

## DISTRIBUTIONAL AND REPRODUCTIVE ASPECTS OF THE BIGEYE THRESHER SHARK (*Alopias superciliosus*) IN THE ATLANTIC OCEAN

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### SUMMARY

*The bigeye thresher shark, Alopias superciliosus is sometimes caught as bycatch in pelagic longline fisheries targeting tunas and swordfish in the Atlantic Ocean. As part of an ongoing cooperative program for fisheries and biological data collection, fishery observer data from various fishing nations and projects were compiled and analyzed. Those data sets include information on geographic location of the observations, as well as size, sex and in some cases maturity stage. A total of 4371 bigeye threshers were recorded throughout the Atlantic Ocean between 1992 and 2013, with the sizes ranging from 70 to 305 cm FL (fork length). Considerable variability was observed in the catch-at-size, with particular emphasis on the tropical region where the mean sizes tended to be smaller than in the other regions. The expected distribution of juvenile and adult specimens also showed considerable variability, and the sex-ratios varied between regions and size classes. Maturity ogives were fitted to data from 642 specimens, with the median sizes at maturity estimated at 208.6 cm FL (corresponding to 349.1 cm TL) for females and 159.2 cm FL (corresponding to 269.8 cm TL) for males. In addition, a segmented regression model (SRM) was used for males, and two breakpoints ( $Bk_1$ : 122.5cm FL,  $Bk_2$ : 173.3cm FL) estimated, identifying transitions between the three different maturity stages for male sharks (immature, maturing and mature). Only a few pregnant females were recorded, always with the presence of two embryos (one per uterus), and were distributed predominantly in the tropical northeast Atlantic closer the African continent, and in the southwest region, with those regions possibly serving as nursery areas for this species. These reproductive parameters, and especially the estimated median sizes at maturity and low fecundity, highlight the vulnerability of this species, reinforcing that the bigeye thresher tends to mature at a larger size than the other species of the Alopiidae family. The biological and distributional patterns presented can help managers adopt more informed and efficient conservation measures for this species.*

**KEYWORDS:** *Alopias superciliosus*; bigeye thresher; size distribution; reproduction; Atlantic Ocean.

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## 1. Introduction

The bigeye thresher (*Alopias superciliosus*), is a large epipelagic and mesopelagic species, occurring circumglobally in tropical and subtropical waters of the Atlantic, Indian and Pacific Oceans (Compagno, 2001). Together with two other species, it belongs to the Alopiidae family (sea foxes) and Lamniformes order, and is characterized by having a remarkably long caudal fin. Thresher sharks have an aplacental viviparous reproductive mode with oophagy, characterized by the developing embryos being nourished by yolk-filled egg capsules that are continuously produced and deposited in the uteri (Gruber and Compagno, 1981; Moreno and Morón, 1992; Gilmore, 1993; Conrath et al., 2004). Similarly to the common thresher (*Alopias vulpinus*) and pelagic thresher (*Alopias pelagicus*), the litter size of the bigeye thresher is commonly two (rarely four) pups, though they grow more slowly and reach maturity at a later age than the other threshers (Moreno and Morón, 1992; Mancini & Amorim, 2006; Romero-Caicedo, 2007, Smith et al., 2008a). In addition, though the bigeye thresher typically occurs in temperate and tropical waters, they can endure colder water temperatures and linger longer at deeper waters than many other pelagic sharks (Gruber and Compagno, 1981; Smith et al., 2008a; IPMA, unpublished data).

Open ocean sharks are one of the least-studied groups of large vertebrates, as the study of wide-ranging and highly migratory fishes that spend most of their lives far from land poses particular difficulties (Pikitch et al., 2008). In the last decade the biological studies and knowledge on life history, genetics, and tagging of these species have been improving. However more research is needed for a better assessment of the impact of fisheries on populations and to facilitate effective management plans for these highly migratory shark species (Camhi et al., 2008a; ICCAT, 2013). Due to the shortage of long time series of information (e.g. catches, fishing effort, changes in abundance) on most pelagic shark populations for stock assessment purposes, demographic models are often chosen to provide initial information and prioritize species for research (Simpfendorfer, 2004). Demographic models rely primarily on life history parameters (e.g. age of sexual maturity, maximum reproductive age, instantaneous rate of natural mortality), thus obtaining this type of biologic data should be essential to estimate species vulnerability to the fisheries and also important for stock assessments (Camhi et al., 2008b, Cortés et al., 2010).

Despite being caught as bycatch in pelagic fisheries, little biological information is available for the bigeye thresher in the Atlantic, probably because of the relative low prevalence observed in surface longline catches (Mejuto and Garcés, 1984; Mejuto, 1985; Castro et al., 2000; Berrondo et al., 2007; Mejuto et al., 2009), which has been estimated at around 0.2% of the total shark bycatches combined for the Atlantic (Mejuto et al. 2009). The only extensive reproductive study available for the species is from the Pacific Ocean (Chen et al., 1997), although some reproductive parameters have been reported from the Atlantic (Stillwell and Casey, 1976; Gruber and Compagno, 1981; Moreno and Morón, 1992; Gilmore, 1993, Amorim et al., 1998) but using limited datasets.

When reviewing the demography of pelagic shark species, several authors ranked the bigeye thresher among the least productive species, highlighting its vulnerability to fisheries impacts (Chen and Yuan, 2006; Cortés, 2008; Smith et al., 2008b). In addition, an Ecological Risk Assessment (ERA) of pelagic sharks caught in Atlantic

pelagic longlines placed the bigeye thresher at high risk, highlighting the urgent need for better basic biological information on this species (Cortés et al., 2010). The International Commission for the Conservation of Atlantic Tunas (ICCAT), responsible for the management of this species in the Atlantic, recently prohibited the retention and commercialization of bigeye thresher sharks caught in the fisheries it manages, recommended the release of live specimens when accidentally captured, and required that both incidental catches and live releases be recorded in accordance with ICCAT data reporting requirements (ICCAT Recommendation 2009/07). Despite this, as shown by Coelho et al. (2012), the hooking mortality of the retained specimens from this species may be high (around 51%) in pelagic surface longline fisheries, and simply releasing the caught specimens may not be the most adequate conservation strategy, as the majority of specimens are captured and discarded already dead. However, it is possible that these high at-haulback mortalities are caused by other factors, such as gear configuration including length and material of branch line, main line, and shortening ratio. The IUCN Shark Specialist Group classifies the bigeye thresher as “Vulnerable in global terms” (according to the IUCN Red List Criteria) and “Endangered” in the Northwest Atlantic and Western central Atlantic (Amorim et al., 2009).

In order to improve the limited information available for this species in the Atlantic, the main objectives of this study were to provide information on 1) the distributional patterns of the bigeye thresher shark caught by pelagic longlines targeting tunas or swordfish in the Atlantic Ocean, particularly in terms of sizes, sex-ratios and proportions of juveniles and adult specimens and 2) the reproductive aspects, particularly in terms of median size at maturity and litter size. The results can be used to better evaluate the status and manage this species in the Atlantic Ocean.

## **2. Materials and methods**

### **2.1. Data collection**

Bigeye thresher shark records and observations were registered within the scope of National or scientific observer programmes. The fishery observers from IPMA (*Portuguese Institute for the Ocean and Atmosphere*), NOAA/NMFS (*National Marine Fisheries Service*), DINARA (*Dirección Nacional de Recursos Acuáticos*), NRIFS (*National Research Institute of Far Seas Fisheries*) and scientific projects of IEO (*Instituto Español de Oceanografía*), collected the data onboard Portuguese, US, Uruguayan, Japanese and Spanish commercial longline vessels targeting tunas or swordfish along the Atlantic Ocean, respectively. Data on bigeye thresher shark sizes by sex was available starting in 1992, 1993, 1997, 2003 and 2003 for the US, Spanish, Japanese, Portuguese and Uruguayan fleets, respectively. US and Uruguayan data were available up to 2010, Portuguese and Japanese data up to 2012, and Spanish up to 2013. For the captured specimens, fishery observers recorded data on specimen size, sex, capture location and date. Additionally, in the Portuguese program, maturity stage was also assessed and recorded whenever a dead specimen was captured while retrieving the longline, and in the Spanish, Portuguese and Uruguayan fleets data the observers recorded, when possible, the presence of pregnant females with the respective characteristics of the embryos.

Data were collected along a wide geographical range. For analysis purposes, the two hemispheres were separated based on the 5°N parallel, as recommended in the ICCAT Manual for shark species (ICCAT, 2006-2009).

Furthermore, the region was divided into six major areas taking into consideration not only the ICCAT sampling areas for sharks (ICCAT, 2006-2009), but also the areas of operation and fishing grounds of these pelagic longline fleets in the Atlantic Ocean. These areas were assigned as follows: Northwest – above 24° N and west of 40°W; Northeast - above 24°N and east of 40°W; Tropical North – between 5° N and 24° N; Equatorial – between 5° N and 5° S; Southwest – below 5° S and west of 20°W; Southeast – below 5° S and east of 20°W (**Figure 1**).

All specimens were measured for fork length (FL), except in the case of the NRIFSF program where the specimens were measured for pre-caudal length (PCL). In those cases, the sizes were converted to FL using the equations estimated by Liu et al. (1998). Within the Portuguese Program, the size of the claspers of males was measured and the maturity stage determined qualitatively, whenever possible. Specimens were considered mature and immature using the following criteria based on the scale proposed by Stehmann (2002): for males, stages 1 (immature) and 2 (maturing) were considered immature while stages 3 (mature) and 4 (active) were considered mature. For females, stages 1 (immature) and 2 (maturing) were considered immature, while stages 3 (mature), 4 (developing), 5 (differentiating), 6 (expecting) and 7 (post-natal/resting) were considered mature (**Table 1**).

## 2.2. Data analysis

Size data were tested for normality with Kolmogorov-Smirnov normality tests (with Lilliefors correction) and for homogeneity of variances, with Levene tests. Given the lack of normality of data and homogeneity of variances, even after transforming the data with square-root and log functions, the specimen sizes were compared between regions, sexes and quarters of the year using non-parametric Kruskal-Wallis tests, and *k*-sample permutation tests using the permutational central limit theorem (Manly, 2007). In the cases for which statistical differences were detected, multiple pairwise comparisons tests were carried out to detect between which categories the differences were significant (Siegel and Castellan, 1988).

The sex-ratios were calculated and compared between regions with contingency tables and Pearson's Chi-squared tests. Further, the sex-ratios were also compared between the seasons of the year and size classes (categorized with the 20% percentiles of the data) taking into account the various regions, using Cochran-Mantel-Haenszel (CMH) chi-squared tests. This test allows detecting eventual seasonality of size related effects in the sex-ratios conditional to each of the regions analyzed.

