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6 **Distribution patterns and indicators of the smooth hammerhead shark**

7 **(*Sphyrna zygaena*) in the Atlantic Ocean**

8

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17

18 **Abstract**

19 The smooth hammerhead shark, *Sphyrna zygaena*, is a pelagic shark occasionally captured as
20 bycatch by industrial pelagic longline fleets in the Atlantic Ocean. Data for this study were
21 collected by fishery observers, between 2003 and 2016. Datasets analyzed included information
22 on catches per unit effort (CPUE), size and sex of smooth hammerhead sharks bycaught by the
23 Portuguese pelagic longline fishery in the Atlantic Ocean. A total effort of 2 523 288 hooks
24 yielded 638 sharks, ranging in size from 123–275 cm fork length. Larger sharks tended to occur
25 in open ocean habitats and smaller specimens in coastal areas. Results confirmed the wide
26 latitudinal range of the species (45°N–35°S), although CPUE was higher closer inshore within
27 the Tropical North and Equatorial regions. An overall sex ratio of 1.4 males for each female was
28 observed, with more males in both inshore and offshore waters. Significant differences in CPUE
29 and size distribution were found between regions, years and quarters of the year. Mean CPUE
30 increased and mean specimen size decreased in the Equatorial region from 2012 onwards. In order
31 to remove fishery-dependent effects from CPUE data, a Tweedie Generalized Linear Model
32 (GLM) was used to create a relative index of abundance (standardized CPUE). The index showed
33 some oscillations in the initial years (2008–2010), followed by a decreasing trend until 2013 and
34 then an increasing trend in more recent years, until 2016. The distributional patterns and indicators
35 presented in this study provide a better understanding of the smooth hammerhead shark's spatio-
36 temporal dynamics and population structure in the Atlantic Ocean and can be used to improve
37 management and conservation measures for this species.

38

39 **Keywords:** pelagic sharks; spatial distribution; size distribution; fisheries; generalized linear
40 model

41

42 **1. Introduction**

43 The smooth hammerhead shark (*Sphyrna zygaena*), is a widespread pelagic species that occurs in
44 temperate and tropical waters, from latitudes of about 60°N to 55°S (Compagno, 1984; Casper *et*
45 *al.*, 2005). This species generally occurs close inshore, however it may also be found over
46 continental and insular shelves to offshore areas, being described as the most oceanic of the
47 hammerhead species (Compagno, 1984; Bester, 2008; Clarke *et al.*, 2015).

48 Like other pelagic species, smooth hammerhead shark is a frequent bycatch in pelagic longline
49 fisheries, although in much lower numbers in comparison to blue shark (*Prionace glauca*) and
50 shortfin mako shark (*Isurus oxyrinchus*) (Buencuerpo *et al.*, 1998; Cortés *et al.*, 2010).
51 Nevertheless, the population structure of the species remains unclear, as the available information
52 is still very limited (Coelho *et al.*, 2011). Moreover, this problem is aggravated by the lack of
53 reliable species-specific data, since hammerhead sharks are often recorded together under the
54 category *Sphyrna* spp. or included in the general sharks group (Camhi *et al.*, 2009).

55 The International Commission for the Conservation of Atlantic Tunas (ICCAT) is the Regional
56 Fisheries Management Organization (RFMO) responsible for the management and conservation
57 of migratory tunas and tuna-like species (including pelagic sharks, such as smooth hammerhead
58 shark) in the Atlantic Ocean and adjacent seas. In 2010, ICCAT adopted several management
59 recommendations to protect smooth hammerhead shark and stated the need of research focused
60 on hammerhead sharks in the Convention area (ICCAT, 2010). Cortés *et al.* (2010) conducted an
61 Ecological Risk Assessment for eleven species of pelagic elasmobranchs, concluding that smooth
62 hammerhead shark was amongst the less vulnerable to overexploitation by pelagic longline
63 fisheries in the Convention area. This was mainly due to a relatively high productivity compared
64 to other pelagic sharks. The smooth hammerhead showed also relatively low interaction with
65 pelagic fisheries, as the species spends part of its life cycle in coastal waters and is therefore less
66 susceptible to capture in those oceanic fisheries. However, Cortés *et al.* (2010) highlighted the
67 urgent need for better biological and distributional information, since there was a high level of
68 uncertainty regarding the life cycle parameters and distribution patterns of this species.

69 Studying spatio-temporal dynamics and population structure of marine species is required to
70 better understand distribution patterns of species and predict potential fishing impacts. This
71 information is therefore crucial for the development of effective fisheries management and
72 conservation strategies. Whilst some recent studies have shown evidence of probable severe
73 decline in the global population of smooth hammerhead shark (Baum *et al.* 2003; Myers *et al.*
74 2007; Ferretti *et al.* 2008), these findings may not represent a full and accurate portrayal of the
75 species' status, as many were based on limited data from logbooks, surveys and public sighting
76 records, which may not adequately sample the smooth hammerhead shark population. In fact,
77 several flaws were identified, mostly related to insufficient sample sizes, poor geographical
78 coverage, misidentification of the species and oversight of the fishing gear specifications and
79 modifications through time (Burgess *et al.*, 2005).

80 The general objective of this study was to provide information on the distributional patterns and
81 indicators of relative abundance of smooth hammerhead shark aiming to fill knowledge gaps for
82 the species in the Atlantic Ocean. Specific objectives of the study were to analyze the catch per
83 unit effort (CPUE), size and sex ratio distribution, provide time series trends, and analyze the
84 seasonal patterns of CPUE and size distributions of smooth hammerhead shark in the Atlantic
85 Ocean.

86

87 **2. Material and methods**

88 **2.1. Data collection**

89 Data were collected across the Atlantic Ocean by scientific fishery observers from the Portuguese
90 Institute for the Ocean and Atmosphere (IPMA) onboard Portuguese pelagic longline vessels.
91 This fleet operates throughout a wide area of the Atlantic Ocean, with spots of high fishing effort
92 around the temperate Northeast and Equatorial regions in oceanic waters. The spatial distribution
93 of the fishing effort is associated with the target species - swordfish (*Xiphias gladius*) and, to a
94 lesser extent, blue shark -, although the characteristics of the vessels of the fleet differ between

95 regions. For example, the vessels operating in the Northeast region of the Atlantic (closer to
96 mainland Portugal and the Azores archipelago) are usually smaller in size and mostly do not have
97 freezer. In contrast, the vessels that concentrate their activity in more distant regions of the
98 equatorial Atlantic are usually larger vessels that can freeze catches (Coelho *et al.*, 2012). The
99 fishing gear typically used by the Portuguese fleet consists of a standard monofilament polyamide
100 mainline set for fishing at depths of 30–70 m. The main line is usually set with five branch lines
101 between pairs of buoys, with each branch line being approximately 18 m in length and a hook in
102 the terminal tackle. The hooks used by the fleet are typically stainless-steel J-style hooks, baited
103 either with squid (*Illex* spp.) or mackerel (*Scomber* spp.). Both monofilament and multifilament
104 wire branch lines are used, but only one type is used per fishing set. Gear deployment traditionally
105 begins at around 17:00, with haulback starting the next day from about 06:00.

106 Between 2003 and 2016, data from a total of 2110 longline sets were collected, which amounted
107 to a total effort of 2 523 288 hooks and yielded 638 smooth hammerhead sharks. The spatial
108 distribution of the sampled areas ranged from 45°N–35°S (lat) and 45°W–10°E (long).

109 For all specimens caught, fishery observers recorded data on fork length (FL), sex, capture
110 location (latitude and longitude), water temperature and date. Catch and effort data were available
111 from 2003–2016, while data on smooth hammerhead shark size and sex were available from
112 2006–2015.

113

114 **2.2. Data analysis**

115 Catch per unit effort (number of specimens caught /1000 hooks), effort (total number of hooks
116 per set) and sex ratio distributions were calculated and expressed geographically using 5° x 5°
117 resolution grids of latitude and longitude (e.g., see Lee *et al.*, 2005; Fernandez-Carvalho *et al.*,
118 2015).

