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DOI: https://doi.org/10.1016/j.ecolind.2019.105942

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Local indicators for global species: pelagic sharks in the tropical northeast Atlantic, Cabo Verde islands region.

Rui Coelho[1,2,*], David Macías[3], Josetxu Ortiz de Urbina[3], Albertino Martins[4], Carlos Monteiro[4], Pedro G. Lino[1], Daniela Rosa[1,2], Catarina C. Santos[1,2], Pascal Bach[5], Hilario Murua[6,7], Pablo Abaunza[3], Miguel N. Santos[1,8].

1: Instituto Português do Mar e da Atmosfera, Portugal (IPMA).

2: Centro de Ciências do Mar do Algarve, Portugal (CCMAR).

3: Instituto Español de Oceanografia, Spain (IEO).

4: Instituto Nacional de Desenvolvimento das Pescas, Cabo Verde (INDP).

5: Institut de Recherche pour le Développement, France (IRD).

6: Centro Tecnológico Experto en Innovación Marina y Alimentaria, Spain (AZTI).

7: Current address: International Seafood Sustainability Foundation, USA (ISSF).

8: Current address: International Commission for the Conservation of Atlantic Tunas, Spain (ICCAT).

*: Corresponding author: Rui Coelho: E-mail: rpcoelho@ipma.pt; phone: + (351)289700500.

Abstract

Pelagic sharks are an important bycatch in pelagic fisheries, especially for drifting longlines targeting swordfish. In the Cabo Verde Archipelago (tropical NE Atlantic), pelagic shark catches can reach a significant proportion of the total catches. Due to the increased concern on the status of pelagic shark species, this study was developed to enhance the current knowledge of those sharks in the Cabo Verde region in comparison to the adjacent areas, especially associated with European Union (EU) pelagic longline fishing activity. Stock status indicators for the two main species, blue shark (*Prionace glauca)* and shortfin mako (*Isurus oxyrinchus*), were developed, based on fisheries data from logbooks and onboard scientific observers, including analysis of size frequency distributions and standardized catch-per-unit-of-effort (CPUE) indexes over time. The standardized CPUEs have been stable or increasing for both species in the past 10 years, indicating no signs of local depletion. In terms of sizes, the blue shark catch is composed mainly of adults, which can be a sign of a stable population. On the contrary, the catch of shortfin mako is composed mainly of juveniles, which in conjunction of a decrease of mean size might be a cause of concern, highlighting possible overfishing on the species in the region. Thirty satellite tags, 25 archival miniPATs and 5 SPOT GPS, were deployed in the Cabo Verde Exclusive Economic Zone (EEZ), showing that those species are highly mobile. The biomass and size distributions were modeled with spatial and seasonal models (GAMs) identifying locations where juveniles are predominantly concentrated and that should be prioritized for conservation. This work presents new information on the status of pelagic sharks in the Cabo Verde region in the context of those highly migratory species, and can now be used to promote more sustainable fisheries in the region.

Key-words:

Indices of abundance; longline fisheries; pelagic sharks; population trends; satellite tagging; spatial models.

1. Introduction

Pelagic sharks are an important component in pelagic fisheries catches, especially for drifting longliners targeting swordfish and tunas (Mejuto et al., 2009; Coelho et al., 2018). Depending on the fisheries, areas and seasons, pelagic sharks can be significant in the overall catch. Blue shark (*Prionace glauca)* and shortfin mako (*Isurus oxyrinchus*) are the two main shark species in those fisheries, and can in some areas and season represent more than 50% of the total longline catch and 90% of the total elasmobranch catch (Coelho et al., 2012). In the Cabo Verde Archipelago (tropical NE Atlantic), pelagic shark catches can also be important for pelagic fisheries (Fernandez-Carvalho et al., 2015a); however, the local status of those populations is not currently assessed. Cabo Verde has a large Exclusive Economic Zone (EEZ) of 734,000 km^2 and, thus, its future sustainability will be largely based on activities related to the use and exploitation of the sea and coastal resources (de Carvalho, 2013). Overall for the Atlantic Ocean, total pelagic fish catches reported to the International Commission for the Conservation of the Atlantic Tunas (ICCAT) in the last few years (2014-2017) were approximately 745,000 t per year. Of those, approximately 76,000 t per year (around 10% of the total catch) represented pelagic sharks, mostly blue shark (approximately 65,000 t per year) followed by shortfin mako (around 6,000 t per year) (ICCAT, 2018).