With the maturity stage data recorded by the Portuguese observer program, maturity ogives were developed to estimate the median size at maturity ( $L_{50}$ ), or length at which 50% of the sharks were mature. For each sex, parameters, standard errors, and 95% confidence intervals (CIs) were estimated. The maturity ogives were fitted by non-linear least-squares (NLS) regression, using the equation:

$$P_{Li} = \frac{1}{1 + e^{-b(L_i - L_{50})}}$$

where  $P_{L_i}$  is the proportion of mature individuals in size class  $L_i$  (using 5cm FL size classes),  $b$  is the slope and  $L_{50}$  is the size at which 50% of individuals mature. Maturity ogives were fitted for both sexes separately and  $L_{50}$  estimates were compared between sexes by analyzing overlaps in the 95% CIs.

The relationship between fork length (FL) and clasper length (CL) was also analyzed using a linear regression model. In addition, a segmented regression model (SRM) was used to estimate the transition points and slopes in the regression between fork length and clasper length. These breakpoints have been defined to identify the three FL intervals with different slopes that represent the three maturity stages of male elasmobranchs: “immature”, “maturing” and “mature” (Segura et al., 2013). Thus, the breakpoints are defined as the values of the explanatory variable (FL) at which the changes in slope occur (Muggeo, 2003). Standard errors were calculated for all the estimated parameters and the coefficients of determination were calculated to test the goodness-of-fit. Furthermore, to assess model adequacy to the data, the Akaike information criterion value (AIC) was calculated for both models (linear regression and SRM).

A logistic-binomial generalized linear model (GLM) was created to determine the influence of each region, sex and quarter of the year on the odds-ratios of capturing juvenile specimens, considering the estimated median sizes-at-maturity. The significance of the model parameters was tested with Wald statistics and likelihood ratio tests (LRT), comparing nested models. Model goodness-of-fit was assessed with the Nagelkerke coefficient of determination ( $R^2$ , Nagelkerke, 1991). The discriminative capacity of the models was determined by the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) curves, with the calculation of the model sensitivity (capacity to correctly detect the event, in this case defined as the capture of juveniles), and model specificity (capacity to correctly exclude the non-events, in this case the capture of adults). Cross validation was carried out using a  $k$ -fold cross validation procedure (with  $k = 10$ ) to estimate the expected level of fit of the models to new data, and to assess eventual over-fitting problems (Fushiki, 2011). Because the models in this study are of the binomial type, the cross validation procedure was used to estimate the misclassification error rate. The odds-ratios of the parameters, with their respective 90% CIs, were calculated and used for model interpretation. The equatorial region and quarter 1 were used as the baseline parameters, and the odds-ratios calculated comparatively for the other regions and quarters of the year, taking into account their interaction effects.

Analysis for this paper was carried out using the R language for statistical computing (R Core Team, 2013). Besides the R core program functions, some additional libraries were used, specifically “segmented” for the SRM models (Muggeo, 2003), “gmodels” for the contingency table analysis (Warnes et al., 2012), “ggplot2” for the graphical analysis (Wickham, 2009), and “maps” (Becker et al., 2013), “maptools” (Bivand and Lewin-Koh, 2013) and “mapplots” (Gerritsen, 2013) for the maps.

### **3. Results**

#### ***3.1. Size distribution***

A total of 4371 bigeye thresher shark specimens were recorded within the scope of this study (2547 from the Spanish fleet, 1211 from Portuguese fleet, 426 from the USA fleet, 134 from the Japanese fleet and 53 from the Uruguayan fleet). The specimens ranged in size from 70 to 305 cm FL (70-300 cm FL for females and 75-305 cm FL for males), covering most of the known size-range of the species. The sample was composed mostly of specimens captured in the tropical north (42.7%) and southeast regions (29.1%), followed by 11.7% in the northwest, 8.3% in the equatorial, 5.1% in the northeast and 3.2 in the southwest (**Figure 1**).

Considerable variability was observed in the size distribution of males and females among the Atlantic regions. The larger-sized specimens tended to be captured mainly in the higher latitudes, predominantly in the northwest and southwest Atlantic, while smaller specimens tended to be captured mainly in the tropical north and northeast areas (**Figure 2**). It was also noteworthy that a very low prevalence of the smaller sized specimens (<150 cm FL) was recorded on all regions (**Figure 2**). These regional trends tended to be common for both males and females, even though some differences between sexes were detected. In general, in the higher northern and southern latitudes, males tended to be larger than females in the eastern regions, while females tended to be larger in the western regions (**Figure 3**). In the equatorial area and tropical north, males also tended to be larger than females (**Figure 3**).

Seasonality also seems to influence the size of captured bigeye thresher sharks. In the northern regions an opposite trend was observed when comparing the northwest and northeast, with sizes tending to increase throughout the year in the northwest and decrease in the northeast, both with similar size ranges (**Figure 4**). In the southeast region sizes remained almost constant throughout the year, in contrast to the southwest region where larger seasonal variability was observed, with smaller specimens caught in the 2<sup>nd</sup> and 3<sup>rd</sup> quarters, and larger ones in the 1<sup>st</sup> and 4<sup>th</sup> quarter (**Figure 4**). In the Equatorial region there was also some tendency for increasing sizes along the year (**Figure 4**).

Size data were not normally distributed (Lilliefors test:  $D = 0.045$ ,  $p\text{-value} < 0.001$ ) and the variances were not homogeneous among regions (Levene test:  $F = 19.17$ ,  $df = 5$ ,  $p\text{-value} < 0.001$ ), sexes (Levene test:  $F = 13.40$ ,  $df = 1$ ,  $p\text{-value} < 0.001$ ) and quarters (Levene test:  $F = 13.83$ ,  $df = 3$ ,  $p\text{-value} < 0.001$ ). Using univariate non-parametric statistical tests revealed that sizes were significantly different among regions (K-W: chi-squared = 301.83,  $df = 5$ ,  $p\text{-value} < 0.001$ ; permutation test: chi-squared = 293.63,  $df = 5$ ,  $p\text{-value} < 0.001$ ) and between sexes (K-W: chi-squared = 26.19,  $df = 1$ ,  $p\text{-value} < 0.001$ ; permutation test: chi-squared = 12.51,  $df = 1$ ,  $p\text{-value} < 0.001$ ), but not among quarters of the year (K-W: chi-squared = 5.20,  $df = 3$ ,  $p\text{-value} = 0.158$ ; permutation test: chi-squared = 7.72,  $df = 3$ ,  $p\text{-value} = 0.052$ ).

### 3.2. Sex ratios

Of the total bigeye thresher sharks recorded, 2039 (46.6%) were females and the remaining 2332 (53.4%) were males, with some local variability recorded in the sex ratios (**Figure 5**). Particularly, there seemed to be some evidence of the presence of more males in coastal waters of central Africa and in oceanic South Atlantic waters,

while around some islands, such as in the Cape Verde archipelago, the sex ratio was biased towards the presence of more females (**Figure 5**).

When comparing the major regions defined in this study there were significant differences in the sex ratios (prop. test: chi-squared: 24.17, df = 5, p-value < 0.001), with the northeast and southeast showing a much higher proportion of males, the northwest and equatorial showing slightly higher proportion of males, while in the southwest and tropical north the sex ratios were very similar between males and females (**Figure 6**). There were also significant differences in sex ratios among seasons when those were compared conditionally within the different regions (CMH test: chi-squared = 25.65, df = 3, p-value < 0.001). A higher proportion of females was observed during the 2nd quarter of the year in the northeast and during the 3rd quarter in the southwest. In contrast, a much lower proportion of females was observed in the 2nd quarter in the tropical north compared to a generally higher proportion of females in this region throughout the rest of the year (**Figure 7**). In the northwest and equatorial regions sex ratios remained relatively constant throughout the year with values approximately 50% for each sex, while in the southeast sex ratios were also relatively constant but with a much higher proportion of males throughout the year (**Figure 7**).

Significant differences were also detected in the sex ratios among sizes tested conditionally within the different regions (CMH test: chi-squared = 33.95, df = 4, p-value < 0.001). A higher proportion of males was observed in the larger size classes in the northeast and southeast, while in the northwest there was a tendency for a higher proportion of females in the larger sizes (**Figure 8**). In the tropical north, equatorial and southwest there were higher proportion of females both in the smaller and larger size classes, and more males in the middle sizes (**Figure 8**).

### 3.3. Median size at maturity

Maturity information was available for 642 specimens, from which 257 were females (232 immature and 25 mature) and 385 were males (157 immature and 228 mature) (**Table 2**). Sample size of mature females was thus low. For this reason, maturity ogives and the clasper length vs. FL relationship were calculated using combined data from all regions.

Estimated maturity ogives are presented in **Figure 9** and the respective equations are:

$$PLi = \frac{1}{1 + e^{-0.06(Li-208.64)}} \quad \text{for females}$$

and

$$PLi = \frac{1}{1 + e^{-0.07(Li-159.24)}} \quad \text{for males.}$$

Female bigeye thresher sharks mature at larger sizes than males (**Table 2**). Differences between sexes were significant because the 95% CIs of  $L_{50}$  do not overlap. Both sexes are late maturing, with females maturing at 208.63 cm FL (79% of the maximum observed size) and males at 159.24 cm FL (61% of the maximum observed

size). The largest immature female was 220 cm FL, while the smallest mature female was 140 cm FL. For males, the largest immature specimen was 203 cm FL, while the smallest mature specimen was 130 cm FL.

The claspers of 372 male specimens were measured and their lengths were plotted against FL (**Figure 10**). A linear regression fitted the FL vs. clasper length data well ( $CL = 0.26FL - 18.97$ ;  $r^2 = 0.96$ ,  $AIC = 143.38$ ), but the SRM had an even higher coefficient of determination and lower value of AIC ( $r^2 = 0.99$ ,  $AIC = 118.25$ ), indicating a better goodness-of-fit to the data than the linear regression. Two breakpoints were estimated for bigeye thresher males with the SRM, resulting in three linear phases such that:

- (1)  $CL = 0.03FL + 5.06$  if  $FL < 122.5$  cm
- (2)  $CL = 0.38FL - 37.97$  if  $122.5 \leq FL \leq 173.3$  cm
- (3)  $CL = 0.2FL - 6.78$  if  $FL > 173.3$  cm

These three linear phases represent the successive maturity stages effectively modeled by the SRM. Thus, phase 1 contains the immature sharks characterized by a subtle slope close to zero; phase 2 represents the transitional “maturing” stage with the steepest slope; and phase 3 presents a flatter slope containing only the mature specimens.

### ***3.4. Litter size and presence of pregnant females***

Overall, 14 pregnant females were observed, plus two that showed signs of recent mating but still had no visible embryos in the uteri. Each of the pregnant females had two embryos, specifically one in each of the uterus.

