

Reproductive biology and population dynamics of the shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, off the southwest Portuguese coast, eastern North Atlantic

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Summary

A total of 262 shortfin mako sharks, *Isurus oxyrinchus*, was sampled from the swordfish longliners operating in the eastern North Atlantic. Most were juveniles, with only 3.4% mature. Based on cohort analysis, average growth was determined as 61.1 cm year⁻¹ for the first year and 40.6 cm year⁻¹ for the second year. There was a marked seasonality in growth, with average monthly rates of 5.0 cm month⁻¹ in summer and 2.1 cm month⁻¹ in winter. Cohort analysis also indicated summer as the probable parturition season, with sharks close to birth size caught in May 2003 and July 2004. Length at maturity for males was estimated at 180-cm fork length using the Schnute model. No females between 210 and 290-cm fork length were caught, although this appears to be the interval where maturation occurs. Gear selectivity was considered as the probable cause for the low number of mature females sampled.

Introduction

The shortfin mako shark, *Isurus oxyrinchus* Rafinesque, 1810, belongs to the family Lamnidae, known as mackerel sharks due to their speed and shape (Compagno, 1984). This pelagic shark is capable of retaining metabolically generated heat (Carey et al., 1981; Bone and Chubb, 1983) that enables its distribution throughout tropical and warm temperate oceans (Compagno, 1984).

Shortfin mako (referred to herein as ‘mako’) are caught as a regular bycatch of commercial fisheries in the Atlantic Ocean that target tunas and swordfish (Hoey, 1984; Casey and Kohler, 1992; Mejuto et al., 1992) and are commercialized worldwide for their meat, fins and jaws (Walker, 1998). Moreno and Morón (1992) argue that makos should not be considered as bycatch, at least not for the eastern North Atlantic surface-drift longliners, due to their high commercial value. Despite this fact, total catches remain unknown, with landings often not reported or reported only as ‘shark’ (Casey and Kohler, 1992; Walker, 1998). Traditionally, both Spanish and Portuguese swordfish fleets use surface-drift longline gear, up to a depth of 18 m (Mejuto et al., 1992).

Genetic studies by Schrey and Heist (2003) concluded that the North Atlantic receives a low number of migrants per generation, creating conditions for a separate stock, hence requiring independent management.

The mako shark presents size and sexual dimorphism, with mature females being larger (maximum size reported 394 cm total length, TL) than males (maximum size reported 284 cm TL) (Stevens, 1983; Compagno, 1984). However, age and growth studies for western North Atlantic mako sharks show both sexes growing at the same rate until they are on average 230 cm fork length (FL) (Casey and Kohler, 1992).

In the literature, size at birth varies from 60–70 (Bass et al., 1975) to 110 cm TL (Gubanov, 1978). The smallest free-swimming shark reported by scientists was 71 cm (Bass et al., 1975); Casey and Kohler (1992) stated that fishermen actually measured makos of less than 63 cm TL in the Grand Banks area. Mollet et al. (2000) concluded TL at birth to average 70 cm.

As for the female size at maturity, values differ greatly between studies, ranging from 180 to 337 cm TL, as reviewed in Mollet et al. (2000). Described parturition periods also vary considerably from winter to summer (Bigelow and Schroeder, 1948; Branstetter, 1981; Stevens, 1983; Uchida et al., 1987; Costa et al., 2002). Temporal analysis of uterus width and gonadosomatic index, plus embryo length-at-age data, led Mollet et al. (2000) to predict a reproductive cycle of 3 years with a gestation time of 8–12 months. The total number of embryos reported varies between 4 and 16 and appears to be positively correlated with maternal size (Mollet et al., 2000). The importance of reproductive and population studies is the necessity of quantifying recruitment for an accurate evaluation of the fishery status (Holden, 1974). Casey and Kohler (1992) noted the need for research on the reproductive biology of the mako shark in all of its Atlantic range; despite this, published studies are still lacking in the eastern North Atlantic. Following the directions of the United Nations Food and Agriculture Organization (FAO, 1998) that request national plans of action toward better management, and the need for extensive biological data from single location fisheries (Mollet et al., 2000), this study aims to investigate the reproductive biology and population dynamics of the shortfin mako shark *I. oxyrinchus* in eastern North Atlantic waters off the coast of Portugal. In order to do so, (i) the reproductive system of mako sharks caught by the swordfish fisheries was examined both external and internally; (ii) estimates for their reproductive parameters are advanced; and (iii) population dynamics based on size, sex ratio, and cohort analysis are addressed.

