidentified (Unk)- were recorded (**Table 1**).

The length range (FL) for all SMA sampled in the Atlantic Ocean for years combined went from 60 to 320cm. The length range (FL) obtained by sex was 60-320cm for females and 60-295cm for males (**Figure 2**) with similar overall length frequency distributions for both sexes. The average size for sexes combined was 145.0cm FL (CI90%:±0.46). The average size for females was 143.9cm FL (CI90%:±0.64) and 147.3cm FL for males (CI90%:±0.65). The cumulative-relative length frequency for all the combined years by sex shows that roughly 50% of females measured ≤135cm FL and 50% of males ≤140cm FL. 50% of the overall specimens observed measured ≤140cm FL (**Figure 3**).

The overall SRo obtained for the Atlantic Ocean of 50.7% females did not differ significantly from 1:1 (*p*=0.06161) (**Table 3**, **Figure 4**). The SRs pattern shows similar proportions between sexes for sizes smaller than 175cm FL. From 175cm FL upwards to 250cm FL a lowered percentage of females is observed, whereas from 250 cm FL upwards females become once predominant (**Figure 5**).

A total of 8,022 females were specifically observed in the Atlantic Ocean to identify internal signs of fertilization (presence or absence of embryos). The results indicated that only 22 females (0.3%) showed embryos (**Table 3**). In the North Atlantic, pregnant females were found between April and December, 7 of which with early-term embryos (April, June, August and December), 8 with mid-term embryos (April, June, July and August) and one female with near-term embryos (June), with overlapping of different stages of development in the embryos being observed during the northern spring and summer. In the South Atlantic, 1 pregnant female was observed with mid-term embryos (August) and 4 with near-term embryos (October and December) (**Table 6**, **Figure 9**).

The minimum, maximum and average length observed of the pregnant females was 250cm, 320cm and 270.1cm FL (CI90%:±5.39), respectively. The cumulative percentage of *F_Pre* approximately shows that 50% of those females measured less than 265cm FL (**Figure 6**).

A total of 243 embryos were observed in 22 pregnant females in the Atlantic Ocean. The average litter size was 11.0 embryos per female (CI90%:±0.90). A minimum number of 5 embryos per litter were observed in a female of 272 cm FL and a maximum of 14 embryos was observed in two females of 283 and 295 cm FL (**Table 4**). It was also possible to measure the size of embryos in 21 pregnant females. The average embryo length was 44.0cm FL (CI90%:±5.22) (**Tables 4** and **6**). The minimum and maximum FL of embryos observed were 14cm and 66cm, respectively.

A number of 20 *F_Pre* were sampled in order to determine the sex of the embryos. The average number of male and female embryos per litter was 5.3 (CI90%:±0.67%) and 5.6 (CI90%:±0.66), respectively. The total number of embryos sexed was 219, 106 males and 113 females. The sex-ratio obtained was 51.6% female, but no significant differences from 1:1 (*p*=0.6852) were achieved (**Table 4, Figure 12**).

The number of embryos found in the right and left uterus in a total of 11 females *F_Pre* resulted in a total of 54 embryos in the right uterus and 61 embryos in the left uterus. The range of embryos found per uterus was from 0 to 8 (right uterus) and 2 to 7 (left uterus). The average number of embryos found in the right uterus was 4.9 (CI90%:±1.05%) and in the left uterus 5.6 (CI90%:±0.68%) (**Table 7, Figure 12**).

All SMA individuals observed in the Atlantic Ocean were found in a very broad SST range from 14.0° to 30.5°C. Similar SST ranges of 15.2°-28.6°C and 15.6°-29.9°C were found for adults in both the NW ($\geq$30°W) and NE (<30°W) Atlantic areas, respectively. However, for the South Atlantic the SST ranges were slightly narrower than for the North Atlantic. In the SE areas (<20°W) SST ranges of 17.6°-28.2°C and 15.4°-29.1°C were found for adult females and males, respectively; while in the SW areas ($\geq$20°W) ranges 19.3°-28.9°C and 17.9°-29.1°C were found for female and male adults, respectively. However, pregnant females were found in narrower SST ranges of 25.2°-26.0°C and 22.8°-28.5°C in the NW ($\geq$30°W) and NE (<30°W) Atlantic areas, respectively. Wider SST ranges in the South Atlantic areas of 19.8°-23.5°C and 21.6°-22.9°C were recorded for the presence of pregnant females in the SE (<20°W) and SW ($\geq$20°W) areas, respectively. The SST range for small specimens ($\leq$120cm FL) was from 14.0° to 29.8°C but no correlation between their distribution and the SST was found. The geographical distribution of small individuals is mapped (**Figure 9**).

It was not possible to establish a correlation between the SST and the 22 pregnant females found in the Atlantic. Nonetheless, the data suggested a possible correlation between the SST and the average size of the embryos present in the aforementioned females (y= -0.1299x+31.208, r²=0.62) in that, the lower the SST, the greater the size observed in the embryos. This fact may be of interest as a means to explain the scarce presence of large females, and particularly of pregnant females -especially of those in advanced stages of gestation- in the oceanic areas of the Atlantic, where a large amount of fishing aimed at tuna and tuna-like species is conducted.

With the above in mind, the overall nominal yield per effort obtained for all the individuals (in number of fish and dressed weight, respectively) was 2.1 fish and 56.9kg DW per thousand hooks. The greatest yields for males, females and combined sexes were obtained mainly of specimens which are more easily accessible to this style of fishing, with sizes of between 120-175cm FL (1.2 fishes, 28.6kg DW per thousand hooks), followed by the size range of 180-245cm FL (0.3 specimens, 20.5kg DW). A low yield was observed for the smallest fishes <120 (0.6 specimens, 5.4kg DW) and the lowest yield was observed in fishes of 250+cm (0.02 specimens, 2.3kg DW) (**Table 9**).

3.3. Indian Ocean

13% of the total observations corresponded to the Indian Ocean with a total number of specimens of 5,673 individuals - 2,550 females; 2,955 males and 168 unidentified (Unk)- observed during the periods 1993-1994 and 1998-2019 (**Table 1**).

The length range (FL) for all SMA sampled in the Indian Ocean for years combined was from 60-325cm. The length range (FL) by sex went from 60-325cm for females and 60-280cm for males (**Figure 2**). Similar overall length frequency distribution for both sexes was found. The average size for sexes combined was 178.0cm FL (CI90%:±0.93). The average size for females was 176.7cm FL (CI90%:±1.4) and 181.7cm FL (CI90%:±1.20) for males. The cumulative-relative length frequency by sex for all years combined shows that roughly 50% of the overall female individuals measured equal to or less than 175cm FL and 50% of males measured less than 185cm FL. For combined sexes this threshold was 180cm FL (**Figure 3**).

The overall SRo obtained for the Indian Ocean was 46.3% of females and was seen to be significantly different to 1:1 (p=0.00000005179) (**Table 3, Figure 4**). The SRs pattern shows similar proportions between sexes for sizes smaller than 180cm FL. However, from this size upwards 260cm FL, the percentage of females is seen to be lowered, becoming once again predominant in sizes over 260cm FL (**Figure 5**).

A total of 2,550 females were specifically observed in the Indian Ocean to identify internal signs of fertilization (presence or absence of embryos). The results showed that only 14 females (0.6%) showed embryos (**Table 3**). In areas situated South of 10ºS, 4 females were found with early-term embryos (June, July, September and October), 9 with mid-term (July, August and September) and 1 with near-term embryos (September) (**Table 6, Figure 9**). Thus, seasonal overlapping in the different stages of embryo development is produced during the austral winter.

The minimum, maximum and average length observed of the pregnant females was 250cm, 305cm and 280.5cm FL (CI90%:±7.20), respectively. The cumulative percentage of *F_Pre* approximately shows that 50% of the females measured were equal to or less than 275cm FL (**Figure 6**).

A total of 159 embryos were observed in 14 pregnant females. The average litter size was 11.4 embryos per female (CI90%:±0.53). A minimum number of 10 embryos per litter was observed in females of sizes of 260, 275 and 281cm FL and a maximum of 13 embryos was observed in females of 280, 290 and 300cm FL (**Table 4**). The size of the embryos of these pregnant females was able to be obtained. The average embryo length observed was 44.9cm FL (CI90%:±4.25) (**Tables 4** and **6**). A minimum and maximum length of embryos observed was 29cm and 63cm FL, respectively. The average of number of embryos found was 6.1 (CI90%:±0.68) and 5.1 (CI90%:±0.57) for male and females, respectively (**Figure 13**). The total number of embryos sexed was 158 (86 males and 72 females). The sex-ratio obtained for those embryos was 45.6% females but no statistical difference was achieved from 1:1 ratio (p=0.301). The range of embryos found per uterus was from 4 to 7 (right uterus) and from 4 to 8 (left uterus). The average number of embryos found in the right uterus was 5.8 (CI90%:±0.80) and 5.6 in the left uterus (CI90%:±1.23) (**Table 7, Figure 13**).

SMA individuals have been observed in a SST range from 12.7º to 31.5ºC. However, the adult specimens observed in the areas of the North Indian Ocean have appeared within a narrow range of SST (27.3º-31.4ºC) with higher values than those observed in other areas of the Indian Ocean, further highlighting the predominant thermal characteristics in the ocean surface system of the North Indian Ocean, whereas in the South Indian Ocean, the data suggested preferential differences in SST ranges according to sex. The males appear to show a preference toward SST from 12.7º to 31.5ºC, while the adult females appear to prefer SST 17.2º to 31.2ºC. For pregnant females the SST range was 18.1º-25.5ºC. The range of SST found for small specimens (≤120cm FL) was 12.7º-29.5ºC. Nevertheless, no correlation was found between their distribution and the SST. **Figure 9** shows the distribution of these small individuals.

A rather weak correlation was found between the SST and the 14 pregnant females observed (y= -0.0691x+40.274, r^2=0.29). Notwithstanding, the data does however suggest that the lower the SST, the greater the size of the embryos (y= -01727x+28.634, r^2=0.64).

An overall nominal yield of 1.0 individuals and 46.8kg DW per thousand hooks, in number and weight respectively, was obtained. The greatest yields of males and females were obtained in the size range of 180-245cm FL (0.5 specimen and 31.6kg DW). The lowest yield was found in the smallest specimens (0.1 individuals and 0.5kg DW) (**Table 9**).

3.4. Pacific Ocean

50% of the available observations of the present study belong to the Pacific Ocean with a total number of 21,326 individuals - 9,333 females; 11,411 males and 582 unidentified (Unk)- recorded during the period 1998-2019 (**Table 1**).

The length range (FL) for all SMA sampled in the Pacific Ocean for years combined went from 60-360cm. The length range (FL) by sex went from 60-360cm for females and to 60-320cm for males, with slight differences by sex in the frequency distribution between the 175-255cm size classes (**Figure 2**). The average size for sexes combined was 159.0cm FL (CI90%:±0.58). The average size for females was 151.5cm FL (CI90%:±0.88) and 167.3cm FL (CI90%:±0.78) for males. The cumulative-relative length frequency for all the combined years by sex and combined sexes shows that roughly 50% of the overall female individuals observed in the Pacific measured less than 145cm FL and 50% of the males observed were ≤165cm FL (**Figure 3**).

The overall SRo obtained was 45.0% female (**Table 3**, **Figure 4**) showing a significant difference from 1:1 ($p=$ 2.2E^{-16}) (**Table 3**, **Figure 4**). The SRs pattern by size class shows similar proportions between sexes for sizes smaller than 170cm FL. From this size upwards to 275cm FL, the percentage of females is seen to be lowered, becoming once again predominant in class sizes over 275cm FL (**Figure 5**).

A total of 9,333 females were specifically observed in the Pacific Ocean to identify internal signs of fertilization (presence or absence of embryos). The results showed that only 56 females (0.6%) showed embryos (**Table 3**). In the North Pacific, 1 pregnant female was found with early-term embryos (December) and 1 with mid-term embryos (December). In the South Pacific, the pregnant females appeared between May and December, 2 with early-term embryos (May and November), 18 mid-term (from August to November) and 33 with near-term embryos (from July to December) (**Table 6**, **Figure 9**).