The occurrence of pregnant females was recorded mainly in two regions of the study area, specifically in the tropical northeast between 1-17°N / 9-32°W, and southwest between 21-36° S / 30- 52°W (**Figure 1**). In the tropical northeast Atlantic, the smallest pregnant female recorded had 210 cm FL and the largest 240 cm FL, and the recorded embryos ranged in size between 30 and 90 cm FL. In the southwest Atlantic, the smallest pregnant female recorded had 209 cm FL and the largest 256 cm FL, with the two females that showed recent signs of mating also recorded in this area and having 207 cm FL. In the southwest Atlantic, the recorded embryos ranged in size between 6 and 73 cm FL, noting that the embryos measuring 6 cm FL were recorded in one female in the early pregnancy stages (with the embryos still encapsulated) in a region closer to the Uruguayan coast.

### ***3.5. Distribution of expected juveniles and adults***

Considerable variability was observed in the distribution of juvenile and adult specimens, when considering sex, region, and season factors, but in general most regions and seasons tended to have a high proportion of juvenile females and adult males (**Figure 11**).

The final estimated logistic-binomial GLM considered the factors sex (deviance explained = 1728.1,  $df=1$ ,  $p$ -value < 0.001), region (deviance explained = 115.5,  $df=5$ ,  $p$ -value < 0.001) and quarter (deviance explained =



0.06,  $df=3$ ,  $p$ -value = 0.553), and also the interaction between quarter and region (likelihood ratio test for nested models: deviance explained = 80.7,  $df=15$ ;  $p$ -value < 0.001). Even though the variable quarter was not significant in terms of single effect, the presence of a significant interaction with region justified having this variable, as well as the interaction, in the model. In terms of goodness-of-fit, the final model had a Nagelkerke  $R^2$  of 0.479 and an AUC of 0.851, with a sensitivity of 71.1% and a specificity of 88.9%. The  $k$ -fold cross-validation procedure resulted in a predicted error for new data of 21.3%.

Compared to the baseline combination (Equatorial region and quarter 1), the odds of capturing juveniles increased in some area-season combinations, whereas they decreased in others. Specifically, the odds-ratios of capturing more juvenile specimens increased significantly in the northeast quarter 4, tropical north quarter 3, southwest quarters 2 and 4, and southeast quarters 2, 3 and 4, and decreased significantly in several regions earlier in the year, specifically in the quarter 1 of the northeast, northwest, southwest and southeast, as well as in the equatorial region in quarters 3 and 4 (**Figure 12**). Additionally, the odds of capturing juvenile males were substantially lower than the odds of capturing juvenile females, with the odds-ratios decreasing by 95.6% (CI: 94.9%-96.3%).

#### 4. Discussion

Differences in the length-frequency distributions and proportions of juvenile and adult specimens were found among the regions of the Atlantic Ocean examined. The most significantly different region seemed to be the tropical north Atlantic, where specimens tended to be smaller and the proportion of juveniles (both males and females) higher. The reasons for these differences are not entirely understood yet, but it is possible that there are migratory and habitat segregation patterns by growth stages between the regions and seasons of the year, with smaller and younger sharks concentrating predominantly in the tropical northern region, while the larger adults seem to prefer the temperate areas of the northern and southern Atlantic. However, it is important to note that the data used in our study comes from several different fleets, with different fishing métiers that target different species, and as such the size ranges and abundance reported by each fleet for each region are also being affected by fleet selectivity. With regards to the spatial distribution of the data, and while part of the observations reported may reflect the species spatial dynamics, they are also being influenced by the sampling effort within each fleet, and are not necessarily representative of the prevalence of the species at each locations.

The maximum sizes observed in our sample (504 cm TL for males and 496 cm TL for females, after conversion from FL) were higher than reported in the literature (484 cm TL reported by Thorpe, 1997; 357 cm TL for males and 422 cm TL for females reported by Liu et al., 1998; 410 cm TL for males and 461 for females reported by Moreno and Morón, 1992). Additionally, the smallest specimens in our sample were 126 cm TL, which is slightly lower than the size at birth of 135-140 cm TL suggested by Chen et al. (1997), and within the 100-140 cm TL suggested by Compagno et al. (2005). This indicates that the sample in our study is covering most of the size classes of the species. However, a very low prevalence of the smaller size classes (particularly specimens with < 150 cm FL) was reported in our study in most of the analyzed regions. This might be related with the fact that the fleets analyzed are operating mainly in oceanic waters, while the smaller sized specimens may be occurring

in other regions not covered in our study, such as more coastal regions where they would be accessible and taken by coastal fleets operating with other fishing gears such as nets and coastal longlines. This higher prevalence of juveniles in more coastal waters has been previously recorded for some other oceanic species, and a similar life history pattern may be occurring with the bigeye thresher shark. Another possible hypothesis would be to consider that the lack of smaller sized specimens might be related with fishing gear selectivity, but given that the bigeye thresher sharks are born at relatively larger sizes, if those smaller specimens were present in oceanic waters then they would likely also be captured by those pelagic longlines. As such, the hypothesis of a life history cycle with the occurrence of smaller specimens in more coastal areas and larger specimens in more oceanic waters is likely to be occurring with the bigeye thresher shark.

As documented for other shark species (Cortés, 2000), the estimated median size at maturity was significantly higher for females (208.6 cm FL, 349.1 cm TL) than males (159.7 cm FL, 269.8 cm TL). Although the number of mature females in the present study was small, these values for the bigeye thresher in the Atlantic are very close to the sizes at first maturity reported by Moreno and Morón (1992) for the Northeast Atlantic (from Cape São Vicente to the Ivory Coast) and Western Mediterranean Sea (340 cm TL for females and 270 cm TL for males, or 200.2 cm FL and 159.9 cm FL respectively). In Taiwanese waters, Chen et al. (1997) reported median sizes at maturity of 336.3 cm TL (estimated 198.2 cm FL) for females and 279 cm TL (estimated 165.2 cm FL) for males, values which are just slightly lower and higher than ours for females and males, respectively. For the northwestern Atlantic, Stillwell and Casey (1976) suggested 350 cm TL (estimated 206 cm FL) as size at first maturity for females and 295 cm TL (estimated 174.3 cm FL) for males, values almost identical to ours for females and a little higher for males. Significant differences between median sizes at maturity have also been reported for the common thresher (*A. vulpinus*) in the north Atlantic, with 216 cm FL for females and 188 cm FL for males (Natanson and Gervelis, 2013) (**Table 3**).

The SRM of male size vs. clasper length predicted that the onset of maturity in male bigeye thresher sharks starts at ca. 122.5 cm FL (first breakpoint) and that all males in the population are mature at ca. 173.3 cm FL (second breakpoint). The fact that the median size at maturity estimated through the maturity ogive ( $L_{50}$  = 159.2 cm FL) is included between the two breakpoints of the regression, seems to support the effectiveness of this method. Furthermore, other authors have used this approach as it provides an objective and direct estimate of the maturity stages of male elasmobranchs (using only clasper measurements) instead of relying on a subjective classification which depends on the observer's ability and may vary between different observers (Segura et al., 2013). In addition, it is a non-invasive method and can be applied to existent common fisheries data (Segura et al., 2013).

The estimated median size at maturity occurs at ca. 79% of the maximum observed size for bigeye thresher females and 61% for males. After examining 164 shark species, Cortés (2000) concluded that on average shark size-at-maturity takes place at about 75% of the maximum observed size. Thus, the values presented here follow this general trend, although our male estimation is a slightly lower than the average. Furthermore, it has been documented that the ratio of size at maturity and maximum observed length ( $L_{50}/L_{max}$ ) ranges from 0.5 to 0.95 for sharks, with most being between 0.65 and 0.8 (e.g. Joung and Chen, 1995). The ratios obtained in the present study are comparable to the values of 0.77 and 0.67 for females and males, respectively, obtained by Moreno and

Morón (1992). Stillwell and Casey (1976) reported a similar ratio to ours (0.77 vs. 0.79) for females in the northwestern Atlantic but a higher value for males (0.79 vs. 0.61). In the Pacific Ocean, Chen et al. (1997) suggested an identical ratio to ours for females (0.79) and higher value for males (0.78). Following the same trend of this study, ratios of 0.8 and 0.7 were estimated in the north Atlantic for female and male shortfin mako, also a Lamniformes species (Natanson et al., 2006). Joung and Chen (1995) proposed three stages of maturity based on the  $L_{50}/L_{max}$  ratio: 1 = early maturity ( $L_{50}/L_{max} < 0.65$ ), 2 = standard maturity ( $0.65 < L_{50}/L_{max} < 0.8$ ), and 3 = late maturity ( $L_{50}/L_{max} > 0.8$ ). The bigeye thresher can thus be considered to follow a standard maturity pattern, with females tending toward late maturity, while males are closer to early maturity.

The fitted logistic-binomial GLM had a high goodness-of-fit with relatively high  $r^2$  and AUC values, and the cross-validation procedure resulted in a low misclassification error rate. Values of AUC between 0.8-0.9, which is the case of the present study, are considered excellent (Hosmer and Lemeshow, 2000), and as such the goodness-of-fit of the presented model also seems very good, with the model having the capacity to correctly predict the capture of juveniles in 71.1% of the cases, while at the same time correctly predicts the capture of adults in 88.9% of the cases. The cross-validation misclassification error rate was estimated at 21.3%, which also seems very reasonable, meaning that most of the times the model is correctly discriminating between the capture of juvenile versus adult specimens under the analyzed variables. One advantage of this model that covered a wide Atlantic region is that it provides a very general overview in terms of large-scale oceanic areas, with the downside of losing some detail in specific regions and seasons. As such, this model and odds-ratios outputs should be regarded mainly as general values in the context of these large-scale oceanic areas, bearing in mind that exceptions are very likely to occur in specific and smaller-scale areas. The tropical north region seemed to differ from the remaining areas because in most seasons the odds of capturing more juveniles than adults increased significantly. Similarly, in some of the other regions there were also increased odds of capturing more juveniles, but those were dependent on specific seasons, as for example in the northeast and northwest regions in the 2nd quarter.

Moreno and Morón (1992) suggested the existence of a nursery area for this species off the Southwestern Iberian Peninsula in the northeast Atlantic. After our study we hypothesize that such an area may exist and possibly extended further south, into the tropical northeast Atlantic and equatorial waters closer to the African continent. This seems to be validated by the fact that smaller and mainly juvenile specimens tended to be captured in this region, but also because a few pregnant females, both mid- and late-term (stages 5- differentiating and 6- expecting), were also recorded in the region. Additionally, the tropical northwestern Atlantic, particularly in areas closer to the Caribbean Sea, may also serve as a nursery as some very small specimens (within the range of sizes at birth described by Chen et al., 1997 and Compagno et al., 2005) were captured in that region. Finally, another cluster of pregnant females was recorded in the southwest Atlantic, some closer to the Rio Grande Rise and a few inside the Uruguayan EEZ and those may also be serving as nursery areas for this species in the South Atlantic. As such, we can hypothesize that at least those areas may constitute nursery areas for the bigeye thresher, but we cannot exclude the possibility of other nurseries along the Atlantic. In some cases we have size observations but without reproductive data, as the observations used in this study depend on the specific objectives of the projects and programs collecting the data. Furthermore, while the geographical coverage of our

study in wide, there are areas not covered and we cannot exclude the possibility of the presence of pregnant females and small juveniles in those areas.