The blue shark is one of the widest ranging of all sharks, found throughout tropical and temperate seas from latitudes of about 60°N to 50°S. It is a pelagic species mainly distributed from the sea surface to depths of about 350 m, even though deeper dives of up to 1000 m have been recorded (Campana et al., 2011). Blue shark is a highly migratory oceanic species, with complex movement patterns and spatial structure probably related to the reproduction cycles and prey distribution (Montealegre-Quijano and Vooren, 2010; Tavares et al., 2012; Coelho et al., 2018). Tagging studies have shown extensive movements with numerous trans-Atlantic migrations probably accomplished by using the major oceanic current systems (Stevens, 1976; Stevens 1990; Queiroz et al., 2005; Silva et al., 2010; Campana et al., 2011). For the north Atlantic, data on the distribution, movements and reproductive behavior suggests a complex reproductive cycle, involving major oceanic migrations associated with mating areas in the north-western Atlantic and pupping areas in the north-eastern Atlantic (Pratt, 1979; Stevens, 1990).

The shortfin mako is also a widespread pelagic shark species, occurring in temperate and tropical waters of all oceans from about 60°N to 50°S. It occurs from the surface to at least 500 m depth, and is occasionally found close to inshore waters where the continental shelf is narrow (Compagno, 2001). Tagging studies in the northwest Atlantic have shown that shortfin makos can make extensive migrations of more than 3,000 km (Casey and Kohler, 1992), even though it has been suggested that trans-Atlantic migrations are not as common as in the blue shark. In the Atlantic, Casey and Kohler (1992) suggests that shortfin mako core distribution in the northwest Atlantic is between 20° to 40°N, bordered by the Gulf Stream in the west and the mid-Atlantic ridge in the east. In the northeast Atlantic it is presumed that the Strait of Gibraltar might be a nursery ground (Buencuerpo et al., 1998 and Tudela et al., 2005). The area between 17° to 35°S off the coast of Brazil seems to be an area of birth, growth and mating in the southwest Atlantic (Amorim et al., 1998).

The blue shark is currently listed as Near Threatened by IUCN, the International Union for the Conservation of Nature (Stevens, 2009), while the shortfin mako is currently listed as Endangered Rigby et al., 2019). In the Ecological Risk Assessments (ERAs) carried out for pelagic sharks in the Atlantic in 2010 and 2012 (Cortés et al., 2010; Cortés et al., 2015), blue shark was shown to have an overall intermediate vulnerability, because it is the most productive of all pelagic shark species. On the contrary the shortfin mako was one of the most vulnerable of all species analyzed, due to its relatively low productivity and high susceptibility.

The latest blue shark stock assessments in the Atlantic were carried out by ICCAT in 2015 (Anon., 2015). For the North Atlantic the stock was unlikely to be overfished and subject to overfishing, even though there were very high levels of model uncertainty reported (Anon., 2015). For the shortfin mako the latest stock assessments were carried out by ICCAT in 2017 (Anon., 2017). The results for the North Atlantic indicated that stock abundance was either below or very close to B_{MSY}, but that fishing mortality was overwhelmingly above F_{MSY}, with a combined 90% probability of the stock being in an overfished state and experiencing overfishing (Anon, 2017). Although the current biomass of the stock was still not very strongly depleted, current fishing mortality levels are unsustainable and can lead to strong population declines in the near future.

Due to the increased concern on the status of pelagic shark species and lack of specific knowledge for the region around the Cabo Verde islands in the tropical NE Atlantic and how local shark components are related to the managed population, this study was developed to enhance the current knowledge of the two main pelagic sharks captured in longline fisheries in the Cabo Verde region, especially associated with European Union (EU) pelagic longline fishing activity. Specifically, the main objectives of this study were to: 1) analyze potential local depletion of sharks in the region, specifically by analyzing trends in the catch composition, catch rates (CPUEs: catch per unit effort) and size distribution for the main species and; 2) identify possible biological and ecological sensitive areas in the region by modeling the spatial distribution of catches of the main species in the region and using the analysis of satellite telemetry tagging data.