119 Catch per unit effort and size data were tested for normality using the Kolmogorov-Smirnov
120 normality test with the Lilliefors correction (Lilliefors, 1967), and for homogeneity of variances

121 with the Levene test (Levene, 1960). Given the lack of normality in the data and heterogeneity of
122 variances, CPUE and specimen size were compared between years, quarters of the year (1st:
123 January-March, 2nd: April-June, 3rd: July-September, 4th: October-December) and regions with
124 nonparametric Kruskal–Wallis tests, Wilcoxon–Man-Whitney tests and k-sample permutation
125 tests using the permutational central limit theorem (Manly, 2007). Sex ratios were compared
126 among regions with contingency tables and Pearson’s Chi-squared tests.

127 Catches were mainly composed of specimens captured in the Equatorial and Tropical North
128 regions of the Atlantic Ocean, hence only these two regions were considered for the sex ratio
129 analysis and for the calculation of yearly/quarterly CPUE and specimen size. The Tropical North
130 region was delimited from 10–30°N, while the Equatorial region extended from 10°N to 10°S.

131 A Generalized Linear Model (GLM) was used to standardize the CPUE time series. By
132 performing a standardization of CPUE, the effects of the covariates considered are removed from
133 CPUE values and those standardized CPUE can then be used as annual indices of abundance. For
134 the CPUE standardization, the response variable considered was CPUE measured as number of
135 individuals caught per 1000 hooks deployed. In the Tropical North and Equatorial regions, the
136 available catch data started in 2005 and was available until 2016. However, data for 2005–2007
137 were not used in the GLM because there was limited information in that period. As smooth
138 hammerhead shark is a bycatch from the fishery, there were many fishing sets with zero catches,
139 resulting in a response variable of CPUE=0. As these zeros can cause mathematical problems for
140 fitting the models, we carried out the CPUE standardization using the Tweedie distribution model
141 (Tweedie, 1984). The Tweedie distribution is part of the exponential family of distributions and
142 is defined by a mean (μ) and a variance ($\phi\mu^p$), in which ϕ is the dispersion parameter and p is an
143 index parameter. In this study, the index parameter (p -index) was calculated by maximum
144 likelihood estimation (MLE). The explanatory variables considered and tested in the model were:
145 Year (2008–2016), Month (January–December) and Area (three areas selected using a GLM-tree
146 area stratification based on the approach of Ichinokawa and Brodziak (2010; Figure 1). The
147 significance of the explanatory variables in the CPUE standardization model was assessed with

148 likelihood ratio tests comparing each univariate model to the null model (considering a
149 significance level of 5%), and by analyzing the deviance explained by each explanatory variable.
150 Goodness-of-fit and model comparison was carried out with the Akaike Information Criteria
151 (AIC) and the pseudo coefficient of determination (R^2). Model validation was carried out with a
152 residual analysis. The final relative index of abundance was estimated by calculating the marginal
153 means of the year factor, also called least square means (LSmeans).

154 All statistical analyses in this work were carried out with the R Project for Statistical Computing
155 version 3.3.2 (R Core Team, 2016). Plots were obtained using library "ggplot2" (Wickham, 2009)
156 and maps drawn using libraries "mapplots" (Gerritsen, 2014) and "shapefiles" (Stabler, 2013).
157 Additional libraries used in the GLM analysis included "tweedie" (Dunn, 2014), "statmod"
158 (Smyth *et al.*, 2015) and "lsmeans" (Lenth, 2015).

159

160 **3. Results**

161 **3.1. CPUE distribution**

162 The spatial distribution of the sampled fishing sets showed that the fishing effort sampled over
163 the 14-year period took place between approximately 50°N and 40°S (Figure 2). The temperate
164 Northeast (30–45°N) and the Equatorial (10°N–5°S) regions represented the major areas of
165 operation of the Portuguese pelagic longline fleet in the Atlantic Ocean, with fishing effort highest
166 in the offshore waters of these regions. The fishing effort ranged between 668 and 2300 hooks
167 per set, with an average effort of 1196 hooks per set.

168 Nominal CPUE ranged from 0.0 to 8.61, with an average CPUE of 0.24. Most sets (85%) showed
169 zero smooth hammerhead shark catches, whilst 13 % had a CPUE between 1 and 3, and 2% had
170 a CPUE of 4 or more. The geographic distribution of CPUE indicated that smooth hammerhead
171 sharks were distributed widely in the Atlantic Ocean, from 45°N to 35°S (Figure 3), although
172 fishing effort was less at higher latitudes. Nevertheless, higher CPUE values were found closer to
173 the African continent, within both the Tropical North and Equatorial regions.

174

175 **3.2. Size distribution**

176 Fishery observers recorded data on specimen size for 559 sharks (including juveniles and adults)
177 caught between ca. 40°N and 30°S (Figure 4). The overall length range was 123–275 cm FL, with
178 a mean size of 195 cm FL. Typically, larger-sized specimens were caught offshore, and smaller-
179 sized specimens caught in more inshore waters, particularly in the Gulf of Guinea. Furthermore,
180 all specimens caught in the offshore waters of the South Atlantic (15–30°S) were 187 cm FL or
181 larger.

182

183 **3.3. Sex ratio distribution**

184 Data on sex was recorded for 562 specimens, caught between ca. 40°N and 30°S, of which 238
185 (42.3%) were female and 324 (57.7%) were male (Figure 5). The overall sex ratio was 1.4 males
186 for each female. Particularly, there seemed to be some evidence of the presence of more males in
187 both inshore and offshore waters of the Atlantic Ocean.

188 The differences observed when comparing the Equatorial and Tropical North regions of the
189 Atlantic Ocean were not statistically significant (proportion test: Chi-squared = 0.541, df = 1, p-
190 value = 0.462).

191

192 **3.4. Yearly and quarterly trends in CPUE**

193 Catch per unit effort was not normally distributed (Lilliefors test: $D = 0.501$, p value < 0.001).
194 Variances were heterogeneous between years (Levene test: $F = 7.121$, df = 10, p value < 0.001)
195 and quarters of the year (Levene test: $F = 19.031$, df = 3, p value < 0.001) and homogenous
196 between regions (Levene test: $F = 3.854$, df = 1, p value = 0.050). Univariate nonparametric
197 statistical tests revealed that CPUE was significantly different between years (K–W: Chi-squared
198 = 124.86, df = 10, p-value < 0.001; permutation test: Chi-squared = 67.67, df = 10, p-value <

199 0.001) and quarters of the year (K–W: Chi-squared = 100.89, df = 3, p-value < 0.001; permutation
200 test: Chi-squared = 54.57, df = 3, p-value < 0.001). The differences between regions were less
201 clear, as the differences were statistically significant when using Wilcoxon-Man-Whitney tests
202 (W-M-W: W = 117870, p-value < 0.001) but not when using permutation tests (permutation test:
203 Chi-squared = 3.85, df = 1, p-value = 0.050).

204 The mean annual CPUE trend followed an oscillatory pattern in both the Tropical North and
205 Equatorial regions (Figure 6), with no catches recorded in 2007. The mean CPUE values were
206 generally lower in the Equatorial region than in the Tropical North region. The mean CPUE
207 tended to increase from 2012 onwards in the Equatorial region, with a recent increase in CPUE
208 also observed for the Tropical North region. Seasonality also seemed to influence CPUE (Figure
209 7). Higher mean CPUE values were recorded in the 3rd quarter of year for the Equatorial region.
210 In the Tropical North, mean CPUE tended to increase over the year, reaching a peak in the 4th
211 quarter.

212

213 **3.5. Yearly and quarterly trends in the size distribution**

214 Size data were not normally distributed (Lilliefors test: D = 0.059, p value < 0.001) and variances
215 were heterogeneous between years (Levene test: F = 6.988, df = 8, p value < 0.001) and quarters
216 of the year (Levene test: F = 4.8207, df = 3, p value < 0.01), but not between regions (Levene test:
217 F = 2.774, df = 1, p value = 0.096). Sizes were compared with univariate nonparametric statistical
218 tests among years (K–W: Chi-squared = 101.74, df = 8, p-value < 0.001; permutation test: Chi-
219 squared = 100.94, df = 8, p-value < 0.001), quarters of the year (K–W: Chi-squared = 14.737, df
220 = 3, p-value < 0.01; permutation test: Chi-squared = 18.987, df = 3, p-value < 0.001) and regions
221 (W-M-W: W = 23964, p-value < 0.001; permutation test: Chi-squared = 25.81, df = 1, p-value <
222 0.001), with statistical differences detected for all cases.