All thresher sharks are listed as “Vulnerable globally” by the IUCN and are known to have vulnerable life history parameters, resulting in a low capacity to recover even from moderate levels of exploitation (Amorim et al., 2009). The size at maturity obtained in the present study reinforces that the bigeye thresher reaches maturity at a larger size than the other species of the Alopiidae family, as stated by Smith et al. (2008a). Assuming that age at maturity is also reached at a late age, and together with its very limited fecundity, this suggests that the reproductive potential of the bigeye thresher is very low. The distributional patterns of sizes and maturity stages in the six regions during different seasons of the year can be used to better inform future management decisions and conservation initiatives for this species in the Atlantic Ocean.

## 5. Acknowledgments

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## 6. References

- Amorim, A., Arfelli C., Fagundes L., 1998. Pelagic elasmobranchs caught by longliners off southern Brazil during 1974-97: an overview. *Mar. Freshwater Res.*, 49: 621-32
- Amorim, A., Baum, J., Cailliet, G.M., Clò, S., Clarke, S.C., Fergusson, I., Gonzalez, M., Macias, D., Mancini, P., Mancusi, C., Myers, R., Reardon, M., Trejo, T., Vacchi, M., Valenti, S.V., 2009. *Alopias superciliosus*. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2. <[www.iucnredlist.org](http://www.iucnredlist.org)>. Downloaded on 01 April 2013.
- Becker, R.A., Wilks, A.R., Brownrigg, R., Minka, T.P., 2013. maps: Draw Geographical Maps. R package version 2.3-6. <http://CRAN.R-project.org/package=maps>.
- Berrondo, L., Pons, M., Forselledo, R., Millar P. & Domingo A., 2007. Distribución espacio-temporal y composición de tallas de *Alopias superciliosus* y *A. vulpinus* observados en la flota palangrera Uruguaya en el océano Atlántico (2001-2005). *Col. Vol. Sci. Pap. ICCAT*. 60(2): 566-576
- Bivand, R., Lewin-Koh, N. 2013. mapproj: Tools for reading and handling spatial objects. R package version 0.8-27. <http://CRAN.R-project.org/package=mapproj>.

- Cailliet, G.M., Bedford, D.W., 1983. The Biology of three Pelagic Sharks from California Waters, and Their Emerging Fisheries: A Review. CalCOFI Rep. Vol. XXIV, 57-69.
- Camhi, M. D., Pikitch, E. K., Babcock, E. A. (Eds.). 2008a. Methods to Improve Understanding of Pelagic Sharks: Demographics, Assessment, and Stock Structure, In: Sharks of the Open Ocean: Biology, Fisheries and Conservation, Blackwell Publishing, Oxford, pp 285-287.
- Camhi, M. D., Pikitch, E. K., Babcock, E. A. (Eds.). 2008b. Life History and Status of Pelagic Elasmobranchs, In: Sharks of the Open Ocean: Biology, Fisheries and Conservation, Blackwell Publishing, Oxford, pp 55-59.
- Campana, S.E., Marks, L., Joyce, W., 2005. The biology and fishery of shortfin mako sharks (*Isurus oxyrinchus*) in Atlantic Canadian waters. Fish. Res. 73, 341–352.
- Castro, J., Serna, J.M., Mácias, D., Mejuto, J. 2000. Estimaciones científicas de los desembarcos de especies asociadas realizados por la flota española de palangre de superficie en 1997 y 1998. Col. Vol. Sci. Pap. ICCAT, 51 (6): 1882-1893.
- Chen, C.T., Liu, K.M., Chang, Y.C., 1997. Reproductive biology of the bigeye thresher shark, *Alopias superciliosus* (Lowe, 1839) (Chondrichthyes: Alopiidae), in the northwestern Pacific. Ichthyol. Res. 44, 227-235.
- Chen, P., Yuan, W., 2006. Demographic analysis based on the growth parameter of sharks. Fish. Res. 78, 374–379.
- Coelho, R., Fernandez-Carvalho, J., Lino, P.G., Santos, M.N., 2012. An overview of the hooking mortality of elasmobranchs caught in a swordfish pelagic longline fishery in the Atlantic Ocean. Aquat. Living Resour. 25, 311–319.
- Conrath, C.L., 2004. Reproductive biology, In: Musick, J.A., Bonfil, R. (Eds.), Elasmobranch Fisheries Management Techniques. APEC Secretariat, Singapore, pp. 133–164.
- Compagno, L.J.V., 2001. Sharks of the world. An annotated and illustrated catalogue of shark species known to date: bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO, Rome.
- Compagno LJV, Dando M, Fowler S. 2005. Sharks of the World. Harper Collins: London.
- Cortés, E., 2000. Life history patterns and correlations in sharks. Res. Fish. Sci. 8, 299-344.
- Cortés, E., 2008. Comparative life history and demography of pelagic sharks, In: Camhi, M. D., Pikitch, E. K., Babcock E. A. (Eds.), Sharks of the Open Ocean: Biology, Fisheries and Conservation. Blackwell Publishing, Oxford, pp 309-322.
- Cortés, E., Arocha, F., Beerkircher, L., Carvalho, F, Domingo, A., Heupel, M., Holtzhausen, H., Santos, M.N., Ribera, M., Simpfendorfer, C., 2010. Ecological risk assessment of pelagic sharks caught in Atlantic pelagic longline fisheries. Aquat. Living Resour. 23, 25–34.
- Fernandez-Carvalho, J., Coelho, R., Erzini, K., Santos, M.N., 2011. Age and growth of the bigeye thresher shark, *Alopias superciliosus*, from the pelagic longline fisheries in the tropical northeastern Atlantic Ocean, determined by vertebral band counts. Aquat. Living Resour. 24, 359–368.
- Fushiki, T., 2011. Estimation of prediction error by using K-fold cross-validation. Stat. Comput. 21, 137–146.
- Gerritsen, H. 2013. mapplots: Data visualisation on maps. R package version 1.4. <http://CRAN.R-project.org/package=mapplots>.
- Gilmore, R.G., 1993. Reproductive biology of lamnoid sharks. Environ. Biol. Fishes. 38, 95–114.

- Gruber, S. H., Compagno, L. J. V., 1981. Taxonomic status and biology of the bigeye thresher *Alopias superciliosus*. US Fish. Bull. 79, 617-40.
- Hosmer, D.W., Lemeshow, S., 2000. Applied Logistic Regression, 2<sup>nd</sup> ed. Wiley, New York.
- ICCAT., 2006-2013. ICCAT Manual. International Commission for the Conservation of Atlantic Tuna. In: ICCAT Publications [on-line]. Updated 2013. <http://www.iccat.int/en/ICCATManual.htm>.
- ICCAT, 2013. 2013 Report of the Inter-Sessional meeting of the sharks species group. Mindelo, Cape Verde – April 8 to 12, 2013. 81pp.
- Joung, S.J., Chen, C.T., 1995. Reproduction in the sandbar shark, *Carcharhinus plumbeus*, in the waters off northeastern Taiwan. Copeia. 1995, 659-665.
- Liu, K., Chen, C., Liao, T., Joung, S., 1999. Age, growth, and reproduction of the pelagic thresher shark *Alopias pelagicus* in the northwestern Pacific. Copeia 1999 (1), 68–74.
- Liu, K.M., Chiang, P.J., Chen, C.T., 1998. Age and growth estimates of the bigeye thresher shark, *Alopias superciliosus*, in northeastern Taiwan waters. Fish. Bull. 96, 482-491.
- Mancini, P., Amorim A., 2006. Embryos of common thresher shark *Alopias vulpinus* in southern Brazil, South Atlantic Ocean. J. Fish. Biol., 69: 318–321.
- Manly, B. 2007. Randomization Bootstrap and Monte Carlo Methods in Biology, 3rd ed. Chapman & Hall/CRC, New York.
- Mejuto, J., 1985. Associated catches of sharks, *Prionace glauca*, *Isurus oxyrinchus*, and *Lamna nasus*, with NW and N Spanish swordfish fishery, in 1984. International Council for the Exploration of the Sea. C.M. 1985/H: 42. 16pp.
- Mejuto, J., Garcés, A.B., 1984. Shortfin mako, *Isurus oxyrinchus*, and porbeagle, *Lamna nasus*, associated with longline swordfish fishery in NW and N Spain. International Council for the Exploration of the Sea. C.M. 1984/G: 72. 10pp.
- Mejuto, J., García-Cortés, B., Ramos-Cardelle, A., Serna, J.M. 2009. Scientific estimations of by-catch landed by the Spanish surface longline fleet targeting swordfish (*Xiphias gladius*) in the Atlantic Ocean with special reference to the years 2005 and 2006. Collect. Vol. Sci. Pap. ICCAT, 64 (7): 2455-2468.
- Muggeo, V.M.R. 2003. Estimating regression models with unknown break-points. Statist. Med. 22, 3055-3071.
- Moreno, J.A., Morón, J., 1992. Reproductive biology of the bigeye thresher shark, *Alopias superciliosus* (Lowe, 1839). Aust. J. Mar. Freshw. Res. 43, 77-86.
- Nagelkerke, N., 1991. A note on a general definition of the coefficient of determination. Biometrika 78, 691–692.
- Natanson, L.J., Gervelis, B.J., 2013. The Reproductive Biology of the Common Thresher Shark in the Western North Atlantic Ocean. T. Am. Fish. Soc. T, 142:6, 1546-1562.
- Natanson, L.J., Kohler, N.E., Ardizzone, D., Cailliet, G.M., Wintner, S.P., Mollet, H.F., 2006. Validated age and growth estimates for the shortfin mako, *Isurus oxyrinchus*, in the North Atlantic Ocean. Environ. Biol. Fish. 77, 367–383.
- Pikitch, E. K., Camhi, M. D., Babcock, E. A., 2008. Introduction to Sharks of the Open Ocean, In: Camhi, M. D., Pikitch, E. K., Babcock E. A. (Eds.), Sharks of the Open Ocean: Biology, Fisheries and Conservation, Blackwell Publishing, Oxford, pp 3-13.