2. Materials and Methods

2.1. Study area and fisheries data collection

The study focused on the Cabo Verde region in the tropical NE Atlantic. Two areas were defined, specifically: i) the Cabo Verde EEZ, and ii) a buffer of 300 nm adjacent to the EEZ (**Figure S1** - Supplemental electronic material).

The data collected and analyzed included EU (Portugal and Spain) pelagic longline fleets fishery logbook and scientific fishery observer data. Those data were compiled and used to provide analysis on the sharks catch composition, catch rate trends and size distributions in the region. Data were available and analyzed between 2006 and 2015, with the exception of 2008 that was not included due to issues related with a switch in database format, which did not allow linking the catch, effort and location (Vessel Monitoring System, VMS) data for that year. All fisheries parameters and indicators were compared between the Cabo Verde EEZ and the neighboring 300 nm buffer area, according to the study areas previously defined.

2.2. Satellite tagging

A total of 30 satellite tags were deployed within this study, specifically 25 miniPATs and 5 Fastloc GPS SPOT tags, both models from Wildlife Computers Inc. One of the GPS SPOT tagged specimens was recaptured after 77 days, and that tag was redeployed on another specimens. As such, of the available tags, 20 miniPATs and 6 GPS SPOTs (5 GPS SPOTs with 1 deployed twice) were deployed in blue sharks and 5 miniPATs were deployed in shortfin makos, all inside the Cabo Verde EEZ during 2016 (**Table S1** - Supplemental electronic material).

For the tagging operations, the sharks were restrained alongside the vessel and handled carefully, with those in the best condition selected for tagging in order to maximize post-release survivorship. Each tagged shark was measured, and the sex and maturity stage determined (juvenile vs. adult, see section 2.3.2 with the used sex specific maturity ogives available in the literature, Anon., 2014). Additional data recorded for each tagged specimen included tagging location (latitude and longitude), date and time.

The miniPATs were rigged with monofilament leaders secured with stainless steel crimps and encased in plastic tubing. Umbrella-type nylon darts (Domeier et al., 2005) were used to attach the tags to the shark dorsal musculature below the first dorsal fin, using the methodology described by Howey-Jordan et al. (2013). For the SPOT tags, the tags were attached with a plastic fin mount system placed in the first dorsal fin provided by the tag manufacturer.

The miniPAT tags archive detailed depth and temperature time-series data and use the light-based information for geo-locations. On the contrary, the Fastloc GPS SPOT tags use GPS based geo-locations that are much faster and provide more precise estimates, but do not record depth or temperature profiles. As such, both tags were used to provide complementary information on the sharks' habitat use and movements.

For estimating geographical daily positions, the Fastloc GPS signals are processed by the tags, compressed and then transmitted over the ARGOS satellite system. For the miniPATs, the daily locations were calculated based on the light levels recorded and using state-space statistical models (GPE3 software, processed through the tag manufacturer web portal). The miniPATs provide observations on twilight, sea surface temperature and dive depth, and the state-space modeling approach uses those observations and the corresponding reference data, along with a simple diffusion based movement model, to generate time-discrete gridded probability surfaces throughout the deployment. The corresponding oceanographic reference data used was that from NOAA Optimum Interpolation SST V2 High Resolution for the sea surface temperature, and from NOAA ETOP01 global relief model, Bedrock version, for bathymetry, respectively. The grids used were 0.25*0.25 degrees of latitude*longitude. From those probability surfaces, the most likely animal locations for a given day/time were derived.

2.3. Analysis of local shark indicators

2.3.1. Catch composition

The relative catch composition of sharks, defined as the species specific shark species in relation to the total shark catches, was calculated and analyzed for the general Cabo Verde EEZ, as well as for the 300 nm neighboring area.

2.3.2. Size distribution

The annual trends in the size frequency distributions and mean sizes for the main shark species were analyzed and plotted by area, sex and quarter of the year. Size data were tested for normality with Kolmogorov-Smirnov normality tests with Lilliefors correction (Lilliefors, 1967), and for homogeneity of variances with Levene tests (Levene, 1960). Specimen sizes were compared between regions (Cabo Verde EEZ and 300nm adjacent area), sexes and quarters of the year using non-parametric k-sample permutation tests (Manly, 2007).