Materials and methods

Study area

From April 2003 to January 2005, shortfin mako sharks were sampled from landings of the Portuguese surface-drift swordfish longline fishery that operates off the southwest coast of Portugal, between 34°N and 39°N in the eastern North Atlantic.

The principal currents acting on the surface waters in the area are: the Portuguese Current, which runs south along the continental coast; the Portuguese Coastal Current, related to the upwelling phenomenon, flowing south during the summer, near the edge of the continental platform; and the Portuguese Coastal Countercurrent during autumn and winter (Ambar, 2003). The predominant wind regime is north in spring and summer, and south in autumn and winter (Frouin et al., 1990). Annual mean surface temperature ranges from 15 to 19°C, with lower monthly temperatures (13°C) during February and highest in September (22°C) (<http://www.nodc.noaa.gov>). This oceanographic data places the Portuguese coast in the transitional area from cold temperate to warm temperate biogeographic regions.

Methods

Sampled vessels were at sea for periods between 5 and 22 days, but usually for 14 days. Hooks were fixed to monofilament instead of metal lines and the usual set consisted of 2000 baited hooks. On board, sharks were refrigerated in a 4°C cold room.

Sampling at the fish house included, whenever possible, weighing of individuals using a floor scale (precision 0.1 kg). Recording of FL and stretched TL (STL) was to the nearest centimeter, measured from the tip of the snout to the caudal fork and to the upper caudal tip, respectively, over the body curve (Skomal and Natanson, 2003). Sex determination was based on external characters; measurements were taken to the nearest half cm of the claspers of males, from the cloaca to the tip, and gonads were collected.

Samples were frozen upon arrival at the laboratory and kept at minus temperatures until further analysis.

For reproductive study purposes, the epigonal organ, as well as males testes and females ovaries, were weighed. Standard measurements used in other shark reproductive biology studies were collected, namely, oviduct width, ovarian efferent pore width, uterus width (at the anterior subdivided uterus), and oviductal gland width for females, plus testes length and width for males. Whenever possible the paired structures were both measured and an average was computed.

FISAT II v.1.1.3 (FAO, 2004) was used to analyze grouped length frequencies for different sampling months with the modal progression analysis tool using both Bhattacharya's method and NORMSEP. Two different sets of grouped length frequencies were used with 5 and 10 cm intervals. Different identifiable cohorts were followed and growth rates computed.

Chi-squared statistics were used to test for deviations from the 1 : 1 M : F sex ratio for different life stages, length intervals, seasons and months, using Statistica v.6.0 (StatSoft Inc., 2001).

Regressions for FL/STL (linear), FL/total weight (power) and FL/dressed weight (power) were obtained by the method of least squares.

In order to test for useful maturity predictors, the various measurements taken from the internal and external reproductive organs were plotted against FL.

Differences between testes from the same mako shark were also tested with Statistica v6.0 (StatSoft Inc., 2001), using a *t*-test for independent samples.

Stehmann's (2002) maturity scale was used in this study, and the degree of claspers calcification was the main character taken into consideration to assign a maturity stage to males. Length at maturity for males was calculated as the FL at which 50% of the individuals were mature, and maturity per size class was estimated using Schnute's (1981) versatile growth model.

Results

Population structure

A total of 262 shortfin mako sharks was sampled at the fishing ports of Sesimbra and Peniche.

Mean FL of mako sharks caught was 126.13 ± 31.67 cm. The largest shark was a 290-cm FL female caught in June 2004; the smallest individual, a 64-cm FL male, was caught in July 2004.

Regressions for conversion of FL into stretched total length (STL) and between total weight (*W_t*) or dressed weight (*W_d*) and FL were computed. They are to be used only for the intervals for which data were available, respectively, 64–290 cm FL for (1) and (2), and 78–290 cm FL for (3).

$$STL \text{ (cm)} = 1.1213[FL(\text{cm})] - 1.4536 \quad (1)$$

$$r^2 = 0.9899 (n = 264)$$

$$W_t \text{ (kg)} = 0.0000244 \times [FL(\text{cm})]^{2.8289} \quad (2)$$

$$r^2 = 0.9718 (n = 221)$$

$$W_d \text{ (kg)} = 0.0000131 \times [FL(\text{cm})]^{2.8766} \quad (3)$$

$$r^2 = 0.9761 (n = 46)$$

The smallest individuals were caught during May 2003 and July 2004; these were close to the reported size at birth (smaller than 70 cm FL and 85 cm STL). Most of the sharks sampled were juveniles (53.4%), followed by young-of-the-year (43.1%); only 3.5% were mature.