- R Core Team 2013, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Romero-Caicedo, A. 2007 Aspectos reproductivos del tiburón rabón *Alopias pelagicus* (Nakamura, 1935) en Manta, Ecuador. En: Martínez-Ortíz J & F Galván-Magaña (eds). Tiburones en el Ecuador: Casos de estudio / Sharks in Ecuador: Case studies. EPESPO - PMRC. Manta, Ecuador. 28-34.
- Segura, A.M., Milessi, A.C., Vogler, R., Galvan-Magana, F., Muggeo, V., 2013. The determination of maturity stages in male elasmobranchs (Chondrichthyes) using a segmented regression of clasper length on total length. *Can. J. Fish. Aquat. Sci.* 70, 830-833.
- Siegel, S., Castellan, N.J., 1988. Non parametric statistics for the behavioural sciences. MacGraw Hill, New York. 399p.
- Simpfendorfer, C. A., 2004 Demographic models: life tables, matrix models and rebound potential, In: Musick J.A., Bonfil R. (Eds.), *Elasmobranch Fisheries Management Techniques*, APEC Secretariat, Singapore, pp. 133–164.
- Smith, S. E., Rasmussen, R. C., Ramon, D. A., Cailliet, G. M., 2008a. The Biology and Ecology of Thresher Sharks (Alopiidae), In: Camhi M. D., Pikitch, E. K., Babcock, E. A. (Eds.), *Sharks of the Open Ocean: Biology, Fisheries and Conservation*, Blackwell Publishing, Oxford, pp 60-68.
- Smith, S. E., Au, D. W., Show, C., 2008b. Intrinsic rates of increase in pelagic elasmobranchs, In: Camhi, M. D., Pikitch, E. K., Babcock, E. A. (Eds.), *Sharks of the Open Ocean: Biology, Fisheries and Conservation*, Blackwell Publishing, Oxford, pp 288-297.
- Stehmann, M.F.W., 2002. Proposal of a maturity stages scale for oviparous and viviparous cartilaginous fishes (Pisces, Chondrichthyes). *Arch. Fish. Mar. Res.* 50, 23-48.
- Stillwell, C. E., Casey, J. G., 1976. Observations on the bigeye thresher shark, *Alopias superciliosus*, in the western north Atlantic. *Fish. Bull.* 74, 221-225.
- Thorpe, T. 1997. First Occurrence and new length record for bigeye thresher in North-East Atlantic. *J. Fish. Biol.*, 50: 222-224.
- Warnes, G.R., Bolker, B., Lumley, T., Johnson, R.C. 2012. *gmodels: various R programming tools for model fitting*. R package version 2.15.3. <http://CRAN.R-project.org/package=gmodels>.
- Wickham, H. 2009. *ggplot2: elegant graphics for data analysis*. Springer, New York.

## Tables

**Table 1.** Maturity stages for the bigeye thresher (*Alopias superciliosus*) used in this study, based on the Stehmann (2002) scale.

Sex	Maturity	Stg	Stage	Description
Male	Immature	1	Immature	Small claspers, shorter than pelvic fins and flexible. Testes small, sperm ducts thread-like.
		2	Maturing	Claspers equal or longer than the pelvic fin, still flexible. Testes larger, sperm ducts beginning to coil.
	Mature	3	Mature	Claspers fully formed and stiff. Gonads enlarged filled with sperm. Sperm ducts tightly coiled filled with sperm.
		4	Active	Claspers dilated and swollen. Testes segmented and well irrigated.
Female	Immature	1	Immature	Ovaries small, their internal structure granulated. Oviducts (uteri) narrow, thread-like.
		2	Maturing	Ovaries somewhat enlarged. Oocytes becoming differentiated to various small sizes. Wider uteri.
		3	Mature	Ovaries large, well rounded and with many oocytes. Oocytes enlarged, all about the same size.
	Mature	4	Developing	Uteri well filled and rounded with seemingly unsegmented yolk content.
		5	Differentiating	Uteri well filled and rounded with segmented content of large yolk. Small embryos.
		6	Expecting	Embryos fully formed, yolk sacs reduced. Embryos can be counted, measured and sexed easily.
		7	post-natal/ resting	Ovaries at resting stage. Uteri empty but still widened.



**Table 2.** Bigeye thresher (*Alopias superciliosus*) observed size ranges and estimated length at 50% maturity ( $L_{50}$ ) with 95% confidence intervals for males and females obtained in this study. LCL is lower confidence limit, UCL is upper confidence limit,  $L_{max}$  is maximum fork length observed.

Sex	Size range (cm FL)				$L_{50}$ (cm)	95% CI		$L_{50} / L$
	Immature	n	Mature	n		LCL	UCL	
Females	100-220	232	140-264	25	208.6	204.8	212.9	0.79
Males	90 - 200	157	130 - 260	228	159.2	156.5	162.0	0.61

**Table 3.** Summary of thresher shark (genus *Alopias*) size at maturity previously reported in the literature, with a comparison to the estimates presented in this study.

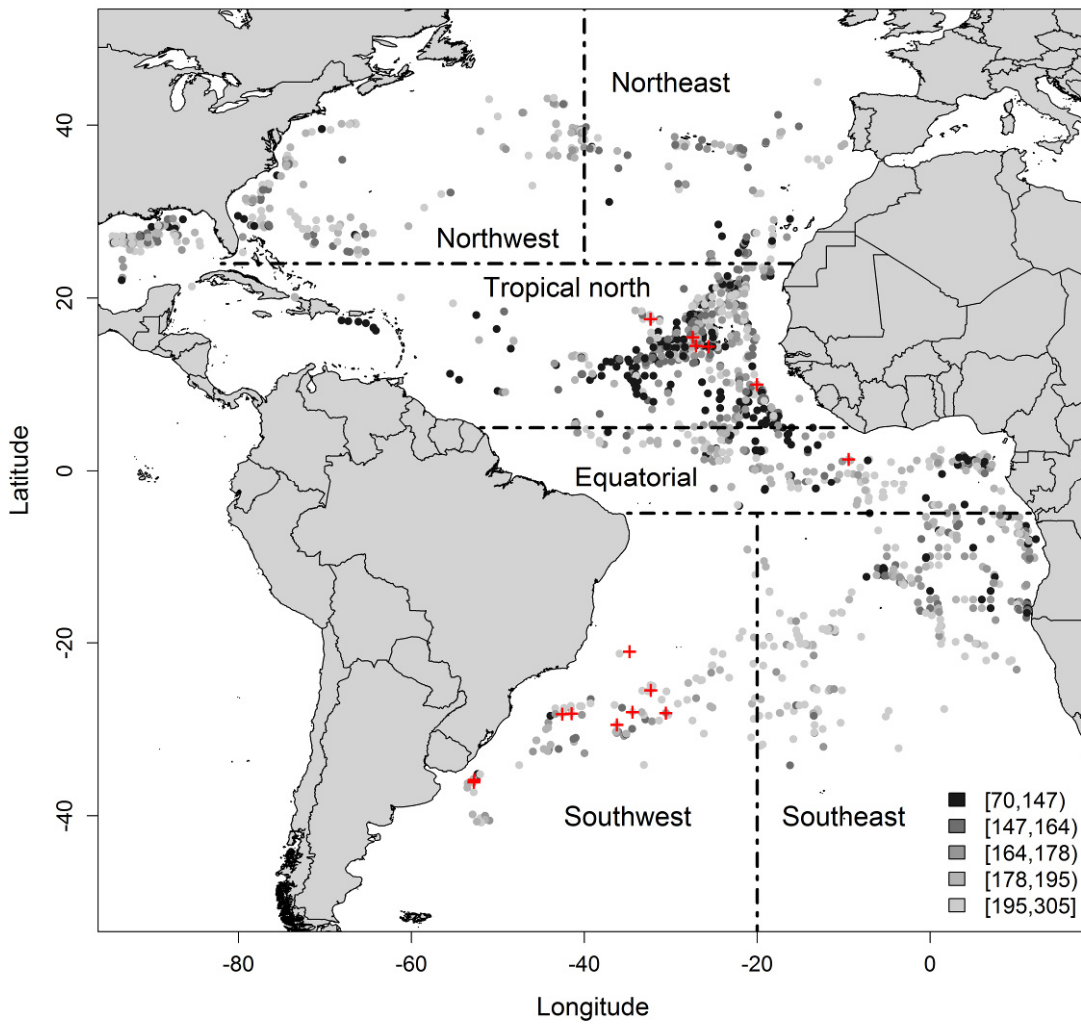
	Size at maturity (cm)		Region	Species
	Males (TL)	Females (TL)		
Current study <sup>*a</sup>	269.8	349.1	Atlantic	<i>A. superciliosus</i>
Moreno and Morón (1992) <sup>b</sup>	270	340	Atlantic	<i>A. superciliosus</i>
Chen et al. (1997) <sup>a</sup>	270–288	332–341	Pacific	<i>A. superciliosus</i>
Stillwell and Casey (1976) <sup>b</sup>	295	350	NW Atlantic	<i>A. superciliosus</i>
Cailliet and Bedford (1983)	333	260-315	Pacific	<i>A. vulpinus</i>
Smith et al. (2008a) <sup>a</sup>	293–311	303	Pacific	<i>A. vulpinus</i>
Natanson and Gervelis (2013) <sup>*a</sup>	333	386	NW Atlantic	<i>A. vulpinus</i>
Liu et al. (1999) <sup>a</sup>	267-276	282–292	Pacific	<i>A. pelagicus</i>

\* Studies that reported the estimates in fork length (FL) and were converted to total length (TL) to facilitate comparison.

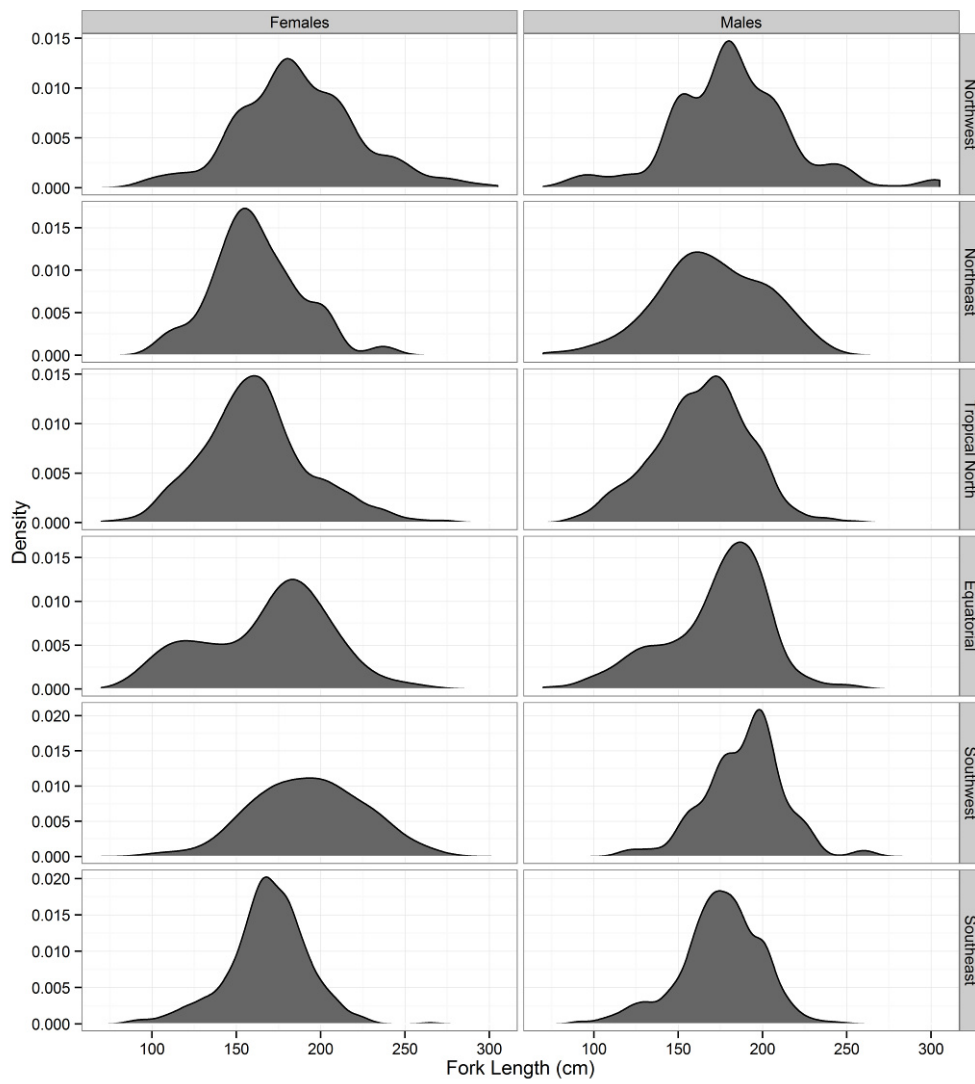
<sup>a</sup>: Studies that reported median size at maturity.