The mean size at first maturity (L_{50}) used to define immature and mature specimens were based on the ICCAT Sharks Working Group report (Anon., 2014) for the North Atlantic shark stocks, as follows:

- Blue shark (males): mean = 200.1 cm Fork Length (FL);
- Blue shark (females): mean = 185.1 cm FL;
- Shortfin mako (males): mean = 182.5 cm FL; range = 180 - 185 cm FL;
- Shortfin mako (females): mean = 286.5 cm FL; range = 275 - 298 cm FL.

2.3.3. CPUE trends and standardization

The time series of catch per unit effort (CPUE) were plotted for blue and shortfin mako sharks, which allowed following the trends over time and assessing seasonality effects in the catch rates. The CPUE time series were standardized in order to remove the fishery-dependent effects (i.e., spatial, seasonal and targeting effects) and estimate relative indexes of abundance that can be used as population status indicators. For the standardization process, the response variable considered was CPUE measured in biomass of live fish (kg) per 1000 hooks deployed. The standardized CPUEs were estimated with statistical models using Generalized Linear Models (GLMs) and Generalized Linear Mixed Models (GLMMs).

Blue shark and shortfin mako data had different characteristics, especially with regards to the percentage of zeros in the datasets. Specifically, the blue shark is relatively common in the catches and has a low percentage of fishing sets with zero catches, while the shortfin mako is rarer in the catches and had a much higher percentage of fishing sets with zero catches. The presence of fishing sets with zero catches results in a response variable of CPUE=0, that can cause mathematical problems for fitting the models, and as such different approaches were tested and applied in each case.

Four different modeling methodologies were initially tested and compared, specifically tweedie, gamma, lognormal and delta lognormal models. For the tweedie models the nominal CPUE was used directly, as the response variable, given that this distribution can handle a certain proportion of zeros (mass) and a continuous distribution for the non-zeros. For the gamma and lognormal models the response variable was defined as the nominal CPUE + constant (c), with c set to 10% of the overall mean catch rate. The value of c=10% of the mean has been recommended by Campbell (2004), as it seems to minimize the bias for this type of adjustments. Further, and in a comparative study, Shono (2008) showed that when the percentage of zeros in the dataset is low (<10%), the method of adding a constant to the response variable performs relatively well. The final tested approach was a delta-lognormal model that uses and combines two different models, specifically a binomial model for the proportion of positive catches and a lognormal model for the expected CPUEs in the positive sets.

The covariates considered and tested in the models were:

- Year: analyzed between 2006 and 2015;
- Seasonal effects (quarters of the year, 4 categories): 1 = January to March, 2 = April to June, 3 = July to September, 4 = October to December;
- Spatial/area effects: tested as 5*5 or 10*10 degree grids;
- Targeting effects: based on the SWO/SWO+BSH ratio of captures.

Interactions between pairs of variables were considered and tested in the analysis and used in the final models, if significant. Specifically, interactions not involving the year factor were considered as fixed factors in GLM type models, while interactions involving the year factor were considered as random variables within GLMM models.

The significance of the explanatory variables, as well as the interactions, were assessed with likelihood ratio tests (LRT) comparing each univariate model to the null model (considering a significance level of 5%), and by analyzing the deviance explained by each covariate. Goodness-of-fit and model comparison was carried out with the Akaike Information Criteria (AIC) and the pseudo coefficient of determination (R^2). Model validation was carried out with a residual analysis. The final estimated indexes of abundance were calculated by least square means (LSMeans or Marginal Means), that for comparison purposes were scaled by the mean standardized CPUE in the time series.

2.4. Spatial models for prediction of catch rates and sizes

Generalized Additive Models (GAM) were used to predict the expected blue shark and shortfin mako shark catch rates (CPUEs) and size distribution as a function of location (latitude and longitude) and quarter of the year. The models used were lognormal GAMs for modeling the CPUEs and Gaussian with identity link for modeling the sizes.