The minimum, maximum and average length observed of the pregnant females was 264cm, 340cm and 307.2cm FL (CI90%:±4.29), respectively. The cumulative percentage of F_Pre approximately shows that 50% measured less than 305cm FL (**Figure 6**). However, a lower FLMat$_{50\%}$ value (FLMat$_{50\%}$= 254cm, equivalent to PCLMat$_{50\%}$= 233cm) was assumed in the assessment of the North Pacific stock (Anon. 2018) based on previous studies of different authors as well as on the value assumed in the North Atlantic stock assessment (Anon. 2017). The higher values found in this study may be due to the availability of samples in the areas surveyed in the Pacific.

A total of 669 embryos were observed in 56 pregnant females. The average litter size was 11.9 embryos per female (CI90%:±0.58). A minimum number of 3 embryos per litter was observed in female sizes 310cm FL and a maximum of 17 embryos was observed in females of 313cm FL (**Table 4**).

The size of the embryos of 55 specimens F_Pre could be obtained, with an average embryo length of 56.3cm FL (CI90%:±2.51) (**Tables 4** and **6**). A minimum size of 33cm was obtained for those embryos, and a maximum size of 75cm. The sex of the embryos was obtained in 55 F_Pre individuals. The average size of male embryos was 6.3cm FL (CI90%:±0.44%) and that of female embryos was 5.6cm FL (CI90%:±0.48) (**Figure 14**). The total number of embryos sexed was 655; 348 males and 307 females. The sex-ratio obtained was 46.9% female, although it was not seen to be statistically different to 1:1 ($p=0.1181$).

In a total of 31 $F\_Pre,$ the number of embryos found in the right and left uterus was recorded, resulting in a total of 179 and 174 embryos in the right and left uteruses, respectively. The range of embryos found per uterus was from 0 to 10 (right uterus) and 1 to 9 (left uterus). The mean number of embryos found in the right uterus was 5.8 (CI90%:±0.65%) and 5.4 in the left uterus (CI90%:±0.52) (**Table 7, Figure 14**).

The SST range in Pacific areas for SMA individuals was from 14.8° to 29.8°C. In the North Pacific, the choice of SST observed in the adult specimens was seen to be higher for the males (16.8°-29.4°C) as well as for the females (19.8°-28.7°C) in relation to those observed in the South Pacific (males: 14.8°-26.7°C, females: 15.2°-26.0°C). Pregnant females were observed in the North Pacific with a narrower SST range (21.4°-23.8°C) than in the South Pacific (16.5°-24.0°C). The range of SST in which the small specimens ($\leq$120cm FL) appear distributed was between 16.8°-28.3°C in the North Pacific and 15.0°-25.2°C in South Pacific areas, but no correlation between SST and their distribution was found (**Figure 9**). Neither was a correlation between the SST and the 56 pregnant females found (y= 0.0268x+12.438, r^2=0.09). Nevertheless, a moderate correlation between the SST and the average size of the embryos was able to be established (y= -0.0951x+26.061, r^2=0.41) in that, the lower the SST, the larger the size of the embryos.

The nominal yields obtained in the Pacific, for both males and females, doubled those obtained in other oceans. For all individuals caught, the nominal yield obtained in number and weight was 3.4 individuals and 136.0 kg DW per thousand hooks. The greatest yield in weight was mainly obtained in the size range 180-245cm FL (1.1 specimens and 78.5kg DW). The lowest yield was obtained in the smallest-sized specimens <120cm FL (0.8 specimens and 5.1kg DW) and in the largest sized 250+cm (0.13 specimens and 19.4kg DW) (**Table 9**).

4. General conclusions and discussion

Important differences in length by sex and sexes combined were observed among the three oceans with very different size frequency distributions of specimens -small or large-. It was possible to distinguish some clear modal classes in some oceans for juvenile individuals probably representing individuals of the zero-, one- or

two-year old classes (**Figure 2**). The maximum size for male and female specimens in this study by ocean was 295cm and 320cm FL from the Atlantic, 280cm and 325cm FL from the Indian, and 320cm and 360cm FL from the Pacific; respectively. Individuals over 300cm FL were extremely rare in our observations. A total of 708 neonate individuals ($\leq$75cm FL) were observed (N=140, 164 and 404 in the Atlantic, Indian and Pacific oceans, respectively). The comparison in the distribution of size frequency in the three oceans for combined sexes shows a greater difference within the Indian Ocean compared to that found in the other two oceans analyzed. Individuals are distributed largely around 180cm in the Indian Ocean, whereas in the Atlantic and Pacific oceans the individuals are mainly distributed around 140cm and 155cm FL, respectively. However, the total size range is approximately the same in the three oceans as a whole, suggesting that the main factor for those size differences is mainly due to the respective availability of the different fractions of each stock in each ocean areas sampled, rather than caused by gear selectivity (**Figure 15**).

Cumulative percentages of the respective length-frequency distribution facilitate the comparisons among oceans and sexes, with females appearing more predominant in the Atlantic Ocean with the largest amount of small individuals observed for sizes $\leq$135cm FL (50%), as well as in the Pacific Ocean for sizes $\leq$145cm FL (50%), while in the Indian Ocean 50% of females were $\leq$175cm. 50% of males in the Atlantic and Pacific oceans were <140cm and $\leq$165cm FL respectively, while in the Indian Ocean they were <185cm FL (**Figure 16**). The size structure difference between sexes in the present paper, with regard to the proportion of individuals in each class (SRs) demonstrates a highly probable size threshold of sexual dimorphism growth and additionally, that females regularly reach larger maximum sizes than males (Barreto *et al.* 2016, Bishop *et al.* 2006).

The SRo values presented slight differences between oceans (50.7%, 46.3% and 45.0% females, for the Atlantic, Indian and Pacific oceans, respectively). The SRo obtained for the Atlantic Ocean did not appear to be significantly different to the 1:1 ratio yet was seen to be significantly different in the Indian and Pacific oceans, suggesting that in the latter cases males were moderately yet significantly more predominant in the surveys conducted in these areas, at least as far as availability and interaction with this fishing style is concerned. The SRo data per square area and ocean indicate a predominance of males in the square areas of the South Atlantic far from the continental limits, likewise in the Indian Ocean (**Figure 4**). A larger predominance of males is observed in square areas of the South West Pacific Ocean, again far from continental limits. This male predominance may suggest areas which are more likely to be mating grounds. However, the sex-ratio changes by size and SRo values can be affected by the size range observed in each case, therefore any possible conclusion should be contextualized.

The SRs values among oceans bear common similarities. Both male and female specimens appear in similar proportions in all oceans up to approximately a size of 175cm FL. This would suggest that a significant differential growth rate according to sex would unlikely appear up until approximately this size or thereabouts. In this respect, we should bear in mind the fact that the size of first maturity described for males would be around 180cm FL (Francis and Duffy 2005) and that this value would be consistent with the possible initial stage of differential development between both sexes, which would be reflected in SRs values. From 175cm FL upwards, the male percentage increases as size increases, probably because of an accumulation of several male ages within very narrow size ranges, with males of sizes > 250cm FL tending to disappear in the Atlantic Ocean, and the SRs changing towards a predominance of females beyond that size, which is consistent with the previously described "*after up to approximately 240cm FL*" (Casey and Kohler 1992). In the case of the Indian and Pacific areas, males almost disappear in catches at around 260 and 275cm FL, respectively, suggesting FL_{max} around those values, where upward sizes show female predominance (**Figure 5**). The increase in the proportion of males in relation to females in certain size ranges and areas has also been described for the North East Atlantic (Mejuto and Garcés 1984). The aforementioned authors described sex-ratios per size for SMA showing a progressive increase in the percentage of males for sizes greater than 170cm FL and more specifically for sizes 200-280cm FL, reaching values of over 80% in the male population in temperate areas between the Iberian Peninsula and the Azores archipelago. Individuals of this species (juveniles, adult females and males) segregate by size and sex several times during their life span (Kohler *et al.* 2002). The distribution of juvenile specimens $\leq$120cm FL, which would include neonates and recruit individuals, is shown along with the location of the pregnant females (**Figure 9**).

Most females observed in all oceans exhibited no signs of fertilization (99.5%) based on the presence of very visible embryos. The sizes of the females in which embryos were seen to be present were $\geq$250cm FL for each of the oceans analyzed. These sizes are similar to those described by other authors who cite mature females at 278cm TL (Joung and Hsu 2005) equivalent to 256cm FL or 254cm FL. A size at maturity for female shortfin makos at 280cm TL (Stevens 1983) was also described and equivalent to 258cm FL or 256cm FL. A median size

at maturity of females from the western North Atlantic was reported at 272 or 275cm FL, larger than that of females of 249 or 252cm FL from the southern hemisphere (Mollet *et al.* 2000) (according to conversions made by Casey and Kohler (1992) or Francis and Duffy (2005), respectively).

The smallest size obtained in this present study, in which pregnant females appeared, was 250cm FL. While this value is not an indicator "*per se*" of the average size of first maturity (FLMat$_{50\%}$), it does however coincide with the size at which the *maximun ovum diameter* began increasing (Francis and Duffy 2005). Our mean maturity size in females was at 270.1cm and 280.5cm FL in the Atlantic and Indian oceans. These results are very consistent with the 275cm FL at which rapid uterus expansion began (Francis and Duffy 2005) and are also similar to the median maturity obtained in New Zealand females (275-285cm FL) (Francis and Duffy 2005). The mean maturity size observed for females in the Pacific was 307.2cm FL, higher than that observed in the Atlantic and Indian oceans and also previously reported for this ocean. However, the smallest female in which embryos were found in the Pacific was 260cm FL -similar to what was observed in the Atlantic and Indian oceans- and the mean size of the embryos observed in this case were already 56.3cm FL. The limited access to many areas of the Pacific may have affected the representativeness of the samples analyzed in the present paper and of the mean value obtained for the Pacific. Notwithstanding, based on studies by other authors, it would be plausible to suggest a mean maturity size of approximately 260cm FL or even lower (Anon. 2018) which would be similar to that described for the Atlantic and Indian oceans. The frequency of gathered sizes for those females which presented embryos, were seen to be different according to the ocean. 50% of pregnant females gathered in rather smaller sizes compared to those of the Atlantic (265cm FL) and to those of Indian Ocean (275cm FL) in relation to those observed in the Pacific (305cm FL) (**Figure 6**).

The presence of potentially reproductive females in the observations conducted by this surface longline fishery was approximately 3% of all females found and 0.5% of females in reproduction-gestation stages, which represents a rather low incidence for this fishery both for adult females as well as for the percentage in gestation. The data suggests that, as in other species of the same family, the scarcity of pregnant females may be explained by the spatial separation of those females from other individuals during pregnancy and parturition, which should not be considered unusual in this species and other taxonomically close-related species. The some mature female tracked using electronic devices over multiple years showed high fidelity to some areas within national EEZ suggesting the possible selection of these areas as parturition grounds (Gibson *et al.* 2021). In addition to the characteristic biological processes and migrations regularly described for these types of species (feeding, reproduction: mating, fertilization, pregnancy, parturition), an additional and ancestral factor must be also considered, and this is the instinct of protection of the offspring which has been consolidated during millions of years from the reproductive behaviour of their extinct ancestors. Many of these shark species seek highly productive areas for the development of the pups while searching for safe places for gestation-parturition far from possible predators, including those of their own species. Therefore, the rare presence of females in gestation processes in the oceanic areas inferred in the present document, and also in other descriptions, should not be considered as a rare case in this and other shark species with the same or similar reproductive strategy.