<sup>b</sup>: Studies that reported size at first maturity from observational data.

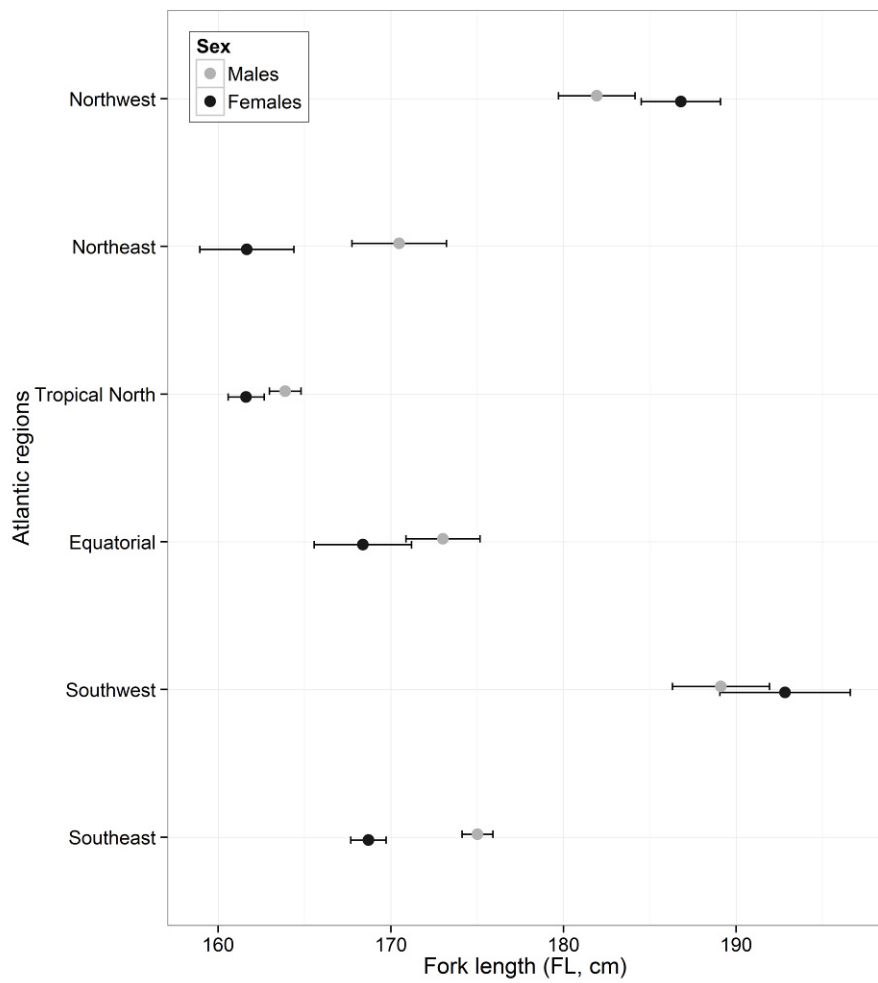
## Figures



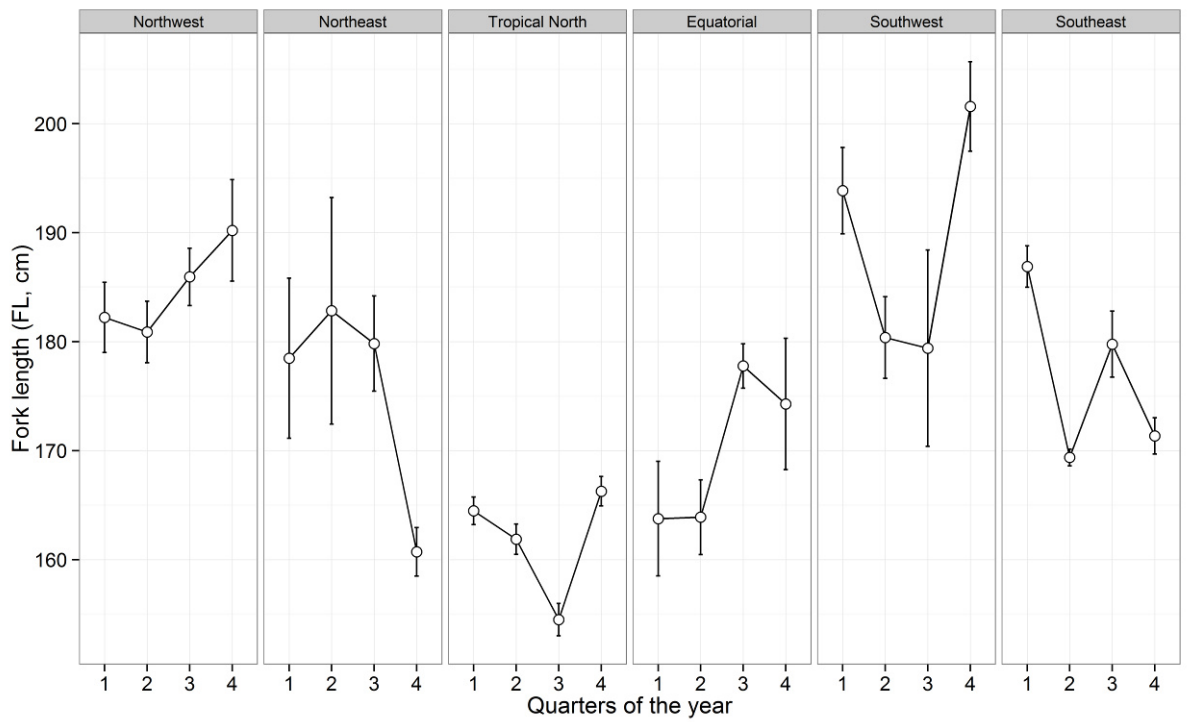
**Figure 1:** Location and sizes (FL, cm) of the bigeye thresher shark (*Alopias superciliosus*) recorded in the six sampling regions of this study. The gray scale of the dots represents specimen sizes, with darker colors representing smaller specimens and lighter colors larger specimens. The categorization of size classes for the map was carried out using the 20% percentiles of the size data. The location of pregnant females recorded by the Spanish, Portuguese and Uruguayan fleets during this study is represented with red crosses.



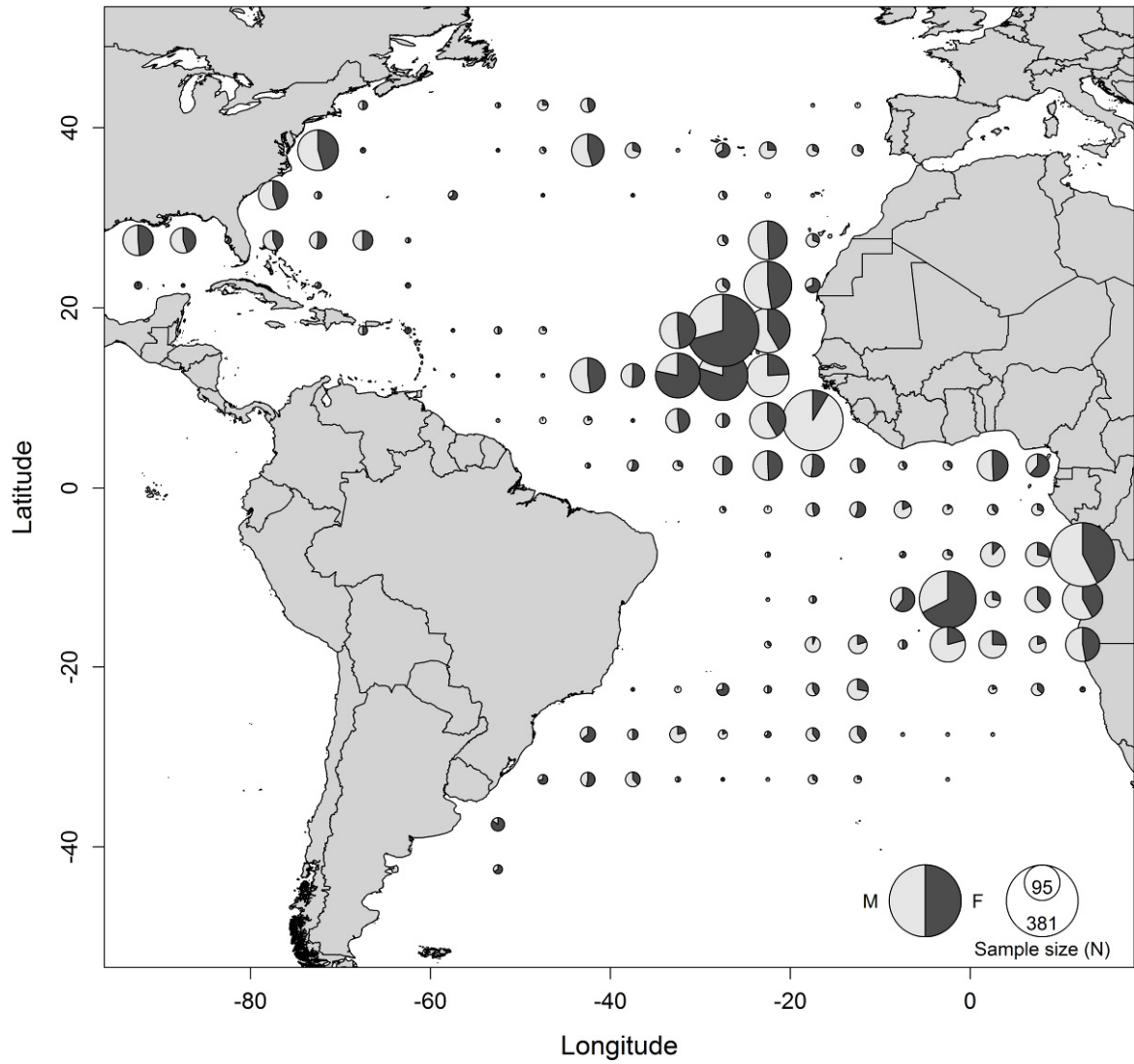
**Figure 2:** Length-frequency distributions of male and female bigeye thresher sharks (*Alopias superciliosus*) caught in six sampling regions of the Atlantic Ocean.