Modal progression analysis with Bhattacharya's method and NORMSEP produced similar results. Cohorts which showed no agreement between the two methods or that had high standard deviations were discarded. Separation of cohorts was most effective at the 10 cm interval (Fig. 1). Sexes were

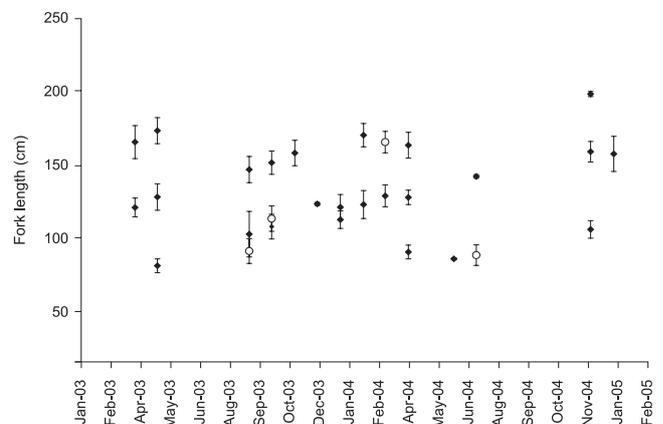


Fig. 1. Plotting of modal classes (black dots) of shortfin mako sharks (bars show standard deviation, circles emphasize secondary and weaker cohorts; n = 93)

analyzed first separately and then compared with sexes pooled. As there were no significant deviations from the pooled sexes, these results are not shown, and growth for the first years was considered sex independent.

Modal classes can be easily followed for the first 2 years of mako life. However, for the first year of life there appears to be a secondary, weaker cohort that is absorbed by the stronger one before completion of the first year.

Average growth was determined as 61.1 cm year⁻¹ for the first year and 40.6 cm year⁻¹ for the second year. Seasonality in growth was observed for the second year, with average monthly growth rates of 5.0 cm month⁻¹ during summer and 2.1 cm month⁻¹ during winter.

According to the NMFS/APECE tagging program, a female captured by rod and reel and tagged in June 2003 near Sesimbra (38°24'N, 9°01'W) with 98 cm STL, was recaptured at 135 cm STL by a Spanish longliner 443 days later after traveling 84 km southwards to 15 nautical miles off Cape S. Vicente (37°01'N, 9°19'W). The computed growth rate for this female was 30.5 cm year⁻¹.

The overall sex ratio was 1.18 : 1, biased toward males, although it varied through the sampling months. The higher M : F ratio was registered during March 2004 (2.57 : 1) and the lowest during May 2004 (0.33 : 1). Statistical analysis run on sex ratio to test for deviations from 1 : 1 showed to be significant for juveniles in the 2003/2004 winter season ($\chi^2 = 5.45$, d.f. = 1, P-value < 0.05) and 2004 spring ($\chi^2 = 4.00$, d.f. = 1, P-value < 0.05) and for pooled life stages in March 2004 ($\chi^2 = 4.84$, d.f. = 1, P-value < 0.05), with a predominance of males in all cases (M : F 2.44 : 1; 2 : 1; 2.57 : 1, respectively).

Male reproductive biology

For reproductive studies, 79 males were sampled from January 2004 to January 2005. However, the internal anatomy could only be evaluated for 68 of them, all caught during 2004. The shortfin mako internal anatomy is characterized by the presence of the epigonal organ. Testes differentiate in the upper region of this organ and appear as a pink coiled streak embedded in the epigonal organ and covered by its membrane. Testes are pinkish-red and present a slightly coiled structure that confers them a lobulate appearance. In all sharks, the two testes were equally developed ($t = 0.12$, d.f. = 38, P-value > 0.05).