Our review of reproductive data showed that SMA females have similar reproductive characteristics in all oceans with similar average litter sizes. The mean litter size of 11.6 pups was much larger than the obtained for other lamnidae species -4 embryos in longfin mako (Compagno 1984), 8.9 in great white shark (Francis 1996), between 2-5 in porbeagle, (Francis and Stevens 2000)-. These results would indicate the high fecundity of litter of this species compared to other closely related lamnidae species. However, some literature indicates and assumes that this species reproduces every 3 years (three-year reproductive cycle) which is not consistent with the two-year reproductive cycle described in other taxonomically closely related yet less abundant species, geographically very restricted to cold waters and with slower growth. Bearing these factors in mind, further studies should be conducted in order to verify the reproductive cycle of SMA. This parameter was discussed in the North Pacific stock assessments case (Anon. 2018) because it is critically important to estimate the correct units of spawning potential in some models and in that case a two-year cycle was assumed as the most likely base case.

The majority of the embryos measured were near-term (43.3%) and mid-term (42.2%). Only 14.4% were early-term embryos. In addition, in the three oceans 24 embryos were sampled of similar size or larger than the smallest free-swimming makos recorded at 63cm FL in the Tuna Longline Database (Duffy and Francis 2010) (**Table 6**). The SRo of the embryos also presented slight differences between oceans but were regarded statistically as not significant differences (51.6%, 45.6% and 46.9% for the Atlantic, Indian and Pacific oceans, respectively).

SST preferences for the total amount of the populations analyzed proved to be very wide. Similar ranges of SST were found in the Atlantic and Pacific oceans, but differed from those found in the Indian Ocean. Different ranges of SST also became apparent in the case of pregnant females. Of particular interest is the high SST in which adult specimens are distributed in areas of the North Indian Ocean (27.3º-31.5ºC) in whose waters no females with embryos have been found. In all cases, the distribution of females with embryos has shown a narrower range of SST than the population as a whole.

The relationship obtained between the SST and the pregnant females has been very weak. On the other hand however, a correlation has been found between the mean size of the embryos and the SST. The lower the SST, the greater the size of embryos observed. It was not possible to find any correlation of the SST with the distribution of small individuals or adult males.

For the total number of years observed, no females with embryos have appeared between the months of January and March in either of the two hemispheres. The females sampled during the first quarter of the year did not present embryos. While they may have presented fertilized eggs, in no case has this information been taken.

A gestation period longer than one year has been previously suggested for this species (Mollet *et al.* 2000). The assumed gestation period of 15-24 months (19 for the line) was suggested from the relationship between embryo length and time of capture. But considering the gestation period, they obtained several slopes taking into consideration 70cm TL for the size-at-birth and concluded that the gestation was around 18 months based on a significant regression with a slope of 3.8cm/month (SE=0.6, n=23). Assuming equally a period of gestation of 18 months we have applied 3.42cm/month as slope for 63cm FL size-at-birth. For the combined data and regardless of the hemisphere considered, the results would indicate that parturition mainly could occur in spring (44.4%) but also in summer (26.7%), autumn (14.4%) and winter (14.4%). Assuming a gestation in excess of 24 months (slope 2.64cm/month) parturition would again mainly occur in spring (34.4%), summer (27.8%), autumn (23.3%) and winter (14.4%). Finally, assuming a gestation of 15 months the parturition would be in spring (50.0%), summer (24.4%), winter (14.4%) and autumn (11.1%).

North Hemisphere: Assuming a period of gestation of 18 months for the North Atlantic Ocean, the parturition would be mainly in autumn (37.5%), followed by spring and winter (25.0%) and summer (12.5%). But differences between eastern and western areas were found. In areas of the North Atlantic at <30ºW, the parturition would mainly be in autumn (42.9%), winter and spring (28.6%) and two pregnant females found at ≥30ºW would indicate that the parturition would be in summer (100%). For the North Pacific Ocean at <180ºE the parturition of two females found with embryos appeared in spring (50%) and summer (50%) (**Table 10**).

South Hemisphere: Assuming the same gestation period (18 months) for the South Atlantic areas at <20ºW the parturition would mainly be in spring (66.7%) and some females would give birth in summer (33.3%). At areas ≥20ºW it would be in spring (100%). Additionally, in S/SW Brazil four pregnant females were found that would give birth in late winter to spring (Costa *et al.* 1995). For the South Pacific Ocean at areas <180ºE the parturition would mainly occur in spring (72.7%), in winter (18.2%) and summer (9.1%). At areas <180ºW the parturition would be in spring (45.2%), summer (28.6%), autumn (14.3%) and winter (11.9%). In this ocean November (spring) was suggested for parturition at about 70cm TL in embryos found in KwaZulu-Natal (Cliff *et al.* 1990) and, in another two females at 56cm and 59cm TL, embryos were found in New South Wales in July and August (winter), which supported parturition in late winter (Mollet *et al.* 2000). For the South Indian Ocean at areas ≥80ºE, the parturition would occur in summer (66.7%) and in spring (33.3%). At areas <80ºE it would be in summer (37.5%) but also in winter and spring (25.0%) and in autumn (12.5%) (**Table 10**).

In summary, results indicated that for both the North and South Hemisphere the parturition would occur throughout the year, regardless of the gestation period considered. In the present study, the main season for parturition for over 18 months of gestation for the Northern Hemisphere was autumn (33.3%) and spring (48.6%) for the Southern Hemisphere. But the weakness of these types of conclusions should be taken into account in most studies due to the low number of observations regularly available and the low prevalence of pregnant females in general and the fact that the effect of seasonality is very different and generally more evident in temperate or colder waters, but minor or nil in subtropical or inter-tropical areas. Despite the huge amount of observations in the present study the same limitation could be considered above all in the North Hemisphere (18 pregnant females observed with embryos) compared to the South Hemisphere (72 pregnant females observed with embryos). Additionally, considering that the effects of seasonality is very different according to the areas-latitudes observed in each study, an apparently evident seasonality in a temperate geographical area does not necessarily imply that it is applicable to the wide range of distribution of these stocks. Therefore, conclusions achieved from local studies should be taken lightly before suggesting generalizations.

The results of the present study partially concur with those of other authors who indicated that the parturition begins mainly in late winter to mid-spring in both hemispheres (Mollet *et al.* 2000). Despite the largest range of sampling in the present study, it was not possible however to clarify conclusively a restrictive seasonality for the parturition processes but rather it suggests that they could occur throughout the year in any ocean / hemisphere. These parturition processes would depend on the development of the embryos. Yet these pregnant females were able to select and access areas with lower SST, highly productive and adequate for the protection of their litter, taking advantage of the currents of each ocean and opting for areas with a higher or lower proximity to insular coasts or to the respective continents. The present study also would suggest wide areas or zones of parturition in any part of the oceans observed. Perhaps the reproductive females, once pregnant, approach areas close to coastal shores, where the waters are colder, either with island preference over continental, or to upwelling areas in order to carry out parturition so that their young may easily access food given that these are areas rich in nutrients and more adequate for the protection of their litters in coastal habitats.

In the Atlantic Ocean, outwith the main oceanic flow of the great marine surface currents, lie extensive areas influenced by the currents of the Canary Islands and Benguela in the East and by the Brazil Current in the West. Females with near-term embryos have been found both in the West as well as in the East Atlantic. Based on the location in which these females have been found, possible areas for parturition could be suggested in the Northeast Atlantic, which would be located in the areas close to Cape Verde and the Annobón Islands (Equatorial Guinea). In the Southeast Atlantic, possible areas of parturition may be those close to the Penguin Islands (Namibia) and in the South West Atlantic, the Santa Catarina Island (Brazil). The presence of neonate specimens found in areas close to the African and South American coasts would support the aforementioned as possible areas of parturition. In addition, new areas of parturition may be suggested to the south of the Azores and in areas close to the Grand Banks, as well as on continental margins of South Africa where neonate specimens have likewise been found (**Figure 9**).

In the case of the Indian Ocean, the whirlpools formed between the North and South Equatorial drift currents should be borne in mind. In general, the waters richest in nutrients would be found in those areas close to the Australian coast, influenced by the cold West Australian Current, and towards the area of Madagascar, the areas influenced by the Agulhas Current. In southern areas of this ocean, several gravid females in different stages of development were found in square-areas close to the 25ºS-065ºE grid, in which a female with near-term embryos was discovered. In this area the northern section of the Central Indian Ridge should be taken into consideration. Several females in different stages of embryonic development were found in longitudes >80ºE, areas which may be influenced by the submarine volcanic plateau referred to as Broken Ridge. The depths and elevations that these underwater plateaux present should be taken into account as an important characteristic which defines many factors within this ocean, much in the same way as do the characteristic flora and fauna. A wide distribution of neonate specimens were also found in southern areas, which may indicate a rather wide area of parturition in this ocean (**Figure 9**).

In the Pacific Ocean, there is a surprising contrast between the east and west coasts with the numerous adjacent seas, each one with their own special characteristics within the oceanic circulation. One in particular is the Peru Current, where the "El Niño" weather phenomenon causes the Peruvian current to move offshore to deeper seas. In this ocean, in the South Pacific areas, the pregnant females were found below the equatorial upwelling, areas in which the cold sub-superficial areas are rich in nutrients. The extensive area in which females with near-term embryos have appeared would suggest very wide areas of possible parturition, spanning 160ºE-160ºW to the north of New Zealand and including the numerous islands of Melanesia and Polynesia. Other females with near-term embryos found between 80º-130ºW would indicate parturition in the areas surrounding Easter Island and the Salas y Gómez Island and also in areas towards Chile around the Desventuradas Islands and the Islands of Juan Fernández. In this part of the South West Pacific there is the Nazca and Salas y Gomez mid-mountain ridge which represents a biological hotspot that houses a large number and diversity of larvae, where higher primary production rates are estimated than for the surrounding oceans (Gálvez-Larach 2009). The appearance of neonate specimens would support the extensive aforementioned as possible areas of parturition. On the other hand, neonate specimens have been found in the North Pacific, both in the East as well as in the West, which may lead to the supposition of other possible areas of parturition in NE Pacific waters, influenced by the cold Oyashio Current, whose waters may arguably constitute the richest fishing ground due to its exceedingly high content in nutrients and the concentration of phytoplankton in the swirls formed on colliding with the Kuroshio Current, along with another possible area towards the coast of Panama.

This widely cosmopolitan distribution of both females presenting embryos and neonate specimens, would lead to very diverse and extensive areas of parturition being considered in all of the oceans studied, even while those areas may not be the areas frequented by oceanic longline fisheries targeted mainly at tuna and tuna-like species (Liu *et al.* 2018).

On the other hand, the nominal yield in weight proved to be slightly higher for males than for females in the Atlantic Ocean. However, in the Indian and Pacific oceans these yields suggest a predominance of male specimens, where the highest nominal yield in weight and in number of fish caught was for males, which would concur with the SRo obtained. Overall, the mean yield obtained for the three oceans was approximately 2 specimens (78.9kg DW) per thousand hooks. This would support the reason behind the relatively low prevalence described for this species in this surface longline fishery, yet at the same time it would suggest a relatively important biomass of this species in relation to other epipelagic species in all of the oceans analyzed and therefore important annual recruitments could be expected. However, this fleet does not have a relevant impact on neonatal individuals and recruits. The scarce occurrence of pregnant females would indicate that this fishery (while it works with part of the reproductive population) scarcely interacts with the fraction of mature or pregnant females in whichever of the oceans / areas where work is carried out, which could be due to the fact that the shortfin mako prefers temperate water around 18ºC (Casey and Kohler 1992) and/or these large pregnant females are likely to be found outwith the oceanic fishing areas surveyed, distributed in deeper waters, or with the ability to escape and not be retained by the fishing gear.

Acknowledgements

References

Abascal F.J., Quintans, M., Ramos-Cartelle, A. and Mejuto, J. 2011. Movements and environmental preferences of the shortfin mako, *Isurus oxyrinchus*, in the southeastern Pacific Ocean. Mar. Biol. 158, 1175-1184. DOI 10.1007/s00227-011-1639-1.

Anislado-Tolentino, V. and Robinson-Mendoza, C. 2001. Edad y crecimiento del tiburón martillo *Sphyrna lewini* (Griffith y Smith 1834) en el Pacífico central de México. Cienc. Mar. 27(4):501-520.