223 The time series of the mean size distribution showed a persistent decreasing trend in fork length
224 in the Equatorial region from 2012 onwards (Figure 8). Whilst length data were more variable in

225 the Tropical North Atlantic, it should be noted that only single specimens were measured in 2009
226 and 2015 for this region, and no size data were recorded in 2007, 2013 and 2014. In terms of
227 seasonality, mean sizes were higher and more regular in the Tropical North region in comparison
228 to the Equatorial region, although size data were lacking for the 2nd quarter of the year in the
229 Tropical North region (Figure 9).

230

231 **3.6. Relative index of abundance**

232 The Tweedie GLM used in the CPUE standardization explained approximately 32% of the
233 variability. The index parameter estimated for the Tweedie distribution was 1.155 and resulted in
234 a distribution that expects 70.4% of zeros, compared to the 75.2% in smooth hammerhead shark
235 CPUE data. All explanatory variables tested (year, month and area effects) contributed
236 significantly for explaining part of the deviance. Seasonal effects were responsible for most of
237 the variability, followed by year effects and finally area effects (Table 1).

238 The final relative index of abundance showed an oscillatory trend in the initial years between
239 2008 and 2010, followed by a decrease in the period between 2010 and 2013. In more recent
240 years, between 2013 and 2016, results showed an increasing tendency in the standardized CPUE
241 series (Figure 10). In general, nominal CPUE and standardized CPUE produced similar trends
242 from 2010 onwards (Figure 10). This final model revealed no problems or outliers in terms of
243 residual analysis (see Supplementary Material).

244

245 **4. Discussion**

246 In light of the global declining trends of several shark stocks, improving the limited information
247 available for smooth hammerhead shark becomes critical for the species conservation and
248 fisheries management. This work provides detailed information on the spatio-temporal dynamics
249 and population structure of smooth hammerhead shark in the Atlantic Ocean. Catch per unit effort,

250 catch at size and sex ratio distributions were analyzed based on detailed data collected by fishery
251 observers onboard Portuguese pelagic longline vessels operating in the Atlantic Ocean, between
252 2003 and 2016. In addition, time series trends and seasonal patterns of CPUE and size
253 distributions were analyzed.

254 In terms of the spatial distribution of CPUE, records of catches ranging from 45°N to 35°S were
255 observed, confirming the wide latitudinal range of this species in the Atlantic Ocean (Compagno,
256 1984; Cortés *et al.*, 2015). Higher CPUE was found closer inshore in both the Tropical North and
257 Equatorial regions. Within these regions, the African west coast (including the Gulf of Guinea)
258 represented an important area of high CPUE. Near-shore waters, as well as islands and seamounts,
259 tend to be sites where many shark species aggregate, and may be used as nursery areas, feeding
260 grounds and/or shelter sites (Olson *et al.*, 1994; Castro *et al.*, 1995; Beck *et al.*, 2001; Queiroz *et*
261 *al.*, 2012; Knip *et al.*, 2010). In addition, smooth hammerhead sharks are reported to occur
262 generally close inshore and in shallow waters, and the Gulf of Guinea is thought to be a possible
263 nursery area for this species (Compagno, 1984; Bester, 2008; Castro *et al.*, 1995). Consequently,
264 the spatial distribution of CPUE is possibly related to environmental conditions off the African
265 west coast and the habitat preferences of the species. Moreover, it is important to highlight that a
266 high percentage of the sets showed zero catches of smooth hammerhead sharks, which may
267 support previous results by Cortés *et al.* (2010) that demonstrated smooth hammerhead shark to
268 be one of the less vulnerable shark species to pelagic longline fisheries in the Atlantic Ocean, due
269 to reduced interactions with the fishing gear.

270 The specimens caught ranged in size from 123–275 cm FL. Larger sharks tended to occur in the
271 open ocean habitat, while smaller-sized specimens seemed to concentrate in more coastal areas.
272 This distribution pattern may be linked to habitat characteristics and migratory behavior, which
273 are in turn related to growth and reproductive state (Coelho *et al.*, 2018). Another possible
274 hypothesis for the size distribution observed is that it may also be affected by fishing gear
275 selectivity (Fernandez-Carvalho *et al.*, 2015). However, the fishing gear analyzed was always
276 shallow pelagic longline sets targeting swordfish, without likely size selectivity issues. Thus, the

277 hypothesis that it relates to life history stages, with the occurrence of smaller specimens in more
278 inshore waters and larger specimens in more oceanic waters, is more likely.

279 In general, the sex ratio data indicated that there was a tendency for the presence of more males
280 in the sampled area, representing an overall sex ratio of 1.4 males for each female. The
281 predominance of one sex over the other in fishery catches may be related to selectivity of the
282 fishing gear, through greater attraction to bait and/or larger sizes (White *et al.*, 2008). Also, partial
283 segregation of sexes has been associated with differential selection of habitats for social, thermal
284 or foraging reasons (Mucientes *et al.*, 2009), which may explain the tendency for females to move
285 to areas outside those in which this longline fleet tends to operate.

286 Since most specimens were captured in the Equatorial and Tropical North regions of the Atlantic
287 Ocean, only data from specimens caught in those two regions were used in the detailed analyses
288 of CPUE and size distributions. Significant differences in CPUE and size distributions were found
289 between regions, years and quarters of the year.

290 Some previous studies suggested that the population of smooth hammerhead sharks in the Atlantic
291 Ocean has likely experienced strong declines (Baum *et al.*, 2003; Myers *et al.*, 2007; Ferretti *et*
292 *al.*, 2008), however these previous findings have also been shown to not necessarily represent a
293 full and accurate portrayal of the species' status (Burgess *et al.*, 2005). From our results, it appears
294 that there has been an increase in mean CPUE, along with a decrease of mean specimen size, in
295 the Equatorial region from 2012 onwards. These results may be related to fishing pressure and
296 the capture of larger specimens over the years, which would cause a decrease in the mean
297 specimen size. Moreover, the standardized CPUE, which can be used as a regional indicator of
298 relative abundance, was not much different from the nominal values, showing similar results and
299 trends from 2010 onwards.

300 It is important to note, however, that the data used in our study may also not fully reflect the
301 complete trends in the Atlantic population of smooth hammerhead shark, since data from only
302 one pelagic longline fleet were considered (Maunder *et al.*, 2006). The data came from oceanic

303 pelagic longlines, set in oceanic waters and targeting mainly swordfish. As such, the results
304 obtained provide mainly a snapshot of the population that is present in these waters and is selected
305 by the shallow setting longline gear targeting mainly swordfish. Also, the possibility of
306 occurrence of smooth hammerhead sharks in the areas not covered cannot be excluded.

307 Despite those limitations, inherent to the fishery-dependent nature of the data, the distribution
308 patterns presented in our study provide an improved understanding of spatio-temporal dynamics
309 and population structure of the smooth hammerhead shark in the Atlantic Ocean. Even though the
310 smooth hammerhead shark is currently a no-retention species in most Atlantic fisheries (ICCAT,
311 2010), it is still captured as bycatch and discarded. The hooking mortality is known to be high
312 (e.g., Coelho *et al.*, 2012), while the post-release mortality is largely unknown. As such, further
313 work is needed to fill knowledge gaps, and better inform future management decisions and
314 implement efficient conservation measures for this species.

315

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327 Humano.