Most of the individuals were immature (maturity stage 1; $n = 65$), with bent claspers and testes not well developed. Eight individuals that had partially calcified claspers were sampled (ranging in size from 157 to 174 cm) and assigned the maturity stage 2, subadults. Most of them presented well-developed testes, even if not with maximal weight, and three of them had some coiling of the epididymi. It was not possible to further investigate if coiling could be a good indicator of the shark's maturity stage, as the meat of the highly prized shortfin mako specimens was going to be exported, dressed but otherwise intact. The mature samples (maturity stage 3) comprised only six sharks (150–245 cm FL), characterized by the presence of fully calcified and thick claspers, well developed and turgid testes and the presence of a spine at the inner margin of the claspers. The epididymis of the mature male appeared as a long, compact, and not coiled white streak. Maturity stage 4, which is active, was not attributed due to the lack of adults for comparison among them.

For males the easiest measurement to take was clasper length, which was registered for all males sampled (Fig. 2a).

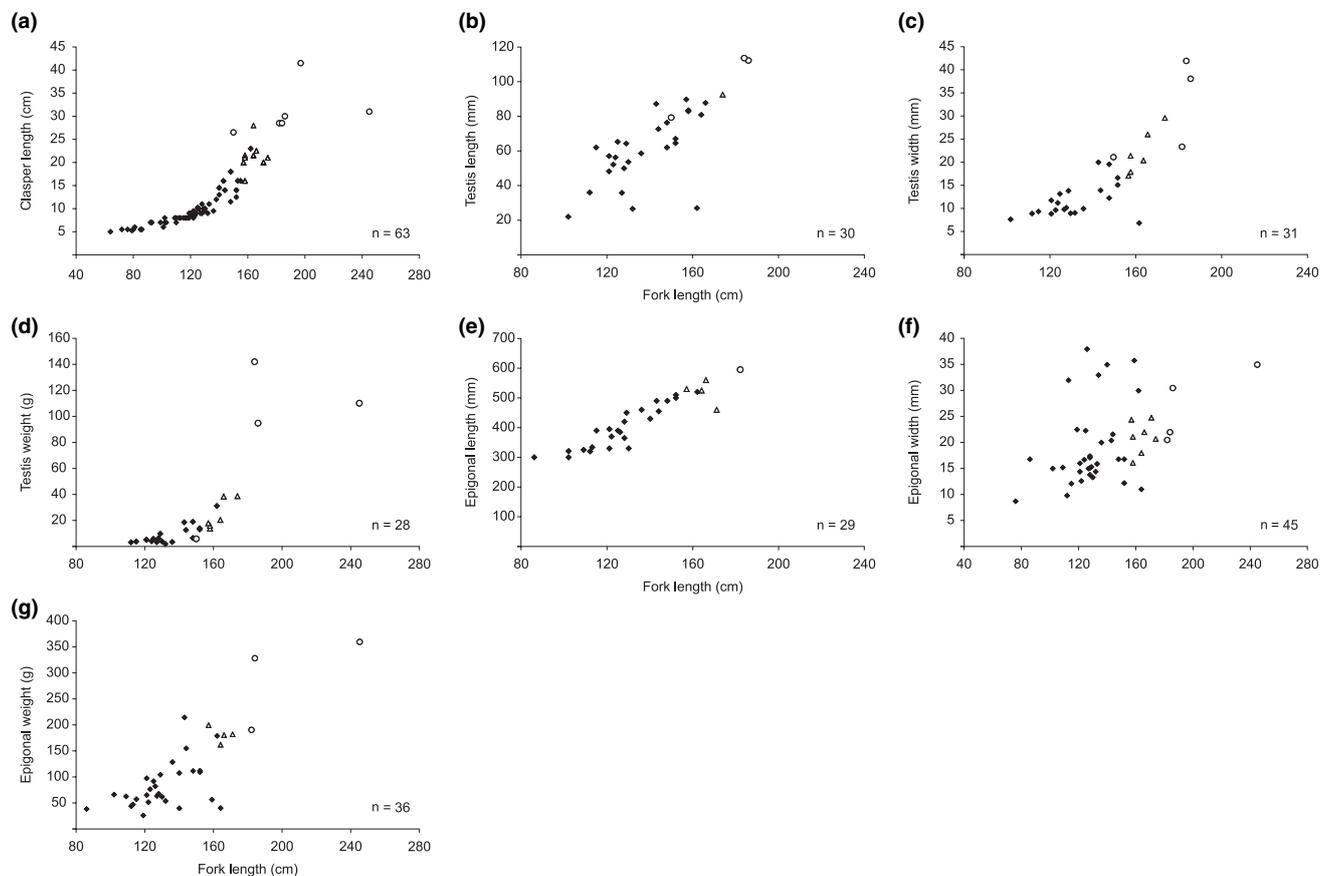


Fig. 2. Plotting of different measurements of shortfin mako male organs against fork length (FL) (■ uncalcified claspers, maturity stage 1; ▲ partly calcified claspers, maturity stage 2; ○ fully calcified claspers, maturity stage 3)

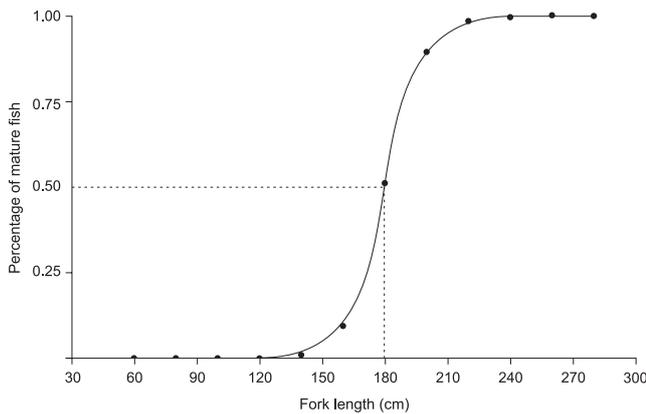


Fig. 3. Cumulative maturity curve for ogives of the shortfin mako males fitted with Schnute model ($n = 79$)

Even with the low number of mature and transitional individuals it was possible to observe the expected sigmoidal curve. To a lesser extent the same pattern was observed in the measurements of the internal organs, even when the individual variability appeared to be greater (Fig. 2b–g). When plotting mean testes width and length against FL (Fig. 2b,c), there is no good separation of immature and subadults, especially in terms of testes width, with an apparent soft transition between stage 1 and stage 3 males. The testes weight remains low until complete maturation of the individual, when its weight increases twofold