Anonymous. 2017. Report of the 2017 ICCAT shortfin mako data preparatory meeting (Madrid, Spain 28-31 March 2017). Collect. Vol. Sci. Pap. ICCAT, 74(4): 1373-146.

Anonymous. 2018. Stock Assessment of shortfin mako shark in the North Pacific Ocean Through 2016. WCPFC-SC14-2018/ SA-WP-11: 121pp.

Barreto R.R., de Farias, W.K.T., Andrade, H., Santana, F.M. and Lessa, R. 2016. Age, Growth and Spatial Distribution of the Liefe Stages of the Shorfin Mako, *Isurus oxyrinchus* (Rafinesques, 1810) Caught in the Western and Central Atlantic. PLoS ONE 11(4): e0153062.

Bishop, S., Francis, M., Duffy, C. and Montgomery, J. 2006. Age, growth, maturity, longevity and natural mortality of the shortfin mako shark (*Isurus oxyrinchus*) in New Zealand waters. Marine and Freshwater Research 57, 143–154.

Camhi, M., Fowler, S.L., Musick, J.A., Bräutigam, A. and Fordham, S.V. 1998. Shark and their Relatives: Ecology and conservation. IUCN/SSC Shark Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK, Occasional Paper of species Survival Commission no. 20. 39 pp.

Casey, J.G. and Kohler, N.E. 1992. Tagging studies on the shortfin mako shark *Isurus oxyrinchus* in the Western North Atlantic. Aust. J. Mar. Freshwater Res., 43(1): 45-60.

Castro, J. 1993. The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. Env. Biol. Fish. 38:37-48

Cliff, G., Dudley, S.F.J: and Davis, B. 1990. Sharks caught in the protective gillnets off Natal, South Africa. 3. The shortfin mako, *Isurus oxyrinchus* (Rafinesque). South African Journal of Marine Science 9:1, 115-126.

Compagno, L.J.V. 1984. FAO species catalogue Vol 4. Sharks of the world: An annotated and illustrated catalogue of sharks species known to date. Part 2 - Carcharhiniformes. FAO Fisheries Synopsis, No.125. FAO, Rome, Italy, pp 251-655.

Cortés, E. 2016. Perspectives on the intrinsic rate of population growth. Methods in Ecology and Evolution 2016 7, 1136–1145.

Costa, F.E.S., Braga, F.M.S., Amorin, A.F. and Arfelli, C.A. 1995. Analysis of mako sharks, *Isurus oxyrinchus*, Rafinesque 1809. Resumos VII Reunião do Grupo de Trabalho sobre Pesca e Pesquisa de Tubaröes e Raias do Brasil, Rio Grande, November 20-24, 1995.

Duffy, C. and Francis, M. 2001. Evidence of summer parturition in shortfin mako (*Isurus oxyrinchus*) sharks from New Zealand waters. New Zealand Journal of Marine and Freshwater Research 35, 319–324.

Francis, M.P. 1996. Chapter 15 - Observations on a pregnant white shark with a review of reproductive biology. Pages 157-172. In A.P. Klimley and D.G. Ainley,.editors. Great white sharks: the biology of *Carcharodon carcharias.* Academic Press, Inc. San diego, CA.

Francis, M.P. and Duffy, C. 2005. Length at maturity in three pelagic sharks (*Lamna nasus, Isurus oxyrinchus, and Prionace glauca*) from New Zealand. Fish. Bull. 103:489-500.

Francis, M.P. and Stevens, J.D. 2000. Reproduction, embryonic development, and growth of the porbeagle shark, *Lamna nasus,* in the South West Pacific Ocean. Fish. Bull. 98:41-63.

Gálvez-Larach, M. 2009. Montes submarinos de Nazca y Salas y Gómez: una revisión para el manejo y conservación. Lat. Am. J. Aquat. Res., 37(3): 479-500. DOI: 10.3856/vol37-issue3-fulltext-16.

Gibson, K.J, Streich, M.K., Topping, T.S. and Stunz, G.W. 2021. New insights into the seasonal movement patterns of shortfin mako sharks in the Gulf of Mexico. Front. Mar. Sci. 8:623104. doi: 10.3389/fmars.2021.623104.

Heupel, M., Carlson, J.K. and Simpfendorfer, C. 2007. Shark nursery areas: Concepts, definition, characterization and assumptions. Mar. Ecol. Prog. Ser. 337:287-297.

Joung, S.J. and Hsu, H.H. 2005. Reproduction and embryonic development of the shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, in the Northwestern Pacific. Zoological Studies 44(4): 487-496.

Kohler, N.E., Turner, P.A., Hoey, J.J., Natanson, L.J. and Briggs, R. 2002. Tag and recapture data for three pelagic shark species: blue shark (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*), and porbeagle (*Lamna nasus*) in the North Atlantic Ocean. Collect. Vol. Sci. Pap. ICCAT, 54(4): 1231-1260.

Liu, K-M., Sibagariang, R.D., Joung, S-J. and Wang, S-B. 2018. Age and Growth of the Shortfin Mako Shark in the Southern Indian Ocean. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science10:577–589, 2018.

Mejuto, J. and Garcés, A.G. 1984. Shortfin mako, *Isurus oxyrinchus*, and porbeagle, *Lamna nasus*, associated with longline swordfish fishery in NW and N Spain. ICES, C.M. 1984/G: 72.

Mollet, H.F., Cliff, G., Pratt Jr, H.L. and Stevens, J.D. 2000. Reproductive biology of the female shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, with comments on the embryonic development of lamnoids. Fishery Bulletin, 98: 299-318.

Mollet, H.F., Testi, A.D., Compagno, L.J.V. and Francis, M.P. 2002. Re-identification of a lamnid shark embryo. Fishery Bulletin, 100: 865–875.

NMFS (National Marine Fisheries Service). 2006. SEDAR 11 stock assessment report. Large coastal complex, blacktip, and sandbar shark. NOAA/NMFS Highly Migratory Species Division, Silver Spring, MD.

Pepperell, J.G. 1992. Trends in distribution, species composition and size of sharks caught by gamefish anglers off South-eastern Australia, 1961-90. Aust. J. Mar. Freshwater Res. 43(1): 213-225.

Restrepo, V. 1999. Notes on analyses of sex ratio at size (SRS) for swordfish. Collect. Vol. Sci. Pap. ICCAT 49(1): 381-386.

Salomon-Aguilar C.A., Villavicencio-Garayzar, C.J. and Reyes-Bonilla, H. 2009. Shark breeding grounds and seasons in the Gulf of California: Fishery management and conservation strategy. Ciencias Marinas (2009), 35(4):369-388.

Semba, Y., Aoki, I. and Yokawa, K. 2011. Size at maturity and reproductive traits of shortfin mako, *Isurus oxyrinchus*, in the western and central North Pacific. Marine and Freshwater Research 62(1): 20-29.

Snelson Jr., F.F., Roman, B.L. and Burgess, G.H. 2008. Chapter 3 - The reproductive biology of pelagic elasmobranchs. In: Sharks of the Open Ocean: Biology, Fisheries and Conservation, pages 24-53. Edited by M.D. Camhi, E.K. Pikitch and E.A. Babcock. Blackwell Publishing.Ltd.

Stevens, J.D. 1983. Observations on reproduction in the shortfin mako *Isurus oxyrinchus*. Copeia, 1:126-130.

Stone, R.B., Bailey, C.M., McLaughlin, S.A., Mace, P.M. and Schulze, M.B. 1998. Federal management of US Atlantic shark fisheries. Fish. Res. 39(2): 215-221.

Table 1. Number of *Isurus oxyrinchus* sampled by ocean and sex during the period 1993-2019.

	ATL	IND	PAC	TOTAL
# Females	8022	2550	9333	19905
# Males	7786	2955	11411	22152
#Unk	154	168	582	904
Total	15962	5673	21326	42961

Table 2. Length frequency (FL cm) by size class of *I. oxyrinchus* sampled in all the oceans by year (1993-2006).

Size/Year	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
60			1		5			1	2	1	9	21	4	6
65		1			16		3	3	1	3	20	39	9	19
70		4	1		15		14	13	17	2	28	33	44	25
75		1			10		19	44	67	4	18	46	52	60
80		4	1	1	1	1	62	75	149	14	12	79	51	88
85	1	3	4		1		37	70	289	35	8	67	67	79
90	2	14	7	4	5		37	216	508	77	57	123	96	75
95		4	9	14	6	5	11	90	370	212	86	98	109	27
100	3	2	7	11	5	2	16	53	159	177	289	125	110	16
105	7	8	6	27	5	8	31	26	66	85	515	69	77	24
110	2	5	5	26		10	40	35	56	48	986	47	38	73
115	2	10	1	26		3	48	66	95	21	996	36	13	98
120	5	8	8	17	4	6	52	106	176	15	691	64	19	113
125	4	15	7	21	4	3	26	107	330	45	294	84	38	138
130	2	21	23	36	6	5	28	97	356	81	325	122	77	162
135	3	28	22	52	5	2	32	75	179	93	453	102	81	100
140	12	26	26	55	5	8	86	72	89	92	571	104	84	82
145	12	40	42	57	12	4	74	88	82	61	451	103	70	52
150	23	59	34	82	13	16	98	98	83	58	320	134	101	80
155	20	69	49	82	11	9	48	71	58	43	210	170	121	72
160	14	77	49	104	26	20	41	46	57	53	192	176	127	124
165	24	92	54	77	20	20	51	53	50	45	117	177	113	108
170	41	104	51	96	25	36	46	45	44	46	121	199	140	97
175	40	90	40	71	38	20	64	29	33	36	82	169	119	102
180	28	86	57	64	26	43	55	36	36	34	91	208	143	109
185	37	70	28	47	27	39	73	35	23	23	72	186	129	112
190	22	52	29	46	31	27	58	31	19	27	75	189	147	110
195	25	62	18	35	15	33	71	31	15	17	57	182	152	95
200	30	53	11	34	18	23	58	25	17	11	58	201	180	94
205	19	32	20	27	14	28	60	19	13	10	58	181	134	67
210	21	30	13	31	11	15	55	25	13	11	56	214	153	76
215	14	24	11	16	11	12	40	16	5	15	48	174	128	63
220	16	17	2	18	15	11	46	15	14	12	54	188	148	73
225	8	19	5	19	4	12	32	11	8	7	41	165	126	59
230	11	6	7	7	7	10	18	7	5	6	31	157	130	39
235	5	7	2	13	4	2	23	4	5	7	21	107	122	33
240	8	5	5	2	5	10	13	8	6	2	16	118	112	38
245	2	3	1	3	4	2	12	4	2	1	15	85	79	34
250		2		3		2	11	4	1	3	15	87	66	28
255	2	3		1			2	4		2	13	53	30	8
260	1	2	2			2	3	1	1	1	7	52	26	13
265	3	1		2	1	3	1		1		5	25	18	5
270	1	3	1	2		1	2	1	1		3	16	4	2
275	1			1	2	2	2			4	1	10	5	3
280	1	2	1					1	1	1	2	11	3	2
285	1	2	1				1			2	6	9	1	1
290	1						1				2	10	2	
295		3					1	2		4	1	5	3	5
300		1					2	2		1	2	10	5	2
305		1							1		1	4	1	
310	1											7	1	3
315											1	4	2	1
320							1	1				7	1	1
325							1				1	1		
330												2	2	
335												2		
340												1	1	
345												1	1	
350												1		
355														
360														
Overall Total	475	1171	661	1227	436	457	1606	1859	3505	1547	7604	5060	3815	2896

Table 2 (cont). Length frequency (FL cm) by size class of *I. oxyrinchus* sampled in all the oceans by year (2007-2019) and total (1993-2019).