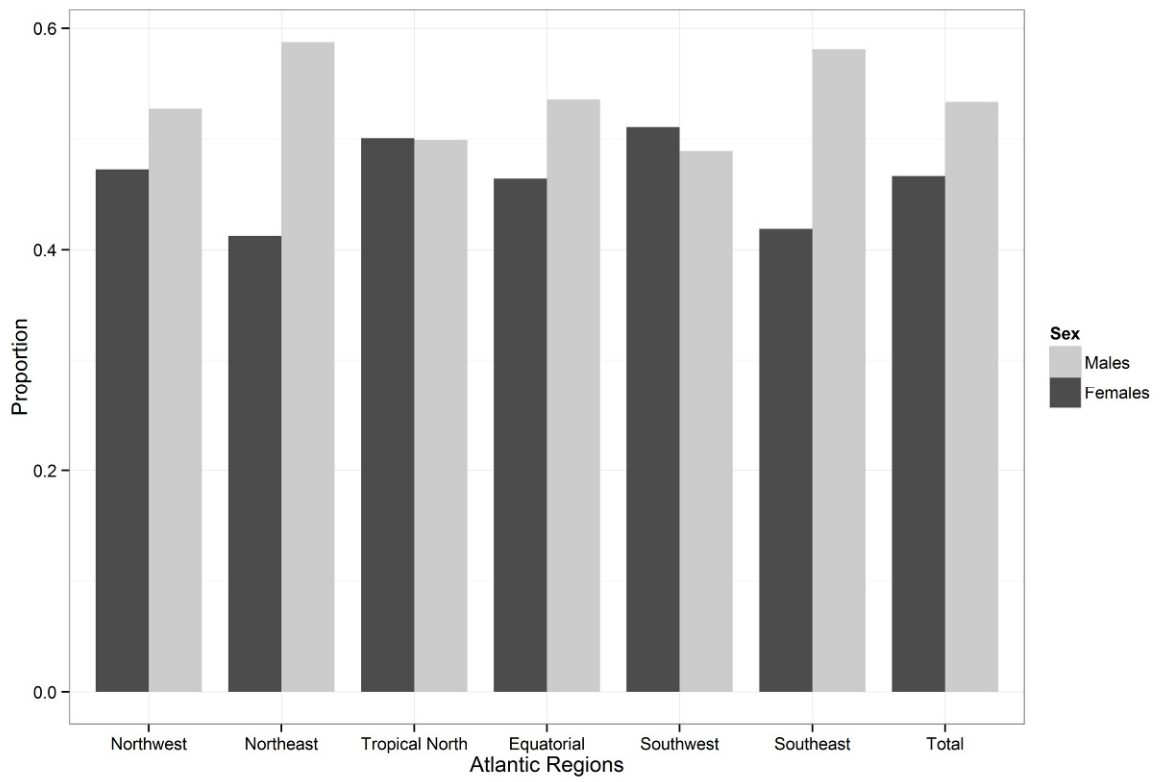
**Figure 3.** Mean sizes of male and female bigeye thresher sharks (*Alopias superciliosus*) caught in six sampling regions of the Atlantic Ocean. The error bars are  $\pm 1$  standard error.



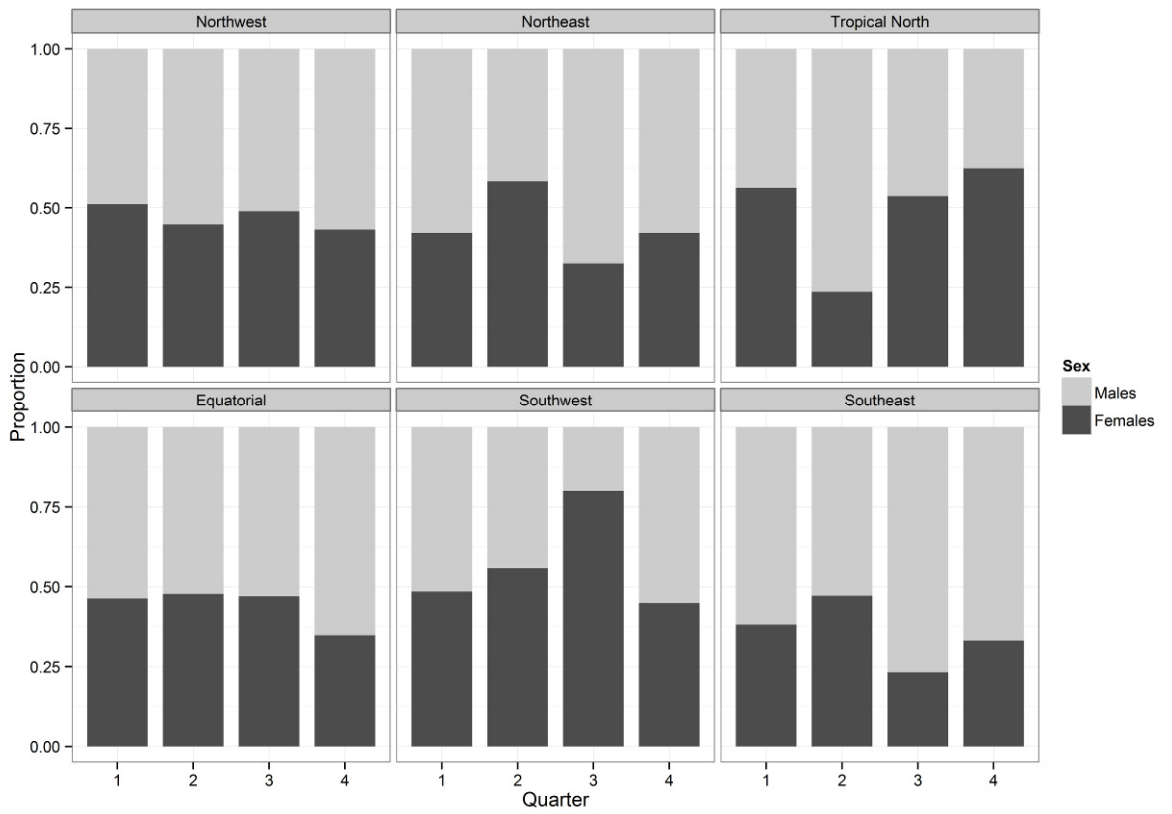
**Figure 4.** Mean size of bigeye thresher sharks (*Alopias superciliosus*) caught in six sampling regions of the Atlantic Ocean during four quarters of the year. The error bars are  $\pm 1$  standard error.



**Figure 5.** Map of the bigeye thresher shark (*Alopias superciliosus*) sex-ratios recorded by 5°x5° degrees squares during this study. The circle sizes are proportional to the sample size (N) in each square.

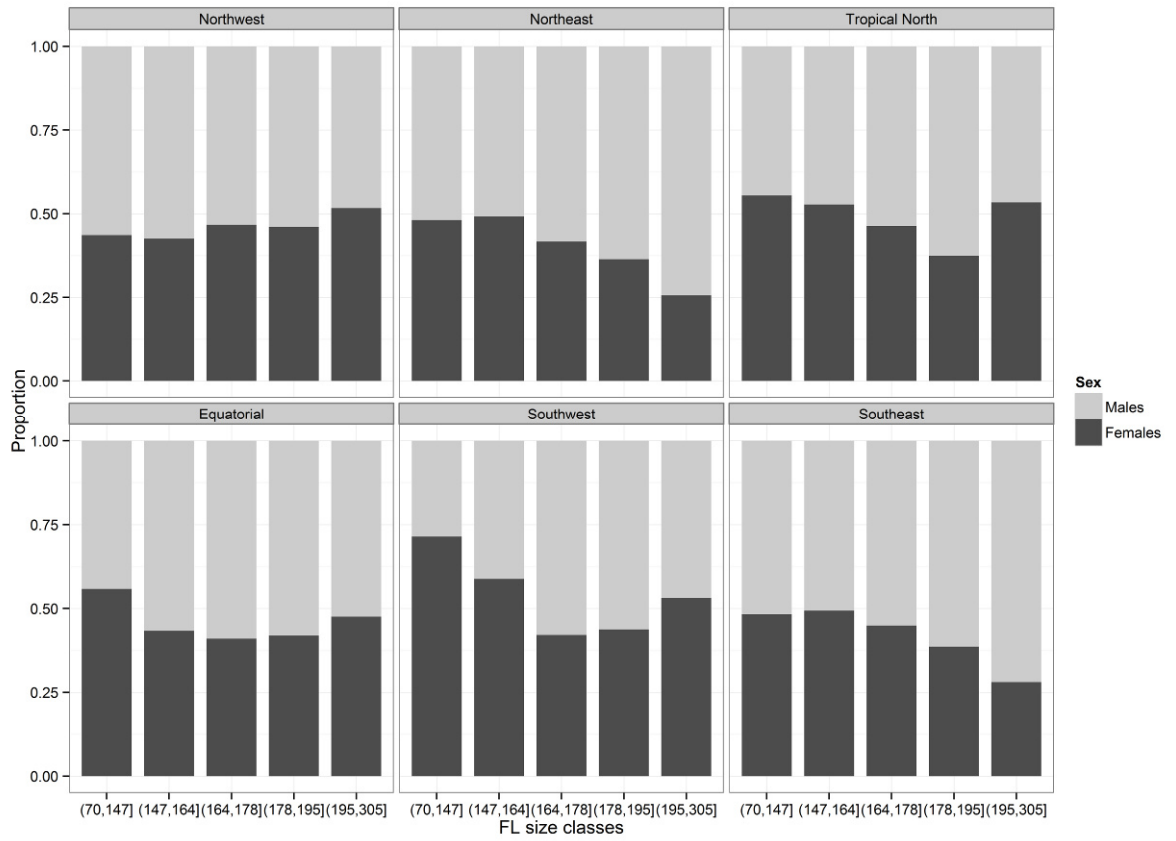


**Figure 6.** Sex ratios of the bigeye thresher shark (*Alopias superciliosus*, all sizes combined) in the six Atlantic regions considered in this study.