328

329 **References**

- 330 Baum, J. K., R. A. Myers, D. G. Kehler, B. Worm, S. J. Harley, and P. A. Doherty.
331 2003. Collapse and Conservation of Shark Populations in the Northwest Atlantic. Am.
332 Assoc. Adv. Sci. 299:389–392. <https://doi.org/10.1126/science.1079777>.
333
- 334 Beck, M. W., K. L. Heck, K. W. Able, D. L. Childers, D. B. Eggleston, B. M. Gillanders, B.
335 Halpern, C. G. Hays, K. Hoshino, T. J. Minello, R. J. Orth, P. F. Sheridan, and M. P. Weinstein.
336 2001. The Identification, Conservation, and Management of Estuarine and Marine
337 Nurseries for Fish and Invertebrates. BioScience. 51:633–641.
338 [https://doi.org/10.1641/0006-3568\(2001\)051\[0633:TICAMO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2).
339
- 340 Bester, C.
341 2008. Smooth Hammerhead. Florida Museum of Natural History.
342 <https://www.floridamuseum.ufl.edu/fish/discover/species-profiles/sphyrna-zygaena>
343 (accessed 5 January 2018).
344
- 345 Buenquerpo, V., S. Rios, and J. Moron.
346 1998. Pelagic sharks associated with the swordfish, *Xiphias gladius*, fishery in the eastern
347 North Atlantic Ocean and the Strait of Gibraltar. Fish. Bull. 96:667–685.
348
- 349 Burgess, G. H., L. R. Beerkircher, G. M. Cailliet, J. K. Carlson, E. Cortes, K. J. Goldman, R. D.
350 Grubbs, J. A. Musick, M. K. Musyl, and C. A. Simpfendorfer.
351 2005. Is the collapse of shark populations in the Northwest Atlantic Ocean and Gulf of
352 Mexico real?. Fisheries 30:19–26. [https://doi.org/10.1577/1548-
353 8446\(2005\)30\[19:ITCOSP\]2.0.CO;2](https://doi.org/10.1577/1548-8446(2005)30[19:ITCOSP]2.0.CO;2).
354
- 355 Camhi, M. D, S. V. Valenti, S. V. Fordham, S. L. Fowler, and C. Gibson.

356 2009. The conservation status of pelagic sharks and rays. IUCN Species Survival
357 Commission Shark Specialist Group, Newbury, UK, 78 pp.

358

359 Casper, B. M., A. Domingo, N. Gaibor, M. R. Heupel, E. Kotas, A. F. Lamónaca, J. C. Pérez-
360 Jimenez, C. Simpfendorfer, W. D. Smith, J. D. Stevens, A. Soldo, and C. M. Vooren.

361 2005. *Sphyrna zygaena*. The IUCN Red List of Threatened Species 2005:
362 e.T39388A10193797.

363 <http://dx.doi.org/10.2305/IUCN.UK.2005.RLTS.T39388A10193797.en>. (accessed 5
364 January 2018).

365

366 Castro, J. A., and J. Mejuto.

367 1995. Reproductive Parameters of Blue Shark, *Prionace glauca*, and other Sharks in the
368 Gulf of Guinea. Mar. Freshw. Res. 46:967–973. <https://doi.org/10.1071/MF9950967>.

369

370 Clarke, S. C., R. Coelho, M. P. Francis, M. Kai, S. Kohin, K. Liu, C. Simpendorfer, J. Tovar-
371 Availa, C. Rigby, and J. J. Smart.

372 2015. Report of the Pacific Shark Life History Expert Panel Workshop. Western and
373 Central Pacific Fisheries Commission.

374

375 Coelho, R., J. Fernandez-Carvalho, S. Amorim, and M. N. Santos.

376 2011. Age and growth of the smooth hammerhead shark, *Sphyrna zygaena*, in the Eastern
377 Equatorial Atlantic Ocean, using vertebral sections. Aquat. Living Resour. 24:351–357.
378 <https://doi.org/10.1051/alr/2011145>.

379

380 Coelho, R., J. Fernandez-Carvalho, P. G. Lino, and M. N. Santos.

381 2012. An overview of the hooking mortality of elasmobranchs caught in a swordfish
382 pelagic longline fishery in the Atlantic Ocean. Aquat. Living Resour. 25:311–319.
383 <https://doi.org/10.1051/alr/2012030>.

384

385 Coelho, R., J. Mejuto, A. Domingo, K. Yokawa, K. M. Liu, E. Cortés, E. V. Romanov, C. Silva,
386 F. Hazin, F. Arocha, A. M. Mwilima, P. Bach, V. O. Zárata, W. Roche, P. G. Lino, B. García-
387 Corté, A. M. Ramos-Cartelle, R. Forselledo, F. Mas, S. Ohshimo, D. Courtney, P. S. Sabarros, B.
388 Perez, C. Wogerbauer, W. P. Tsai, F. Carvalho, and M. N. Santos.

389 2018. Distribution patterns and population structure of the blue shark (*Prionace glauca*)
390 in the Atlantic and Indian Oceans. *Fish Fish.* 19:90–106.
391 <https://doi.org/10.1111/faf.12238>.

392

393 Compagno, L. J. V.

394 1984. *FAO Species Catalogue: Vol. 4, Part 2 Sharks of the World: An Annotated and*
395 *Illustrated Catalogue of Shark Species Known to Date.* Food and Agriculture
396 Organization of the United Nations, Rome.

397

398 Cortés, E., F. Arocha, L. Beerkircher, F. Carvalho, A. Domingo, M. Heupel, H. Holtzhausen, M.
399 N. Santos, M. Ribera, and C. Simpfendorfer.

400 2010. Ecological risk assessment of pelagic sharks caught in Atlantic pelagic longline
401 fisheries. *Aquat. Living Resour.* 23:25–34. <https://doi.org/10.1051/alr/2009044>.

402

403 Cortés, E., A. Domingo, P. Miller, R. Forselledo, F. Mas, F. Arocha, S. Campana, R. Coelho, C.
404 Da Silva, F. Hazin, and H. Holtzhausen.

405 2015. Expanded ecological risk assessment of pelagic sharks caught in Atlantic pelagic
406 longline fisheries. *Collect Vol. Sci. Pap. ICCAT.* 71:2637-88.

407

408 Dunn, P. K.

409 2014. Tweedie: Tweedie exponential family models. R package version 2.2.1.
410 <http://CRAN.R-project.org/package=tweedie>.

411

412 Fernandez-Carvalho, J., R. Coelho, J. Mejuto, E. Cortés, A. Domingo, K. Yokawa, K. M. Liu, B.
413 García-Cortés, R. Forselledo, S. Ohshimo, A. Ramos-Cartelle, W. P. Tsai, and M. N. Santos.
414 2015. Pan-Atlantic distribution patterns and reproductive biology of the bigeye thresher,
415 *Alopias superciliosus*. Rev. Fish Biol. Fish. 25:551–568. [https://doi.org/10.1007/s11160-](https://doi.org/10.1007/s11160-015-9389-7)
416 [015-9389-7](https://doi.org/10.1007/s11160-015-9389-7).
417
418 Ferretti, F., R. A. Myers, F. Serena, and H. K. Lotze.
419 2008. Loss of large predatory sharks from the Mediterranean Sea. Conserv. Biol. 22:952–
420 964. <https://doi.org/10.1111/j.1523-1739.2008.00938.x>.
421
422 Gerritsen, H.
423 2014. Mapplots: Data Visualisation on Maps. R package version 1.5. [http://CRAN.R-](http://CRAN.R-project.org/package=mapplots)
424 [project.org/package=mapplots](http://CRAN.R-project.org/package=mapplots).
425
426 ICCAT
427 2010. Recommendation by ICCAT on hammerhead sharks (family Sphyrnidae) caught in
428 association with fisheries managed by ICCAT. ICCAT Recommendation 2010-08.
429 <http://www.iccat.es/Documents/Recs/compendiopdf-e/2010-08-e.pdf>. (accessed 5
430 January 2018).
431
432 Ichinokawa, M., and J. Brodziak.
433 2010. Using adaptive area stratification to standardize catch rates with application to
434 North Pacific swordfish (*Xiphias gladius*). Fish. Res. 106:249–260
435
436 Knip, D. M., M. R. Heupel, and C. A. Simpfendorfer.
437 2010. Sharks in nearshore environments: Models, importance, and consequences. Mar.
438 Ecol. Prog. Ser. 402:1–11. <https://doi.org/10.3354/meps08498>.
439