Size/Year	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	1993-2019
60	1	7		4	3	1					4	3		73
65	3	11	1	14	2	1	1	2		1		1		151
70	2	15	2	109	14	4	4	4	1	1	2	3	4	361
75	8	8	5	3	14	6	16	7	3				1	392
80	15	10	10	1	23	27	24	13	5		1			667
85	16	9	9	1	24	42	35	2	9	1	1		1	811
90	14	8	2	2	34	28	35	1	19	1	2	2		1369
95	12	19	2	3	33	11	18		23		2			1164
100	17	20	5	6	36	9	10		20	1	7			1106
105	15	13	8	3	16	1	5	1	9		12	1	1	1039
110	22	16	19	12	17		10		1	1	21	1	2	1493
115	29	11	31	5	16	8	16		2		23	1		1557
120	69	26	35	14	36	4	47		7		19	1	1	1543
125	71	44	34	6	52	10	65		37		13		1	1449
130	117	43	31	28	82	26	107	5	68	2	6			1856
135	119	34	26	36	79	42	65		68	1	9	3		1709
140	52	51	31	33	61	41	49	2	47	1	17		2	1699
145	55	72	53	27	63	13	17	5	21	1	22	2		1499
150	66	86	82	41	89	14	36	11	28	3	22	3	1	1681
155	61	64	64	25	73	18	45	16	34	13	33	3	3	1485
160	100	67	72	46	105	19	46	28	31	18	38	4	4	1684
165	75	56	72	55	59	27	37	14	43	16	32	13	3	1503
170	72	63	52	49	79	21	46	30	33	20	31	17	8	1612
175	86	32	64	36	71	20	59	40	20	17	29	13	6	1426
180	85	64	67	46	90	20	51	32	22	16	28	19	12	1568
185	59	44	40	29	66	8	46	25	20	20	29	15	8	1310
190	66	62	42	39	85	12	45	28	18	24	29	24	20	1357
195	55	46	44	15	61	7	36	13	9	15	30	11	7	1157
200	54	52	36	19	73	15	36	13	9	19	13	21	11	1184
205	42	30	21	24	56	10	27	17	4	12	12	13	7	957
210	33	31	17	20	48	7	20	11	11	6	15	7	6	956
215	23	24	17	16	43	5	17	10	6	8	7	6	1	760
220	33	26	14	14	45	5	15	9	5	3	6	7	3	814
225	20	12	9	17	30	4	10	3		4	4	6	3	638
230	30	22	8	16	41	5	8	4	1	1	3	3	2	585
235	17	13	7	10	25	2	4	2	1	5	4	4	1	450
240	17	29	11	8	30	1	2	4	2	1	3	5	4	465
245	9	17	5	13	35	3	2	4		1		2	2	340
250	11	7	10	11	23	1	7	3	1			2	2	300
255	6	7	1	3	17		4	1	1		1	2	2	163
260	2	3	1	3	19	1	4	1	1		2	1	2	151
265	5	1	3	3	6	1	1	2	1					88
270	1	3	1	1	3						2		1	49
275	2	2			7			1						43
280	2	2		6	2		1				1	2	1	42
285		1	1	4	2		1					1		34
290	7	1		3	3	2	1				1			35
295	1			1	2		1					1		30
300	2		1	3	1		3	1						35
305				2	7			1						18
310	2	1		3	6	2					1			27
315	2		1	1	2		1				1	3		19
320		1		7	3	2					1			25
325				2	4									9
330				2	1			1	1					9
335			1											3
340					1									3
345				2										4
350		1	1											3
355														0
360		1												1
Overall Total	1683	1288	1069	902	1918	506	1136	367	642	237	535	227	132	42961

Table 3. Number of *Isurus oxyrinchus* sexed (F+M)#, number of females sampled (F#), overall sex-ratio% (SRo), number of pregnant females (F_Pre#), percentage of pregnant females relative to the females analyzed (F_Pre%) by ocean.

	ATL	IND	PAC	TOTAL
(F+M)#	15808	5505	20744	42057
F#	8022	2550	9333	19905
SRo (%)	50.7	46.3	45.0	47.3
F_Pre#	22	14	56	92
F_Pre%	0.27	0.55	0.60	0.46

Table 4. Number of pregnant females (F_Pre#) of *Isurus oxyrinchus* observed, average litter size observed (Ave_N_emb), confidence interval, maximum and minimum number of embryos, total number of embryos sexed (N_emb_sexed), number of female embryos (N_emb_Fem), number of male embryos (N_emb_Male), overall sex-ratio of the embryos found (SRo), average size and confidence interval (Ave_FL_emb) and minimum and maximum size of embryos.

	ATL	IND	PAC	TOTAL
F_Pre#	22	14	56	92
Ave_N_emb	11.0	11.4	11.9	11.6
CI90%	0.90	0.53	0.58	0.43
Min_N_emb	5	10	3	3
Max_N_emb	14	13	17	17
N_emb_sexed	219	158	655	1032
N_emb_Fem	113	72	307	492
N_emb_Male	106	86	348	540
SRo (%) emb	51.6	45.6	46.9	47.7
Ave_FL_emb	44.0	44.9	56.3	51.6
CI90%	5.22	4.25	2.51	2.28
Min_FL_emb	14	29	33	14
Max_FL_emb	66	63	75	75

Table 5. Average number of embryos (Ave_N_emb) and average length of embryos (Ave_FL_emb) with their respective confidence intervals (CI90%) by length class of the pregnant females (FL_F_Pre) observed in *Isurus oxyrinchus* for all the oceans and years combined.

FL_F_Pre	Ave_N_emb	CI90%	Ave_FL_emb	CI90%
250	10.3	0.95	39.3	9.00
255	12.0	0.00	44.0	0.00
260	10.3	1.18	49.3	7.03
265	11.6	0.99	39.7	10.59
270	9.8	2.17	54.7	8.51
275	9.8	1.09	59.3	9.09
280	11.9	0.95	43.2	10.97
285	11.3	1.45	49.5	9.04
290	12.0	1.39	52.9	1.22
295	11.2	1.41	58.5	6.86
300	13.0	0.85	54.3	6.99
305	12.8	0.79	51.3	9.62
310	9.5	3.03	58.9	12.02
315	13.8	1.03	53.2	8.50
320	13.2	0.68	59.3	9.07
325	11.3	3.64	61.2	7.89
330	13.0	1.64	59.5	12.34
335	15.5	0.82	56.0	18.09
340	11.5	1.11	33.5	0.00

Table 6. Average size (cm) of the embryos (Ave_FL_emb) found by size of pregnant females (FL_F_Pre) by hemisphere, ocean and month.

Hem.	Ocean	Month	FL_F_Pre	Ave_FL_emb	Hem.	Ocean	Month	FL_F_Pre	Ave_FL_emb
N	ATL	4	260	23	S	PAC	10	260	59
N	ATL	4	263	48	S	PAC	10	273	65
N	ATL	4	320	14	S	PAC	10	277	70
N	ATL	6	254	46	S	PAC	10	280	67
N	ATL	6	260	29	S	PAC	10	280	65
N	ATL	6	266	29	S	PAC	10	310	66
N	ATL	6	268	27	S	PAC	10	323	75
N	ATL	6	295	66	S	ATL	10	263	59
N	ATL	7	258	44	S	PAC	10	287	55
N	ATL	7	265	51	S	PAC	10	294	41
N	ATL	7	270	50	S	PAC	10	297	67
N	ATL	7	265	45	S	PAC	10	298	48
N	ATL	8	250	43	S	PAC	10	300	47
N	ATL	8	282	32	S	PAC	10	307	55
N	ATL	8	272	46	S	PAC	10	314	60
N	ATL	12	283	32	S	PAC	10	318	45
N	PAC	12	285	44	S	PAC	10	324	42
N	PAC	12	340	33	S	PAC	10	326	60
S	PAC	5	310	36	S	PAC	10	329	70
S	IND	6	260	30	S	PAC	10	332	52
S	IND	7	281	35	S	PAC	10	339	45
S	IND	7	290	45	S	PAC	11	282	56
S	PAC	7	313	71	S	PAC	11	321	71
S	PAC	7	320	60	S	PAC	11	264	53
S	IND	8	301	54	S	PAC	11	290	55
S	IND	8	308	40	S	PAC	11	290	45
S	ATL	8	260	54	S	PAC	11	294	62
S	PAC	8	302	46	S	PAC	11	295	46
S	PAC	8	303	63	S	PAC	11	306	44
S	IND	9	262	46	S	PAC	11	309	66
S	IND	9	272	52	S	PAC	11	310	40
S	IND	9	275	47	S	PAC	11	317	48
S	IND	9	275	37	S	PAC	11	318	55
S	IND	9	279	63	S	PAC	11	323	68
S	IND	9	280	53	S	PAC	11	323	54
S	IND	9	292	48	S	PAC	11	324	70
S	IND	9	300	49	S	PAC	11	327	65
S	PAC	9	290	68	S	PAC	11	327	42
S	PAC	9	318	75	S	PAC	11	331	67
S	PAC	9	296	63	S	PAC	11	340	34
S	PAC	9	310	41	S	ATL	12	264	64
S	PAC	9	320	58	S	ATL	12	266	59
S	PAC	9	320	50	S	PAC	12	292	60
S	ATL	10	278	62	S	PAC	12	301	66
S	IND	10	252	29	S	PAC	12	335	67

Table 7. Total number of embryos observed per uterus (right, left) in *I. oxyrinchus*, average number of embryos per uterus and confidence intervals (CI90%) by ocean and all the oceans combined.

	Right_U			Left_U		
	N	Ave.	CI90%	N	Ave.	CI90%
ATL	54	4.9	1.05	61	5.6	0.68
IND	29	5.8	0.80	28	5.6	1.23
PAC	179	5.8	0.65	174	5.4	0.52
TOTAL	262	5.6	0.50	263	5.6	0.39

Table 8. Nominal catch rates per thousand hooks of *Isurus oxyrinchus* , in number of specimens (CPUE#) and in weight (CPUEw) -kg dressed weight:DW-, by sex and combined sexes for the Atlantic, Indian and Pacific oceans.

	Female		Male		Female+Male+Unk	
	CPUE#	CPUEw	CPUE#	CPUEw	CPUE#	CPUEw
ATL	1.07	27.78	1.04	28.60	2.13	56.87
IND	0.43	20.77	0.50	25.06	0.97	46.83
PAC	1.51	53.15	1.84	80.64	3.43	136.01

Table 9. Nominal catch rates per thousand hooks of *Isurus oxyrinchus* , in number of specimens (CPUE#) and in weight (CPUEw) -kg dressed weight:DW-, by sex, combined sexes and size range for the Atlantic, Indian and Pacific oceans.

ATL	Female		Male		Female+Male+Unk	
Size range	CPUE#	CPUEw	CPUE#	CPUEw	CPUE#	CPUEw
<120cm	0.31	2.85	0.27	2.52	0.59	5.41
120-175cm	0.60	14.49	0.57	13.84	1.18	28.60
180-245cm	0.15	8.56	0.20	11.83	0.34	20.54
>=250cm	0.01	1.87	0.00	0.42	0.02	2.32

IND	Female		Male		Female+Male+Unk	
Size range	CPUE#	CPUEw	CPUE#	CPUEw	CPUE#	CPUEw
<120cm	0.05	0.23	0.04	0.21	0.10	0.49
120-175cm	0.17	5.31	0.16	4.93	0.33	10.47
180-245cm	0.20	12.21	0.29	18.76	0.50	31.58
>=250cm	0.02	3.02	0.01	1.16	0.03	4.29

PAC	Female		Male		Female+Male+Unk	
Size range	CPUE#	CPUEw	CPUE#	CPUEw	CPUE#	CPUEw
<120cm	0.42	2.62	0.37	2.31	0.84	5.14
120-175cm	0.67	16.12	0.64	16.14	1.34	32.95
180-245cm	0.35	23.18	0.77	54.45	1.13	78.47
>=250cm	0.07	11.23	0.06	7.74	0.13	19.45

Table 10. Percentage of possible season of parturition of *Isurus oxyrinchus* by area, ocean and hemisphere for a period of gestation of 18 months.