to threefold (Fig. 2d). The epigonal organ length increases linearly with FL (Fig. 2e), as would be expected since it runs along the abdominal cavity and its primary function, hematopoiesis, is not sex related. Integrating all data, length at onset of maturity can be estimated as 150–180 cm FL. Maturity per size class was estimated using Schnute’s (1981) versatile growth model. The iterative process estimated the following parameters: $x_1 = 196$ cm; $B = 1.10$; $f = 18.00$; and $g = 0.18$. Length at 50% maturity (i.e. L50) yielded approximately 180 cm (Fig. 3).

Female reproductive biology

A total of 32 females was internally examined; all were clearly immature except for a 290-cm FL female caught in June where the ovary comprised 0.072% of body weight ($W_t = 293$ kg) and the maximum ovum diameter was 4.9 mm. The oviductal gland was 38.3 mm wide and the two uteri were equally developed, averaging 47.1 mm.

Different female reproductive tract measurements (Fig. 4a–e) reveal that the oviduct width shows high individual variation until 150 cm FL, and appears to increase slightly thereafter. The ovary efferent pore increases with FL (Fig. 4d), despite that all plotted individuals are immature and have no macroscopically visible ovary. The oviductal gland appears to have the same diameter for a wide range of immature FLs indicating a late development in the maturation process. The largest immature female sampled was 210 cm FL.

Discussion

Modal progression analysis identified the first two cohorts, which according to Pratt and Casey (1983) should present higher annual growth, which they did. However, the results obtained show slightly higher growth rates (61.1 cm year⁻¹ for the first year and 40.6 cm year⁻¹ for the second) than Pratt and Casey’s (1983) results (50 cm year⁻¹ for the first year and 32 cm year⁻¹ for the second). There is also an apparent seasonality in growth, with the highest growth increment occurring at the beginning of summer and the lowest during winter. This could be due to an increase in food availability and water temperature. Since this is an endothermic species (Bone and Chubb, 1983), the less energy needed to maintain body temperature, the more energy is available for growth.