440 Lee, P. F., I. C. Chen, and W. N. Tzeng.
441 2005. Spatial and temporal distribution patterns of big- eye tuna (*Thunnus obesus*) in the
442 Indian Ocean. *Zool. Stud.* 44:260-270.
443
444 Lenth, R.
445 2005. Lsmeans: Least-Squares Means. R package version 2.20-2. [http://CRAN.R-](http://CRAN.R-project.org/package=lsmeans)
446 [project.org/package=lsmeans](http://CRAN.R-project.org/package=lsmeans).
447
448 Levene, H.
449 1960. Robust tests for equality of variances. *Contrib. to Probab. Stat.* 1:278–292.
450
451 Lilliefors, H. W.
452 1967. On the Kolmogorov-Smirnov test for normality with mean and variance unknown.
453 *J. Am. Stat. Assoc.* 62:399–402.
454
455 Manly, B. F. J.
456 2007. *Randomization, bootstrap and Monte Carlo methods in biology*, 3rd ed. Chapman
457 & Hall/CRC Press, Boca Raton, FL.
458
459 Maunder, M. N., J. R. Sibert, A. Fonteneau, J. Hampton, P. Kleiber, and S. J. Harley.
460 2006. Interpreting catch per unit effort data to assess the status of individual stocks and
461 communities. *ICES J. Mar. Sci.* 63:1373–1385.
462 <https://doi.org/10.1016/j.icesjms.2006.05.008>.
463
464 Mucientes, G. R., N. Queiroz, L. L. Sousa, P. Tarroso, and D. W. Sims.
465 2009. Sexual segregation of pelagic sharks and the potential threat from fisheries. *Biol.*
466 *Lett.* 5:156–159. <https://doi.org/10.1098/rsbl.2008.0761>.
467

468 Myers, R. A., J. K. Baum, T. D. Shepherd, S. P. Powers, and C. H. Peterson.
469 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean.
470 Science. 315:1846–1850. <https://doi.org/10.1126/science.1138657>.
471

472 Olson, D., G. Hitchcock, A. Mariano, C. Ashjian, G. Peng, R. Nero, and G. Podesta.
473 1994. Life on the Edge: Marine Life and Fronts. Oceanography 7:52–60.
474 <https://doi.org/10.5670/oceanog.1994.03>.
475

476 Queiroz, N., N. E. Humphries, L. R. Noble, A. M. Santos, and D. W. Sims.
477 2012. Spatial dynamics and expanded vertical niche of blue sharks in oceanographic
478 fronts reveal habitat targets for conservation. PLoS One 7.
479 <https://doi.org/10.1371/journal.pone.0032374>.
480

481 R Core Team.
482 2016. R: A language and environment for statistical computing. R Foundation for Statistical
483 Computing, Vienna, Austria. <http://www.R-project.org/>.
484

485 Smyth, G., Y. Hu, P. Dunn, B. Phipson, and Y. Chen.
486 2015. Statmod: Statistical Modeling. R package version 1.4.21. [http://CRAN.R-](http://CRAN.R-project.org/package=statmod)
487 [project.org/package=statmod](http://CRAN.R-project.org/package=statmod).
488

489 Stabler, B.
490 2013. Shapefiles: Read and write ESRI shapefiles. R package version 0.7.
491 <http://CRAN.R-project.org/package=shapefiles>.
492

493 Tweedie, M. C. K.
494 1984. An index which distinguishes between some important exponential families. In:
495 Statistics: Applications and New Directions. Proceedings of the Indian Statistical Institute

496 Golden Jubilee International Conference. Indian Statistical Institute, Calcutta, pp. 579-
497 604.
498
499 White, W. T., C. Bartron, and I. C. Potter.
500 2008. Catch composition and reproductive biology of *Sphyrna lewini* (Griffith & Smith)
501 (Carcharhiniformes, Sphyrnidae) in Indonesian waters. J. Fish Biol. 72:1675–1689.
502 <https://doi.org/10.1111/j.1095-8649.2008.01843.x>.
503
504 Wickham, H.
505 2009. ggplot2: Elegant graphics for data analysis. Springer-Verlag, New York, NY.
506 <http://ggplot2.org>.
507

508 **Tables**

509 **Table 1 - Deviance of the parameters used for the CPUE standardization with a Tweedie**
 510 **GLM.**

Tweedie model (R²=32%)					
Parameter	Df	Deviance	Resid. Df	Resid. Dev.	Significance (p-value)
Null			973	1452	
Year	8	212	965	1240	< 0.01
Month	11	231	954	1009	< 0.01
Area	2	41	952	968	< 0.01

511 Deviance of the parameters used for the CPUE standardization with a Tweedie GLM. For each
 512 parameter it is indicated the degrees of freedom used, the deviance explained, the residual degrees
 513 of freedom, the deviance after incorporating each parameter and the significance (p-value) of each
 514 parameter. It is also indicated the coefficient of determination value (pseudo R²).

515 **Figure captions**

516 **Figure 1 - Spatial area stratification.** Spatial area stratification for smooth hammerhead shark
517 CPUE captured by the Portuguese pelagic longline fleet in the Tropical North and Equatorial
518 regions of the Atlantic Ocean. 1, 2 and 3 are the labels of the final areas selected by the GLM-
519 tree algorithm.

520 **Figure 2 - Spatial distribution of the sampling effort.** Spatial distribution of the sampling effort
521 (fishing effort in number of hooks) analyzed for this work, from the Portuguese pelagic longline
522 fleet in the Atlantic Ocean, between 2003 and 2016.

523 **Figure 3 - Spatial distribution of the catch per unit effort.** Spatial distribution of smooth
524 hammerhead shark CPUE (n/1000 hooks) analyzed for this work, by the Portuguese pelagic
525 longline fleet in the Atlantic Ocean, between 2003 and 2016.

526 **Figure 4 - Location and size distribution of smooth hammerhead shark.** Location and size
527 distribution (FL, cm) of smooth hammerhead shark recorded for this study between 2006 and
528 2015. The color scale of the dots represents specimen sizes, with darker colors representing
529 smaller specimens and lighter colors, larger specimens. The categorization of size classes was
530 carried out using the 0.2 quantiles of the data (values in the legend represent the lower and upper
531 limits of each size class).

532 **Figure 5 - Sex ratios of smooth hammerhead shark.** Sex ratios of smooth hammerhead shark,
533 recorded in 5°x5° squares, between 2006 and 2015. The circle diameter is proportional to the
534 sample size (N) in each square.

535 **Figure 6 - Time series of the mean CPUE.** Time series of the mean CPUE of smooth
536 hammerhead shark, caught in the Tropical North and Equatorial regions of the Atlantic Ocean,
537 between 2005 and 2016. Bars represent the \pm standard error of the mean.

538 **Figure 7 - Mean CPUE by quarter of the year.** Mean CPUE of smooth hammerhead shark,
539 caught in the Tropical North and Equatorial regions of the Atlantic Ocean during the four quarters
540 of the year, between 2005 and 2016. Bars represent the \pm standard error of the mean.