	Winter	Spring	Summer	Autumn
North ATL <30ºW	28.6	28.6	0	42.9
North ATL ≥30ºW	0	0	100	0
NORTH ATL	25.0	25.0	12.5	37.5
North PAC <180ºE	0	50.0	50.0	0
NORTH PAC	0	50.0	50.0	0
NORTH HEMISPH.	*22.2*	*27.8*	*16.7*	*33.3*
South ATL <20ºW	0	66.7	33.3	0
South ATL ≥20ºW	0	100	0	0
SOUTH ATL	0	80.0	20.0	0
South IND ≥80ºE	0	33.3	66.7	0
South IND <80ºE	25.0	25.0	37.5	12.5
SOUTH IND	14.3	28.6	50.0	7.1
South PAC <180ºE	18.2	72.7	9.1	0
South PAC <180ºW	11.9	45.2	28.6	14.3
SOUTH PAC	13.2	50.9	24.5	11.3
SOUTH HEMISPH.	*12.5*	*48.6*	*29.2*	*9.7*
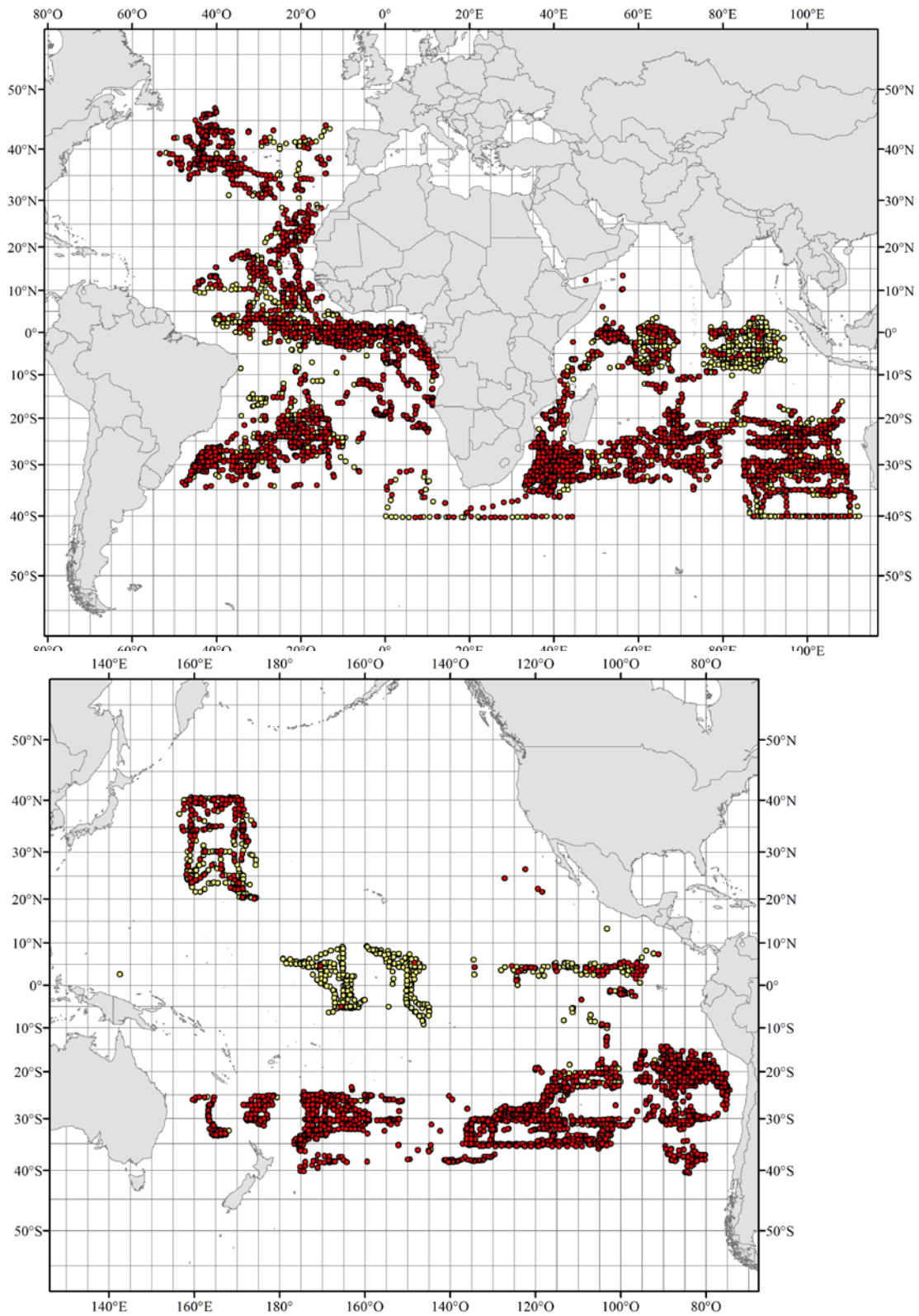
Figure 1. Map of the sets observed during the period 1993-2019 in the Atlantic, Indian (upper panel) and Pacific (lower panel) (positive sets with observations of *I. oxyrinchus* are colored in red).
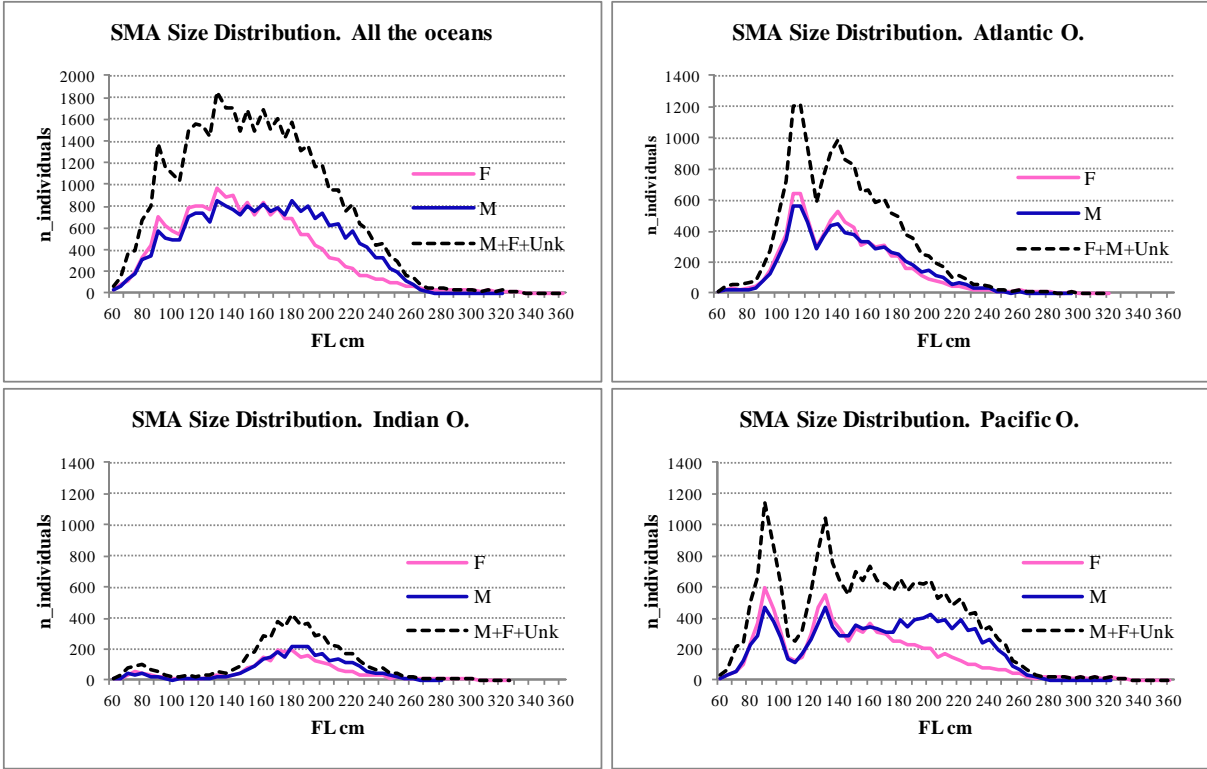
Figure 2. Size distribution (FL cm) of *Isurus oxyrinchus* by sex and combined sexes for the oceans as a whole and by ocean.
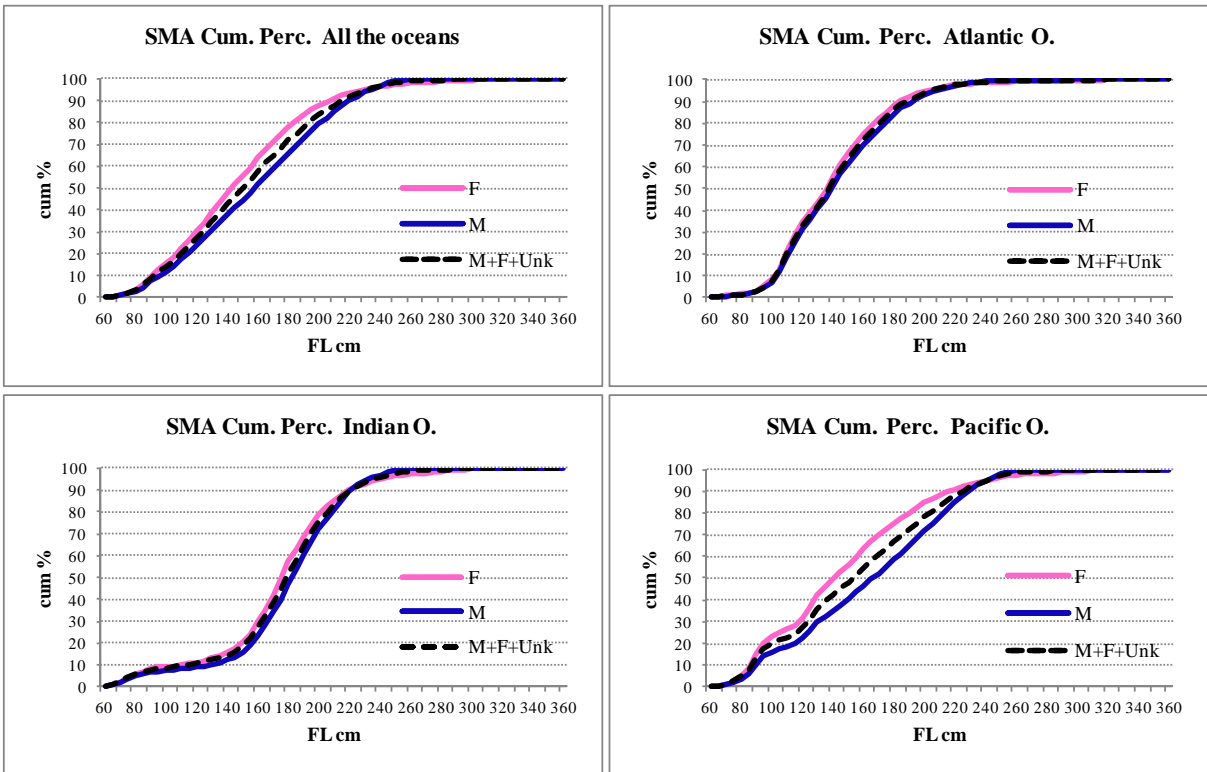
Figure 3. Cumulative percentages of *Isurus oxyrinchus* length frequencies by sex and combined sexes for all oceans and for the Atlantic, Indian and Pacific Ocean.
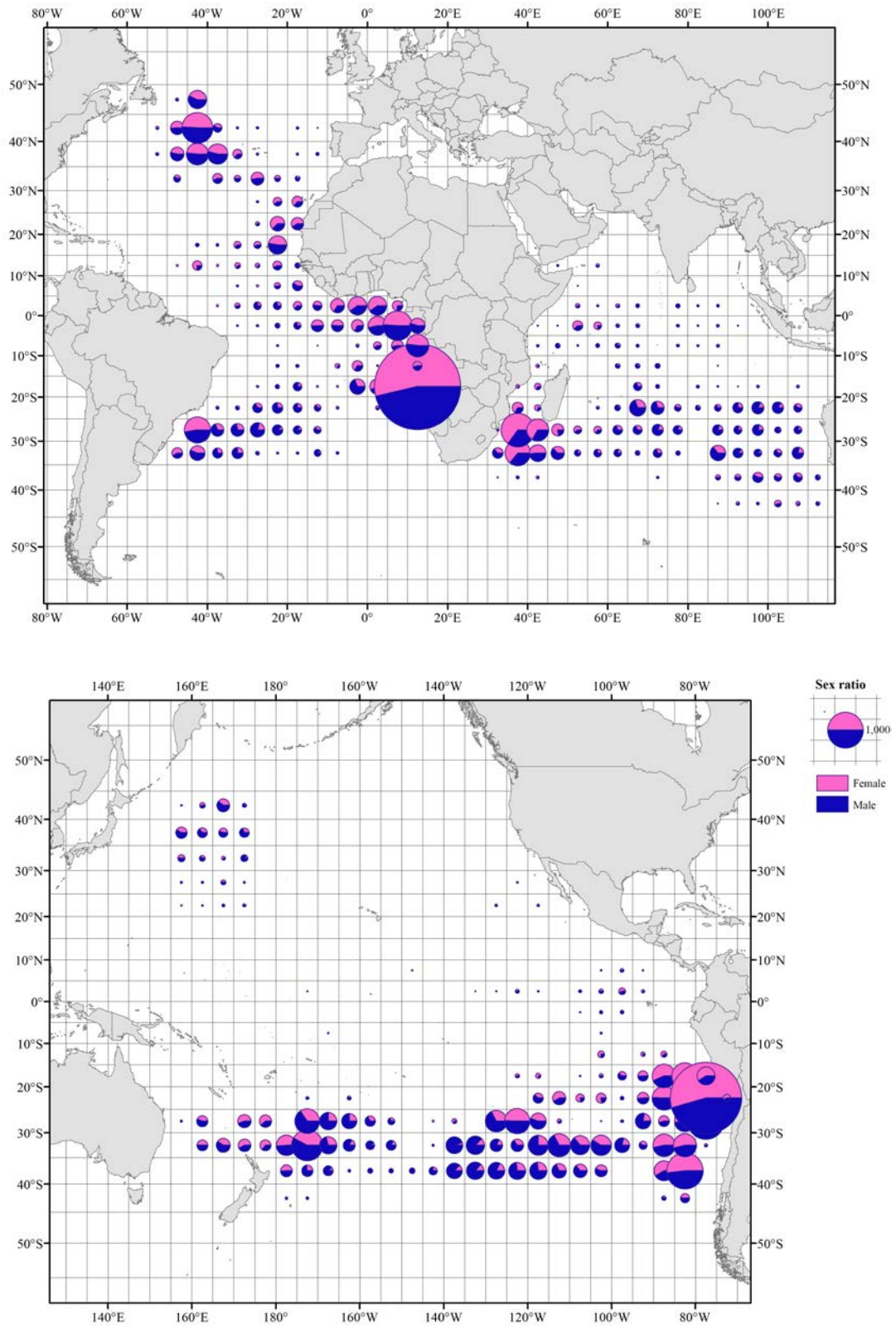
Figure 4. Overall sex ratio (SRo) of *Isurus oxyrinchus* by square 5°x5° and ocean.
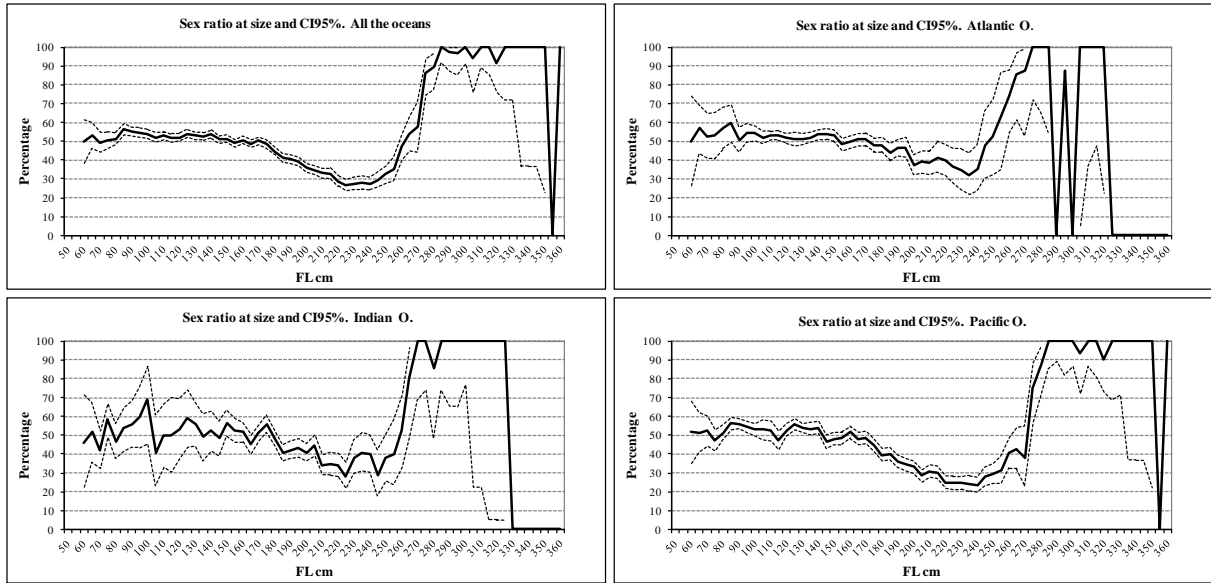
Figure 5. Sex ratio at size (SRs) values and their CI95% of *Isurus oxyrinchus* obtained for all of the oceans and by ocean.
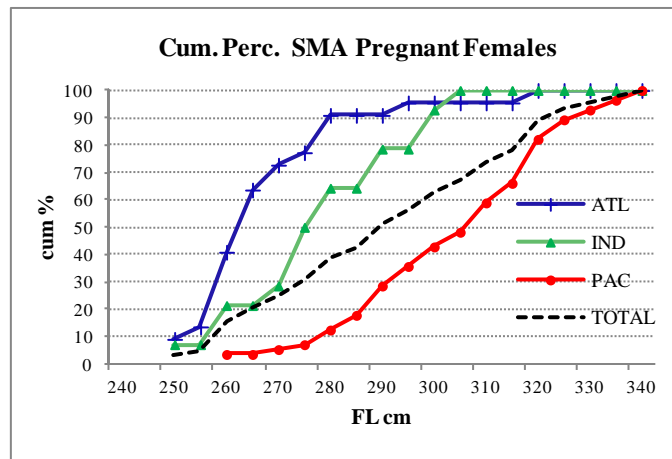
Figure 6. Cumulative percentages of pregnant female length frequencies (*Isurus oxyrinchus*) by ocean and whole oceans.
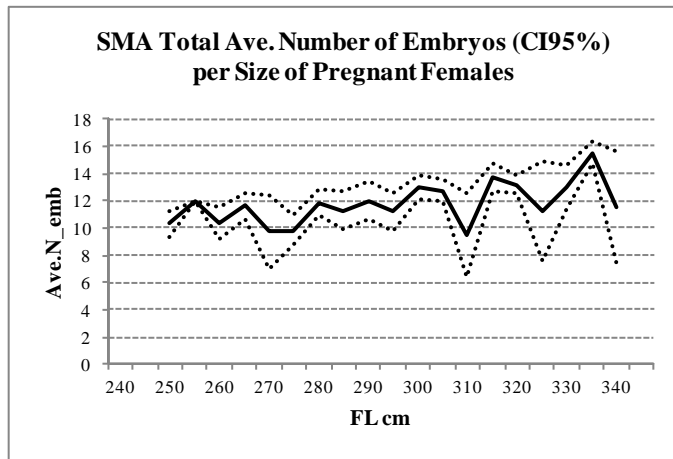