Lack of sex differences in cohort analysis for the first years of life is in accordance with previous studies reporting that male and female mako sharks grow at the same rate until they reach about 200 cm FL (Casey and Kohler, 1992; Campana et al., 2005). Cohort analysis was not more informative since sampled shortfin mako sharks display high individual variability.

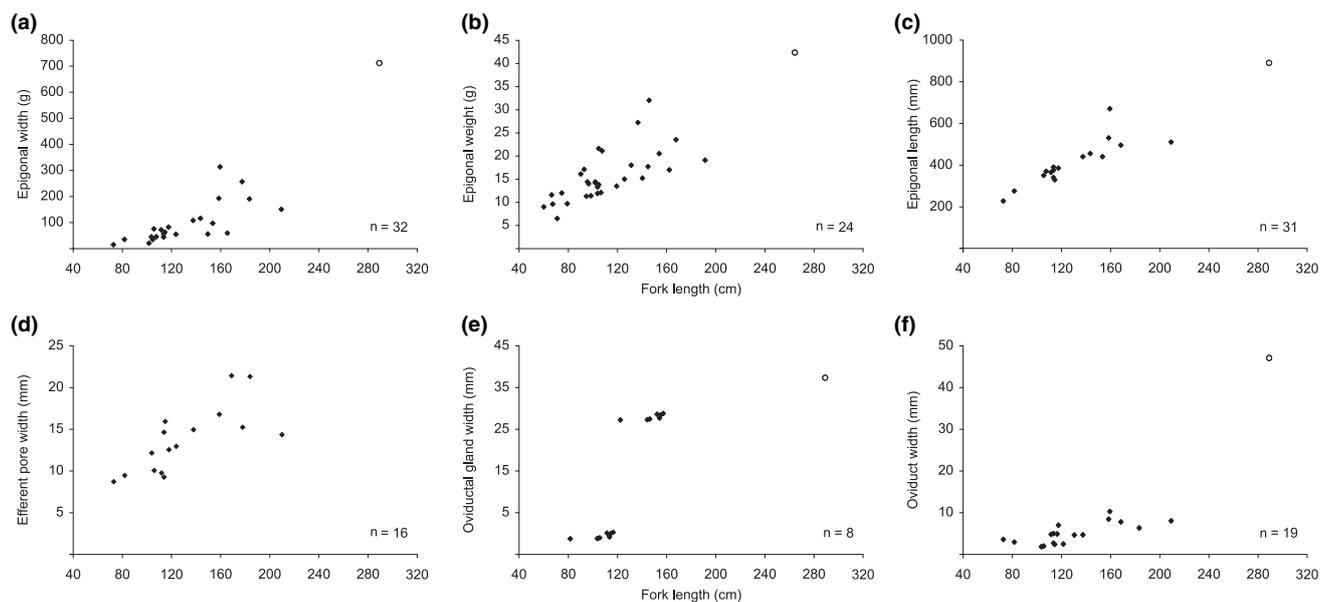


Fig. 4. Plotting of different measurements of shortfin mako female internal organs against fork length (FL) (■ immature; ○ mature)

The capture of the smallest individuals in the summer months suggests that parturition occurs either prior or during this season. Early summer as the parturition season is in agreement with Bigelow and Schroeder (1948), Gilmore (1993) and Costa et al. (2002). However, this disagrees with Mollet et al. (2000) who, reviewing worldwide shortfin mako data, concluded that late winter to mid-spring was the parturition period in both hemispheres. The second and weaker cohort might, however, represent a secondary pupping season occurring earlier in the year.

The lack of sampled large shortfin makos might be explained by the greater strength of larger sharks (Pratt and Casey, 1983). The fishery from which the makos were sampled operates with monofilament longline gear without a metal ending before the hook. In the case of the sampled large female, fishermen reported that it jumped out of water and fought for over 1 h. It is thus comprehensible that fishermen sometimes opt for cutting the lead line.

According to Pratt and Casey (1983), young-of-the-year mako sharks are not caught by conventional fishing gear in the western North Atlantic. However the same trend was not observed in the sampled area, where a great number of young-of-the-year was caught. Given the preference of juvenile shortfin makos that were tracked in California, for the upper mixed layers (80% of the time was spent in the upper 12 m) and taking into account that larger makos dive deeper (Sepulveda et al., 2004), juvenile sharks are expected to be the most frequently captured life stage, as was observed in this study.