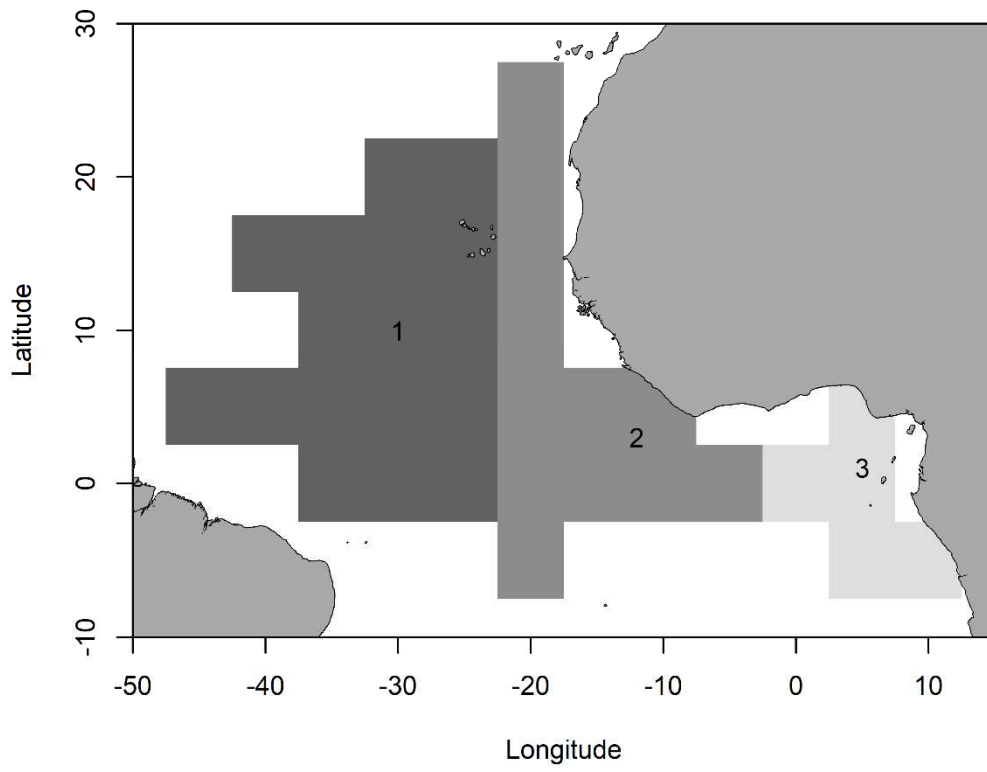
541 **Figure 8 - Time series of the mean sizes.** Time series of the mean sizes (FL, cm) of smooth
542 hammerhead shark, caught in the Tropical North and Equatorial regions of the Atlantic Ocean,
543 between 2006 and 2015. Numbers between brackets represent the sample size for each year. Bars
544 represent the \pm standard error of the mean.

545 **Figure 9 - Mean sizes by quarter of the year.** Mean sizes (FL, cm) of smooth hammerhead
546 shark, caught in the Tropical North and Equatorial regions of the Atlantic Ocean during the four
547 quarters of the year, between 2006 and 2015. Numbers between brackets represent the sample
548 size for each quarter of the year. Bars represent the \pm standard error of the mean.

549 **Figure 10 - Results of the CPUE standardization with a Tweedie GLM.** Results of the CPUE
550 standardization with a Tweedie GLM (black line), that represents a relative index of abundance
551 for smooth hammerhead shark, with the respective 95% confidence intervals (gray lines). The
552 triangles represent the nominal CPUE series. The vertical dotted line symbolizes the entry into
553 force of the ICCAT Recommendation on hammerhead sharks (ICCAT, 2010).

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555 Figure 1



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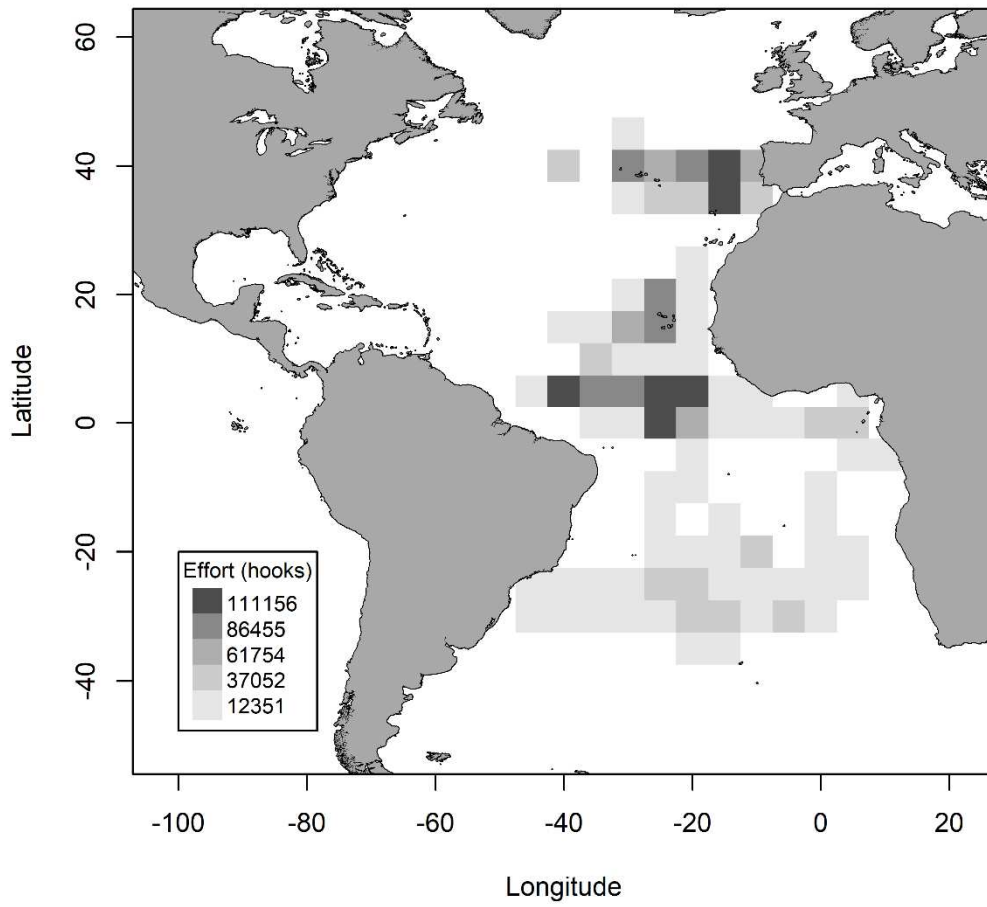
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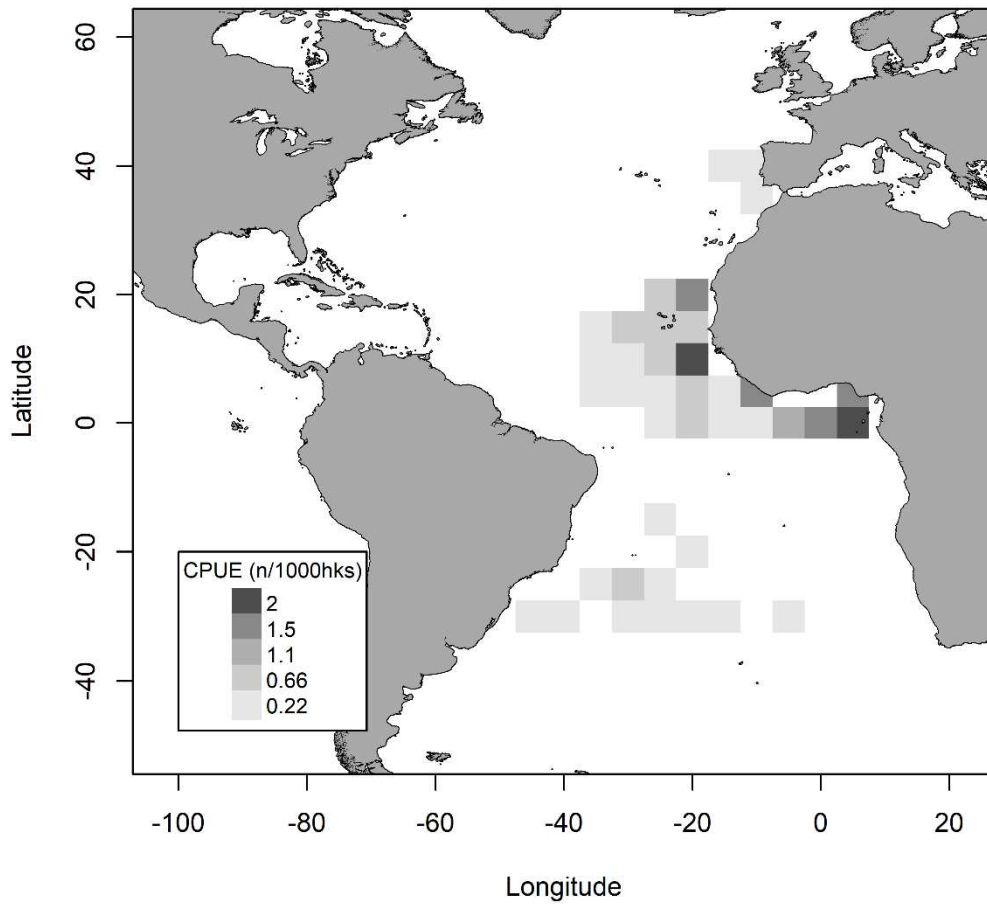
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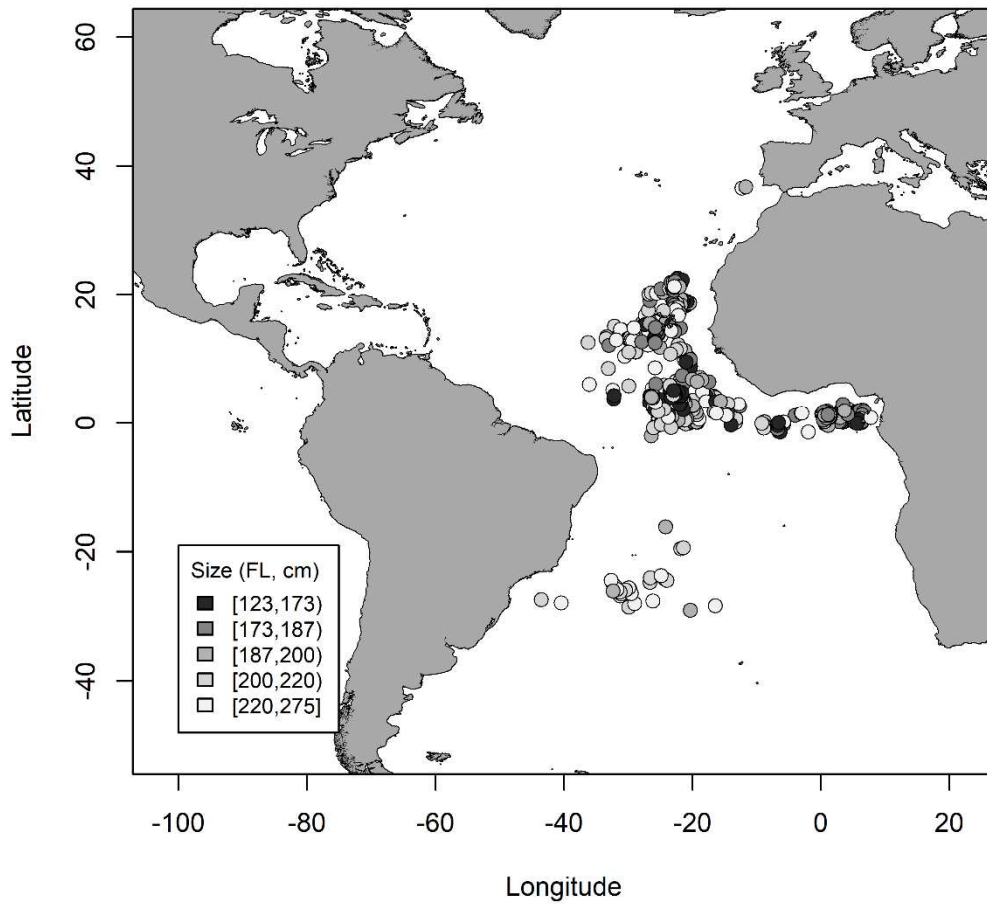
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573 Figure 3