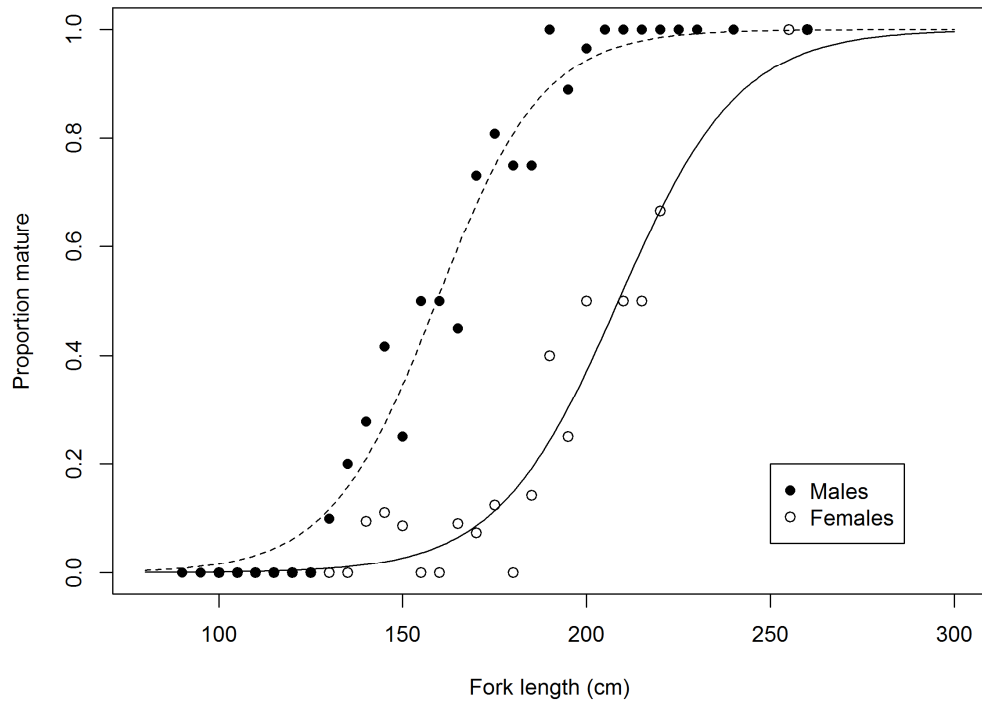


**Figure 7.** Sex ratios of bigeye thresher sharks (*Alopias superciliosus*, all sizes combined) per quarter of the year, in the six regions of the Atlantic considered in this study.

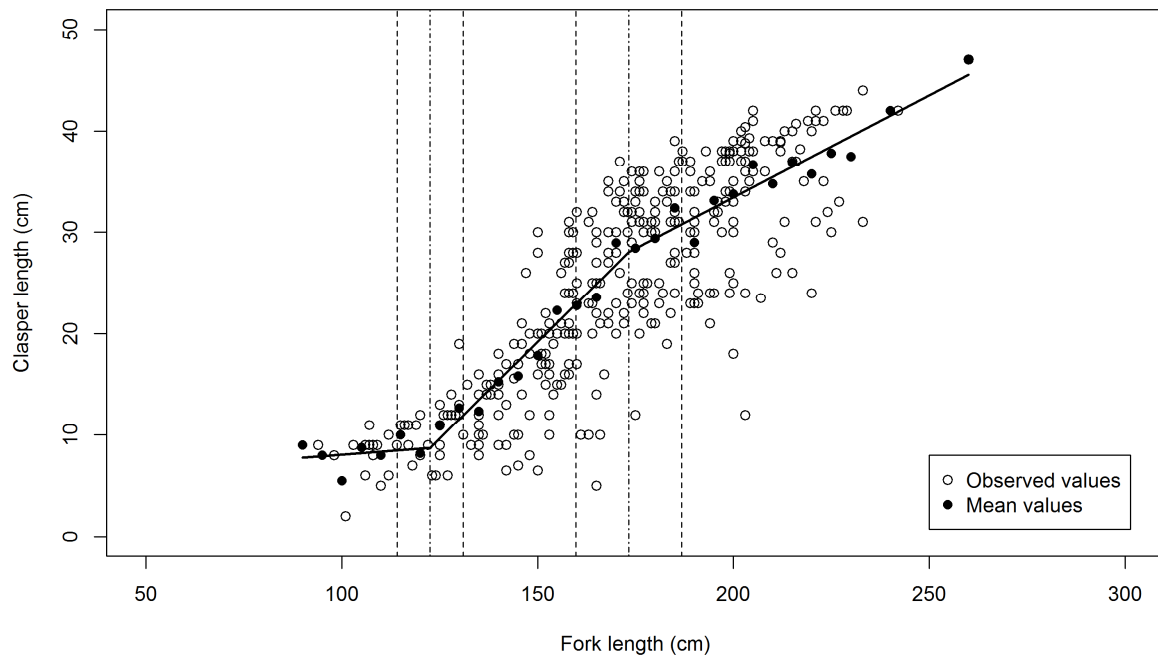




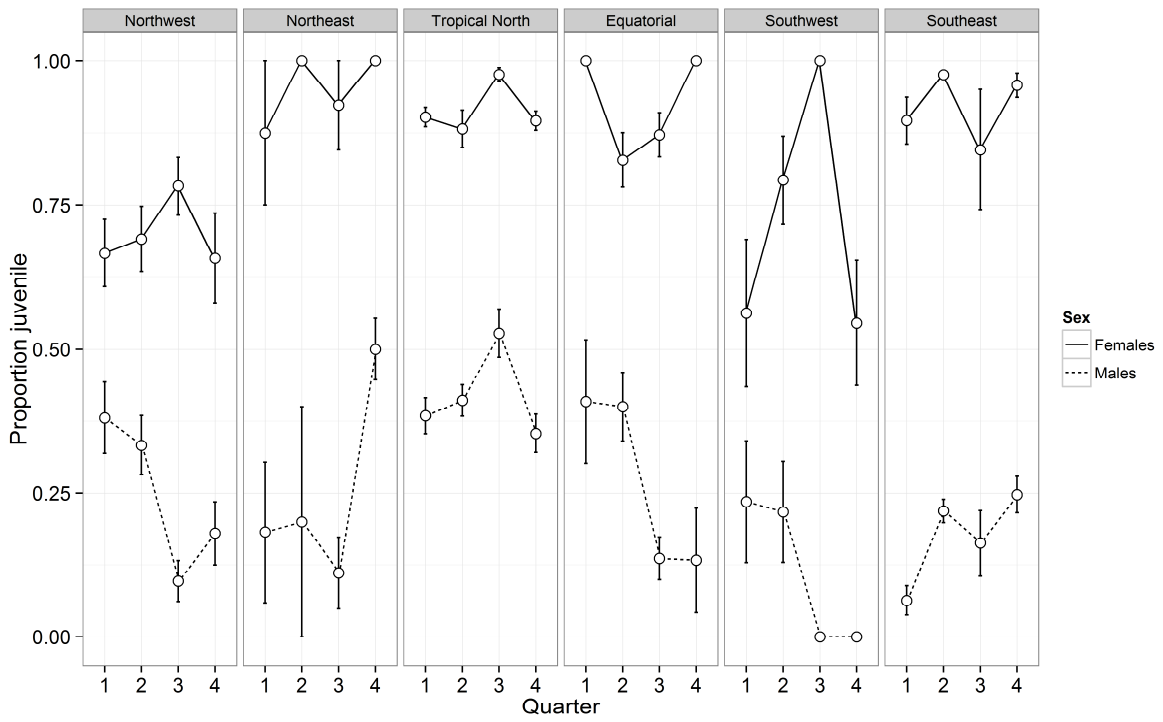
**Figure 8.** Sex ratios of bigeye thresher sharks (*Alopias superciliosus*) per size class, in the six regions of the Atlantic considered in this study. The categorization of size classes carried out using the 20% percentiles of the size data.



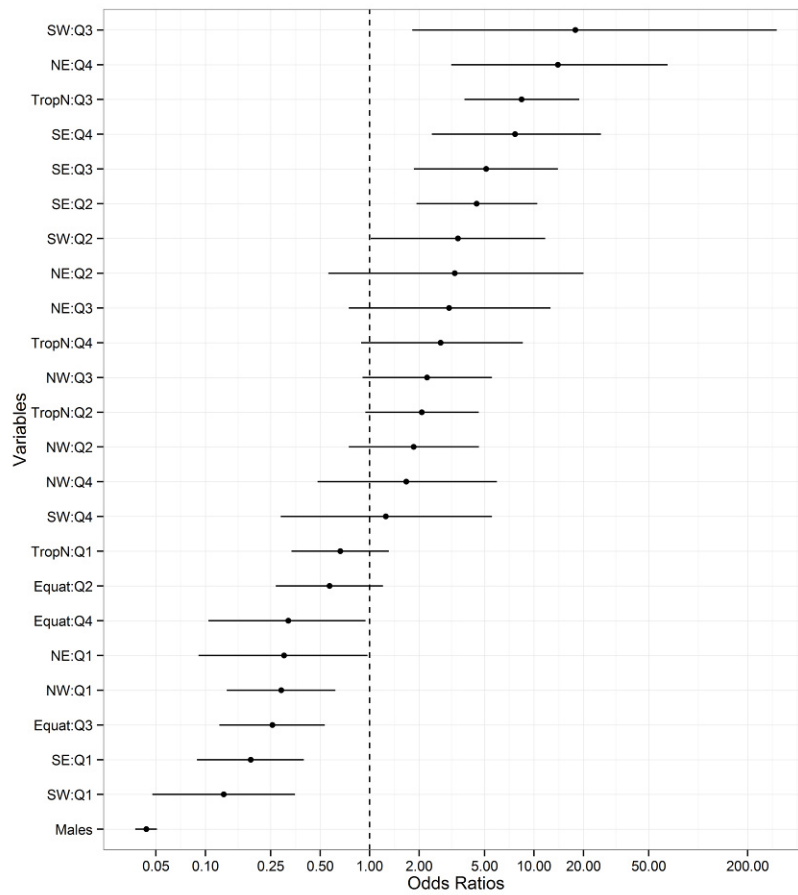
**Figure 9.** Observed mature:immature ratio by size class (dots, black for males and white for females) and fitted maturity ogives for male and female bigeye thresher sharks (*Alopius superciliosus*). Sizes were grouped into 5 cm FL classes.



**Figure 10.** Clasper length vs. fork length (FL) of male bigeye thresher sharks (*Alopias superciliosus*). The black line represents the segmented fitted model between fork length and clasper length. For calculating the segmented model, the median clasper size of 5-cm size classes was used instead of the original clasper sizes. The dot-dash lines represent the estimated breakpoints and the associated dash lines, their 95% confidence intervals.



**Figure 11.** Proportion of juvenile bigeye thresher sharks (*Alopias superciliosus*) caught in the six sampling regions of the Atlantic Ocean in each quarter of the year. The error bars are  $\pm 1$  standard error. The size range considered was 70-300 cm FL for the females and 75-305 cm FL for the males.



**Figure 12.** Odds ratios (with 90% confidence intervals) of capturing juvenile (<159.2 cm FL for males and <208.6 cm FL for females) bigeye thresher sharks (*Alopias superciliosus*) in each of multiple region:quarter combinations, as well as for the single effect for sex. The x-axis is in a base 10 logarithm scale.