Overall sex ratio points to either a greater abundance, or to a greater availability of males to the fishing gear, due to prey preference, habitat occupation or other behavioral trait. The sex ratio for young-of-the-year is not significantly different from 1 : 1, as previously reported by Stevens (1983). The important bias of sex ratio toward males in juveniles could be attributed to a higher female mortality, female immigration, gear selectivity or a highly fluctuating sex ratio over time. Muñoz-Chápuli (1985) states that there is a segregation of sexes by the parturition period, with the females moving to warmer waters and the males to colder waters, suggesting that it is to protect the neonates and young-of-the-year against predation by adults and juveniles. Ultimately, this is not necessarily a logical explanation, since the density of larger predators, especially of shark species, is greater in warmer waters and tropical habitats. Still, if displacement to warmer waters in fact happens, females could be migrating before reaching maturity, explaining the male predominance among juveniles. The movement southwards of the recaptured immature female supports this hypothesis. Sex ratio seasonality could also be indicative of reproduction driven migrations.

Regarding the male reproductive biology it is possible to advance an estimate of length at maturation around 180 cm FL, based on the length of claspers and degree of calcification. This is a slightly smaller length when compared with the 195 cm FL reported by Stevens (1983). Bass et al. (1975) in his compilation of data on *I. oxyrinchus* reported mature males from sizes of 225 cm TL or larger for South African waters. This could be indicative of earlier maturation in terms of size in the North Atlantic waters compared with the South Atlantic.

All except one of the females caught were immature, suggesting that they do not reproduce in these waters (Gilmore, 1993). Nevertheless, the presence of a 290 cm FL mature or maturing female questions that hypothesis, and

raises the possibility of unavailability more than absence from the area.

Pregnant shortfin makos have only been captured between 20° and 30°N or S (Gilmore, 1993). Due to the lack of mature females in other areas, it is thought that females migrate to these latitudes to give birth. Nevertheless, there is no information about the area where mating occurs, since males appear more abundant at higher latitudes. Casey and Kohler (1992) suggested that adult females may remain farther offshore, however this reality does not apply to these waters, since the coastal areas are not productive enough to invite sharks. If there is spatial segregation it could be in the water column, with females spending more time in deeper waters or just an effect of gear selectivity. Schrey and Heist (2003) have suggested mako females to be philopatric to pupping grounds while males entail longer distance movements, based on microsatellites and mtDNA population structure. The Schrey and Heist (2003) hypothesis is strengthened by the 3-year reproductive cycle of female mako sharks. Should parturition occur at the same time in both hemispheres, then an entrainment to another cycle would highly compromise reproductive fitness. Other problems emerge from this theory, since young-of-the-year with 71 cm STL (close to the reported birth size) were caught off the Portuguese coast in July. Do these sharks have such low growth rates? Or are mako sharks from the eastern North Atlantic born smaller? In addition, if these sharks were born at lower latitudes and use surface waters, it is highly improbable that they are migrating north against the Portuguese current.

Mollet et al. (2000) reported the median TL at maturity of females from the western North Atlantic to be greater than that of females from the Southern Hemisphere. The data of the only 290-cm FL female that appeared to be mature, while never having reproduced (no signs of a spent uterus and no striations), supports this idea of later length-at-maturity when compared with South Atlantic sharks.

The efferent pore is known to enlarge as the ovary matures and reaches maximum size when ovulation peaks (Gilmore, 1993). As immature females do not have a macroscopically visible ovary (Stevens, 1983), efferent pore size appears to be a useful parameter to evaluate the maturity state in earlier stages.

Ovarian weight for the only mature female comprised 0.07% of its body weight, a value inferior to the reported interval for mature females by Stevens (1983). According to Mollet et al. (2000), the reproductive parameters of the 290-cm FL shortfin mako are below all values of mature females in terms of uterus width, among the transitions from immature to mature in terms of oviductal gland width and among the highest values for mature females' ova diameter. This requires further investigation and sampling of females from the eastern North Atlantic, especially as no females from this area were analyzed in Mollet et al. (2000).

This study provides some insight on the biology of shortfin mako sharks in the eastern North Atlantic. However, concerning the reproductive traits of females, parturition grounds and migration patterns further research should be carried out; these questions are of greater importance, given the high percentage of immature individuals caught in these waters.

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