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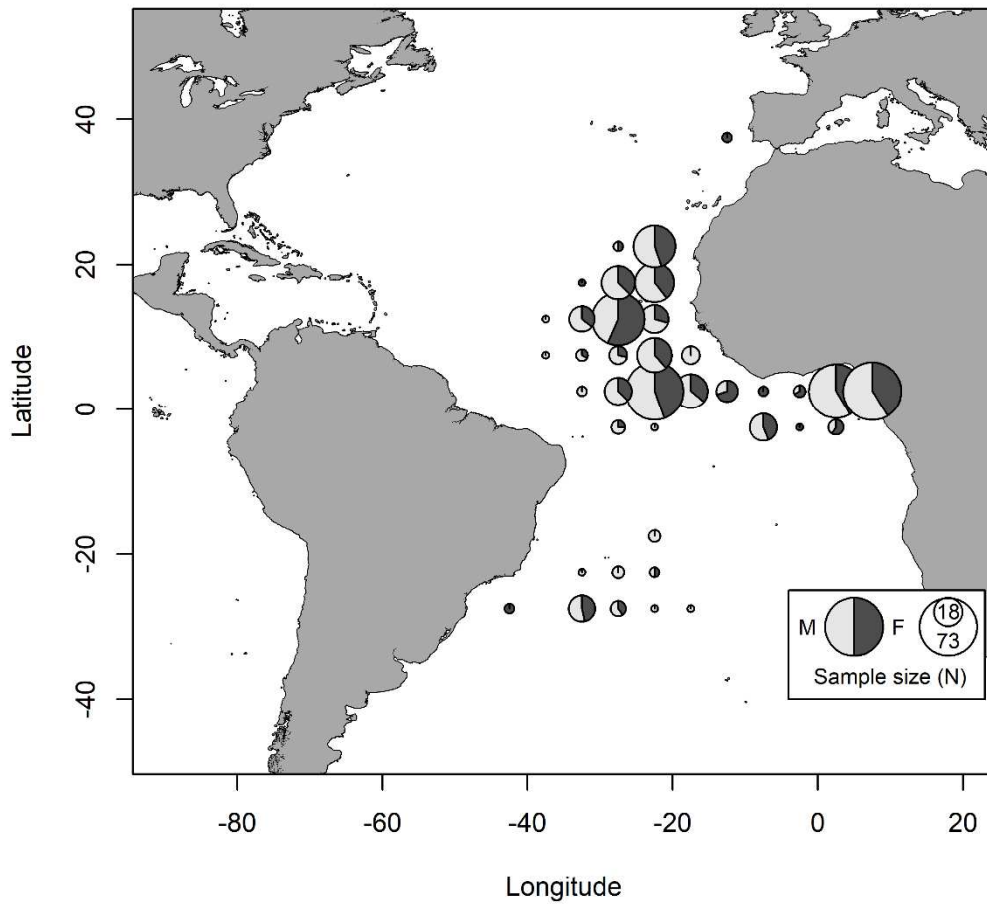
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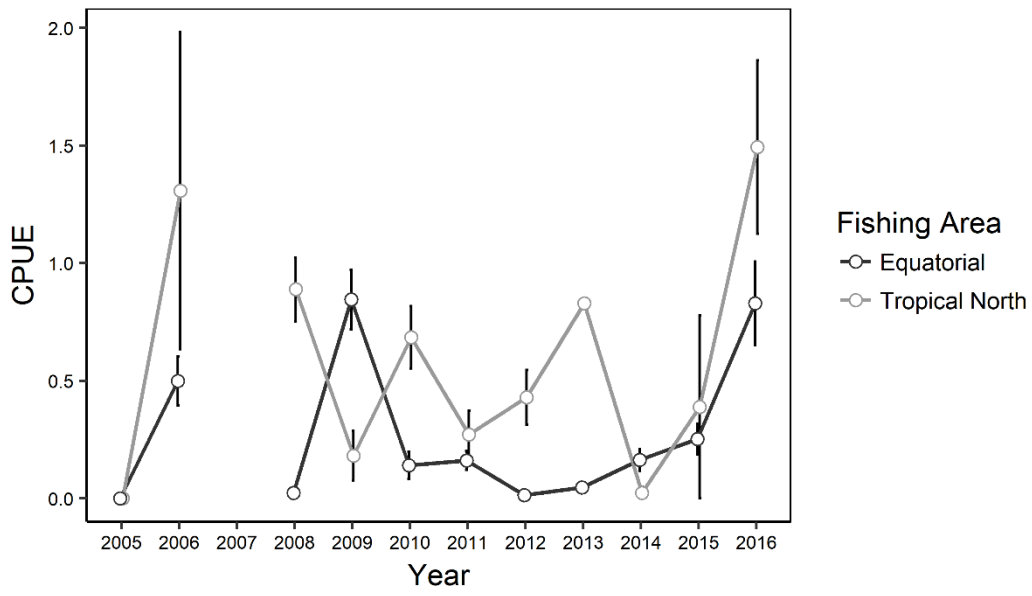
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591 Figure 5