Figure 7. Average number of embryos of *Isurus oxyrinchus* per size class of pregnant females observed in all of the oceans and their respective confidence intervals (CI95%).
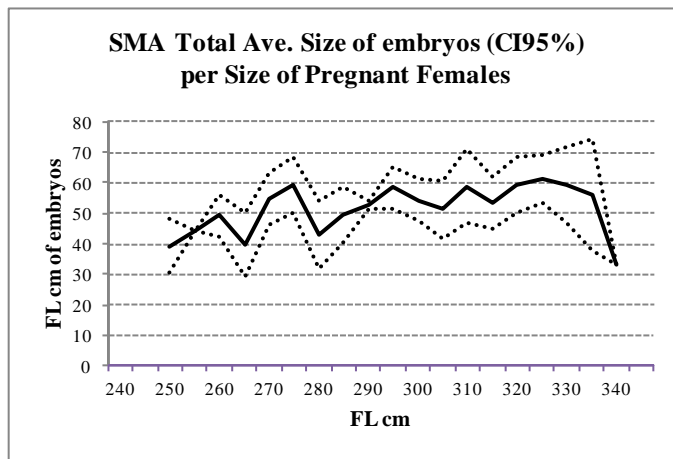
Figure 8. Average length (FL cm) of embryos of *Isurus oxyrhinchus* and their confidence intervals (CI95%) per size class of pregnant females observed in all of the oceans.
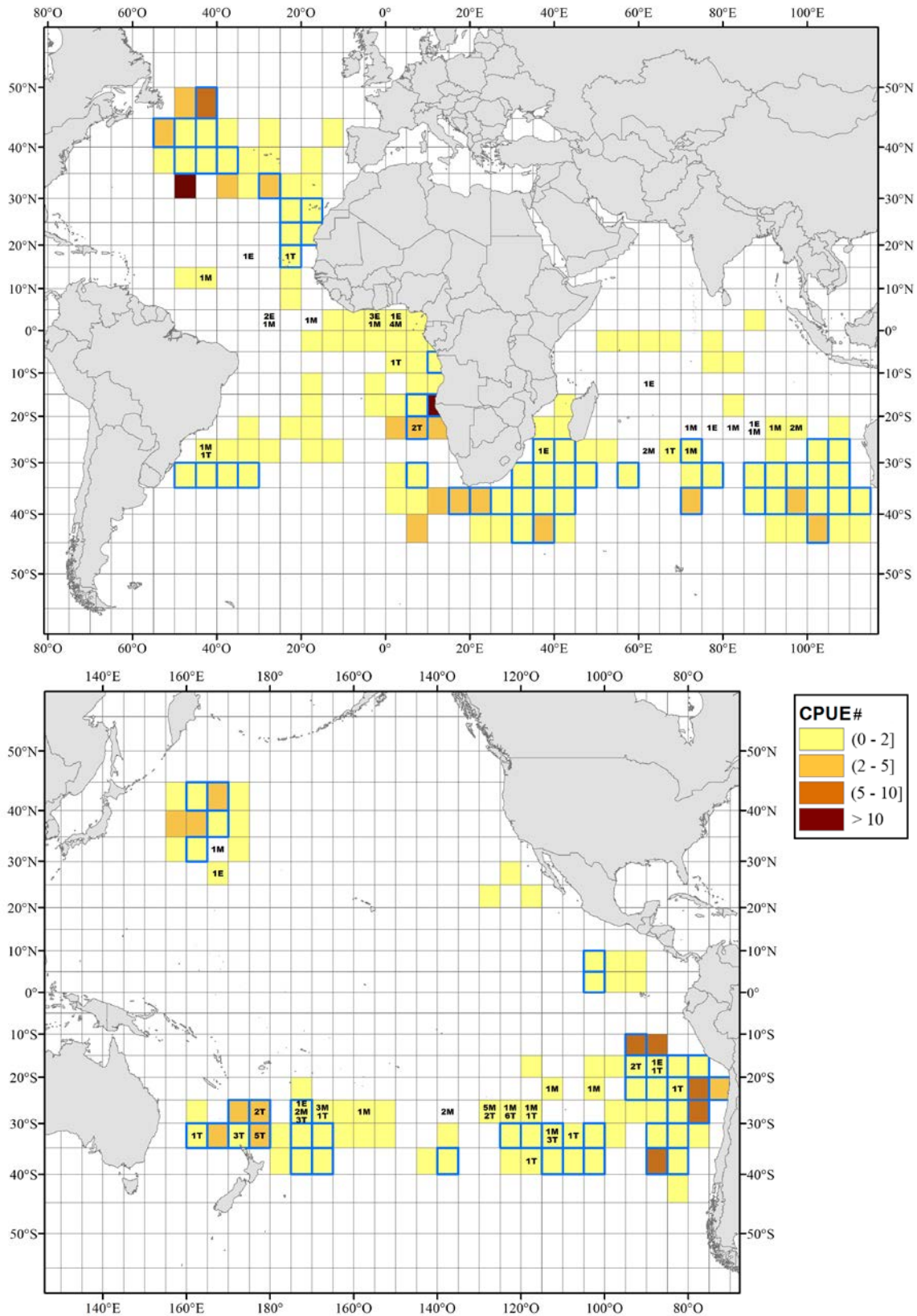
Figure 9. Distribution of individuals ≤120cm FL and location of pregnant females found with different states of embryos (E:early-, M: mid-, T: near-term) in the Atlantic, Indian and Pacific oceans during the 1993-2019 period. The blue grids illustrate that at least one SMA of FL size ≤ 75cm was captured.
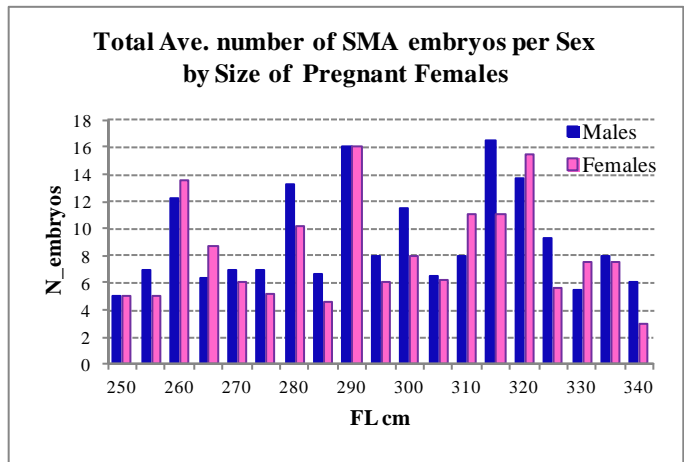
Figure 10. Average number of male and female embryos by pregnant female size class observed in all the oceans combined.
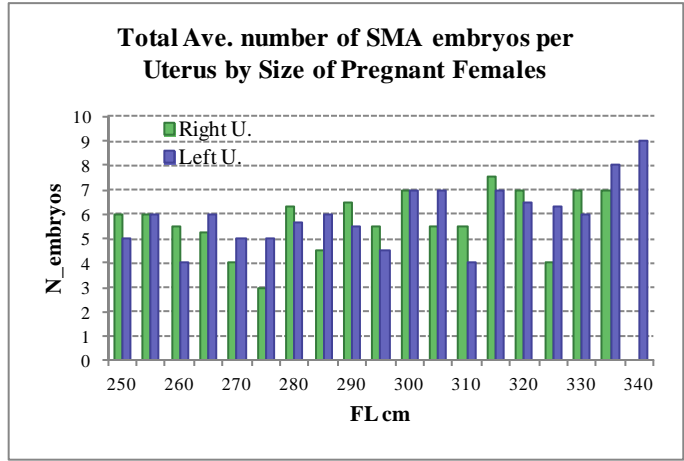
Figure 11. Average number of embryos per uterus and by pregnant female size class observed in all the oceans combined.
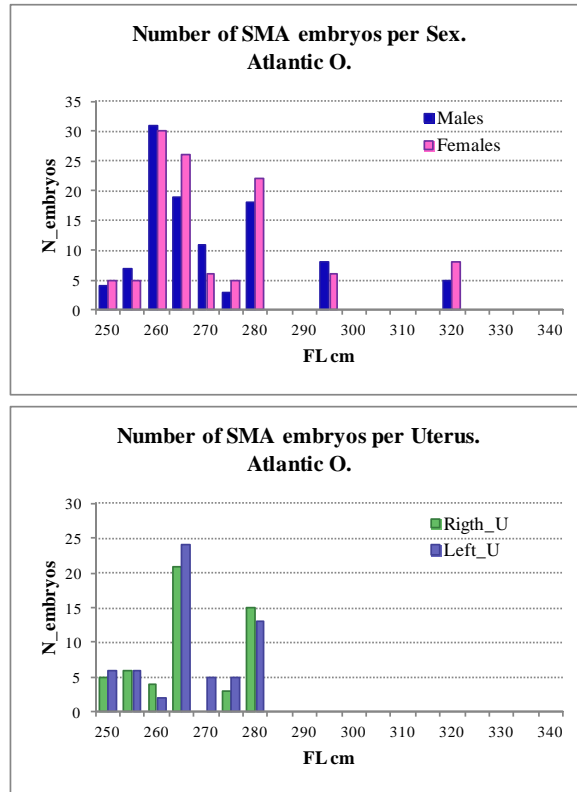
Figure 12. Number of embryos, male and female (upper), and number of embryos per uterus (lower), by size class of pregnant females sampled in the Atlantic Ocean.
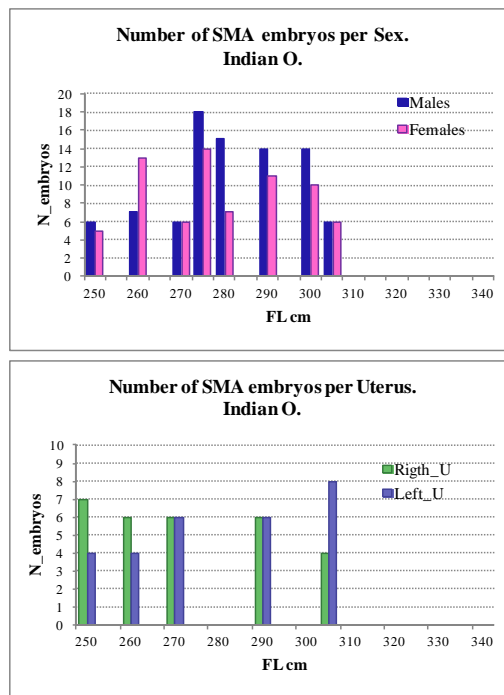
Figure 13. Number of embryos, male and female (upper) and number of embryos per uterus (lower), by size class of pregnant females sampled in the Indian Ocean.
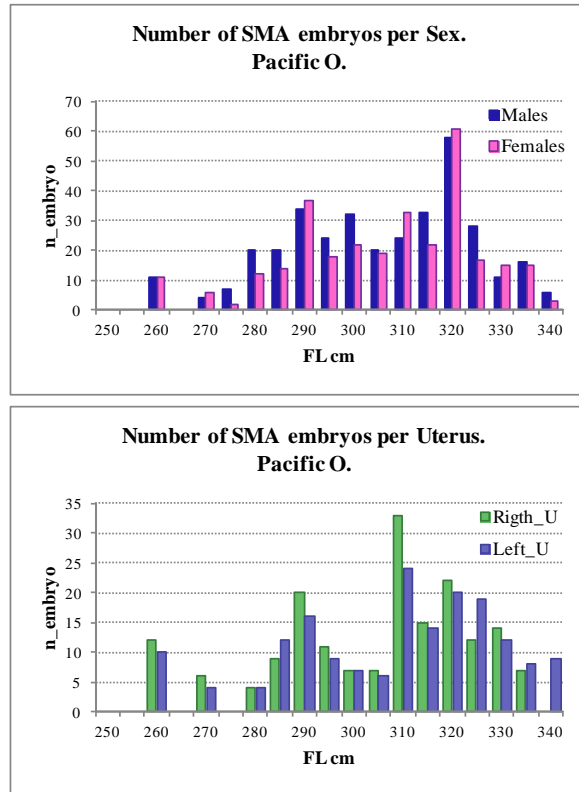
Figure 14. Number of embryos, male and female (upper), and number of embryos per uterus (lower), by size class of pregnant females sampled in the Pacific Ocean.
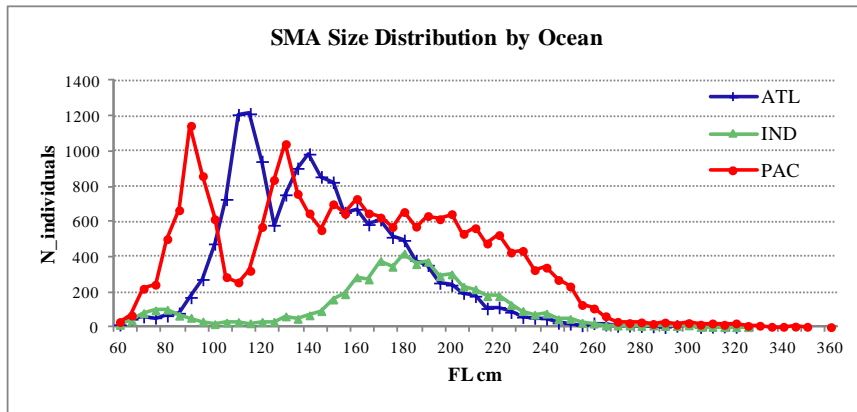