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602 Figure 6



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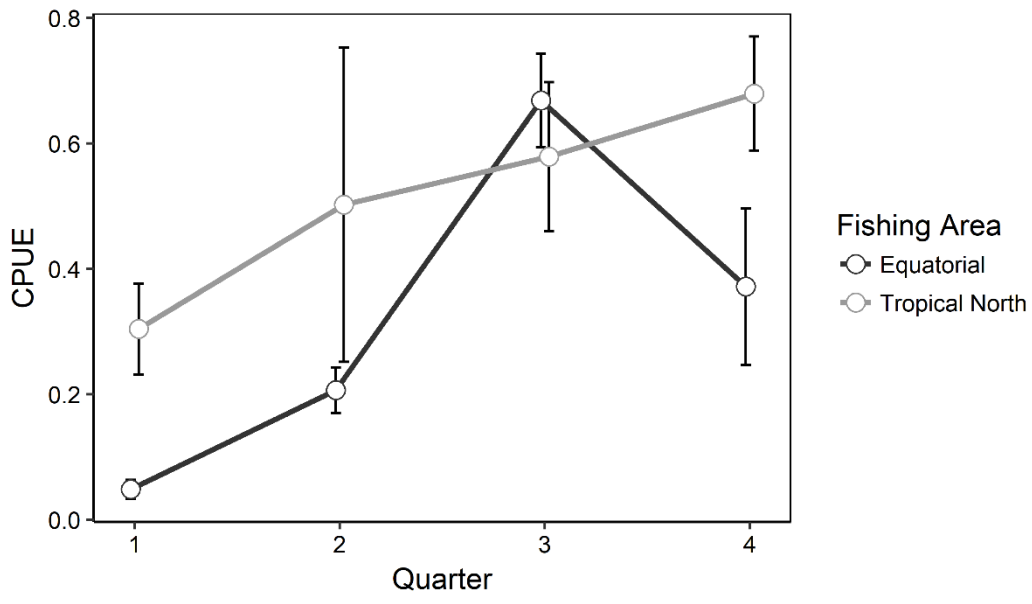
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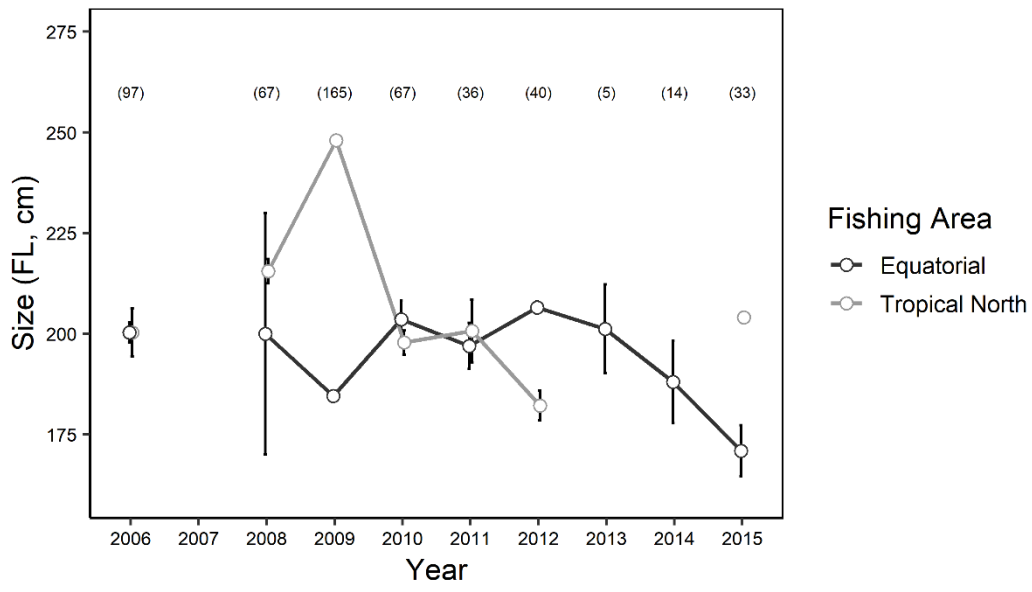
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629 Figure 8



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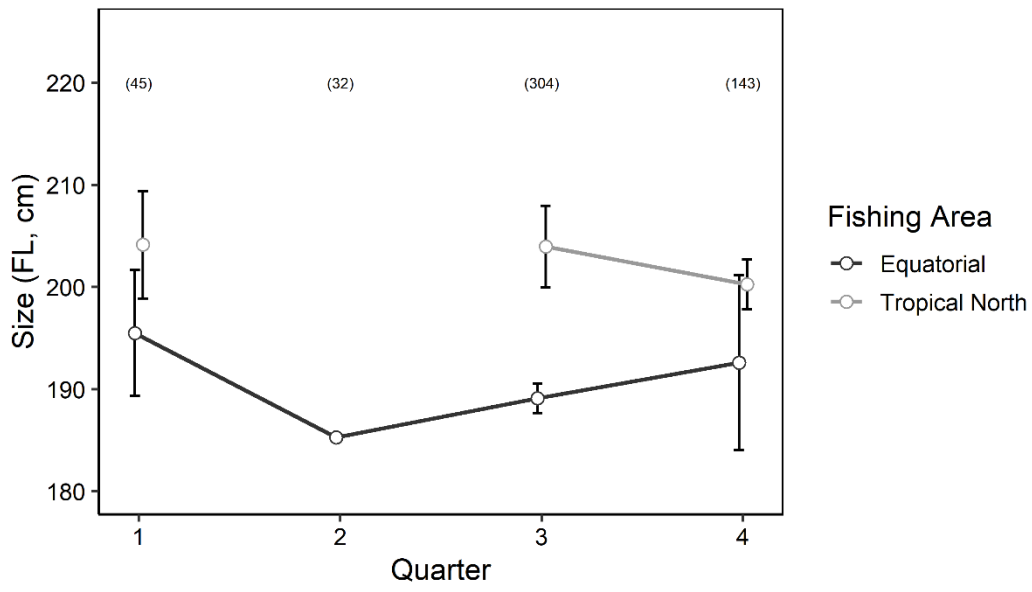
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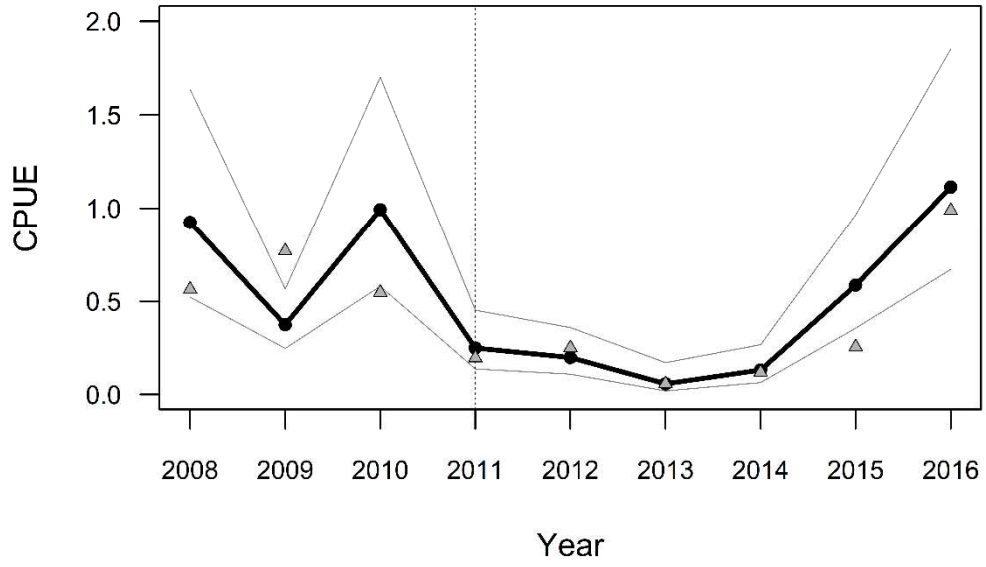
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648 Figure 10



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