Figure 15. Size distribution (FL cm) of *Isurus oxyrinchus* by ocean and years combined.
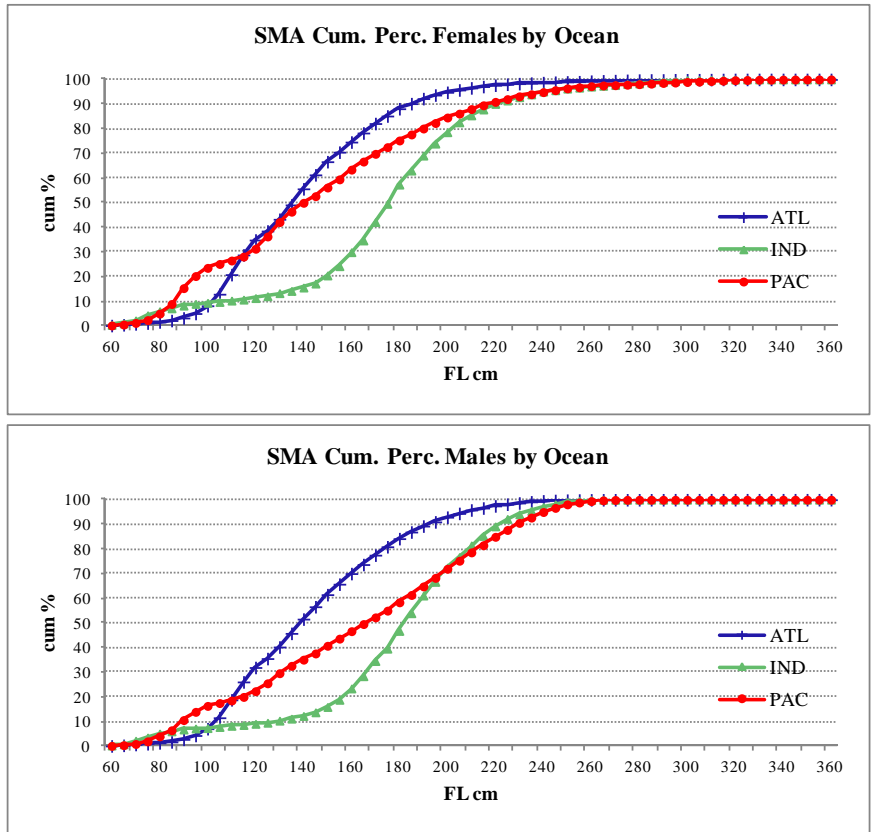
Figure 16. Cumulative percentages of female and male length frequencies (*Isurus oxyrinchus*) by ocean.