The predictors in the models were given by the smooth functions of latitude and longitude plus a parametric component for the quarters of the year. The smooth terms for the location covariates were estimated by maximum likelihood with thin plate regression splines (Wood, 2003). The significance of the model parameters was tested with LRT comparing nested models, including the significance of the interactions between latitude, longitude and quarter of the year. Goodness-of-fit was assessed with the Akaike Information Criterion (AIC; Akaike, 1973) and with the final deviance explained. A residual analysis was carried out for model validation. The expected mean catch rates and sizes were mapped along the study area and for each quarter of the year.

All analysis in this study was carried out using the R language for statistical computing v3.4.0 (R Core Team, 2017), with the following additional libraries: “car” (Fox and Weisberg, 2011), “ggplot2” (Wickham, 2009), “gmodels” (Warnes et al., 2013), "KernSmooth" (Wand, 2015), “lme4” (Bates et al., 2013), "lsmeans " (Lenth, 2014), “maps” (Becker et al., 2013), “mgcv” (Wood, 2006, 2011), “perm” (Fay and Shaw, 2010), “plyr” (Wickham, 2011), "raster" (Hijmans, 2016) and "tweedie" (Dunn, 2013).

3. Results

3.1. Local shark indicators

3.1.1. Catch composition

The catch composition of elasmobranchs in the study area is largely dominated by blue shark (BSH) followed by shortfin mako (SMA) (**Table 1**). Other less frequent elasmobranch species occasionally captured in the region include the bigeye thresher (BTH) (*Alopias superciliosus*), silky shark (FAL) (*Carcharhinus falciformis*), longfin mako (LMA) (*Isurus paucus*), oceanic whitetip (OCS) (*Carcharhinus longimanus*), crocodile shark (PSK) (*Pseudocarcharias kamoharai*) and smooth hammerhead (SPZ) (*Sphyrna zygaena*) (**Table 1**). Most of those other species are either no-retention species in ICCAT and/or listed in CITES, and therefore are mostly released or discarded.

Table 1. Catch composition (percentage, in weight) of major shark species captured in the Cabo Verde EEZ and adjacent waters of the tropical NE Atlantic.

FAO code	**Species**	**Species composition (%)**		
		EEZ	**300 nm**	**Combined**
BSH	Blue shark	93.4	94.5	94.1
SMA	Shortfin mako	4.7	3.3	3.8
SPZ	Smooth hammerhead	0.2	0.3	0.3
FAL	Silky shark	0.3	0.3	0.3
OCS	Oceanic whitetip	0.1	0.1	0.1
BTH	Bigeye thresher	<0.1	<0.1	<0.1
SKH	Other elasmobranchs	1.2	1.4	1.3

3.1.2. Size distribution of the major shark species

In terms of size distribution, blue sharks caught in the Cabo Verde region are relatively large specimens with mean sizes of 210.9 cm FL (SD=17.9) inside the Cabo Verde EEZ and 205.3 cm FL (SD=21.5) in the 300 nm adjacent waters (**Figure 1**). Those differences observed in the mean sizes in the two areas were significant (K-Sample Asymptotic Permutation Test: Chi2 = 88.9, df = 1, p-value < 0.001), meaning that in the Cabo Verde EEZ the blue sharks are significantly larger than in the adjacent waters. Considering that the estimated blue shark mean size at first maturity for the North Atlantic is 185 cm FL for females and 200.1 cm FL for males (Anon., 2014), the catch of blue sharks in the Cabo Verde EEZ and neighboring waters is likely composed mainly by adults. The size distribution is also narrower in the EEZ.

For the shortfin mako the mean sizes were 149.4 cm FL (SD=24.5) inside the Cabo Verde EEZ and 142.2 cm FL (SD=36.6) in the adjacent waters. In this species the observed differences between areas were also statistically significant (K-Sample Asymptotic Permutation Test: Chi2 = 13.4, df = 1, p-value < 0.001), meaning that in the Cabo Verde EEZ shortfin makos are also significantly larger than in the adjacent waters (**Figure 1**). Considering that the estimated shortfin mako mean size at first maturity for the North Atlantic is 275-298 cm FL for females and 180-185 cm FL for males (Anon., 2014), the catch of shortfin makos in both regions is likely composed mainly by juveniles. Again for shortfin mako the size distribution of the catches showed a wider distribution outside the EEZ of Cabo Verde.

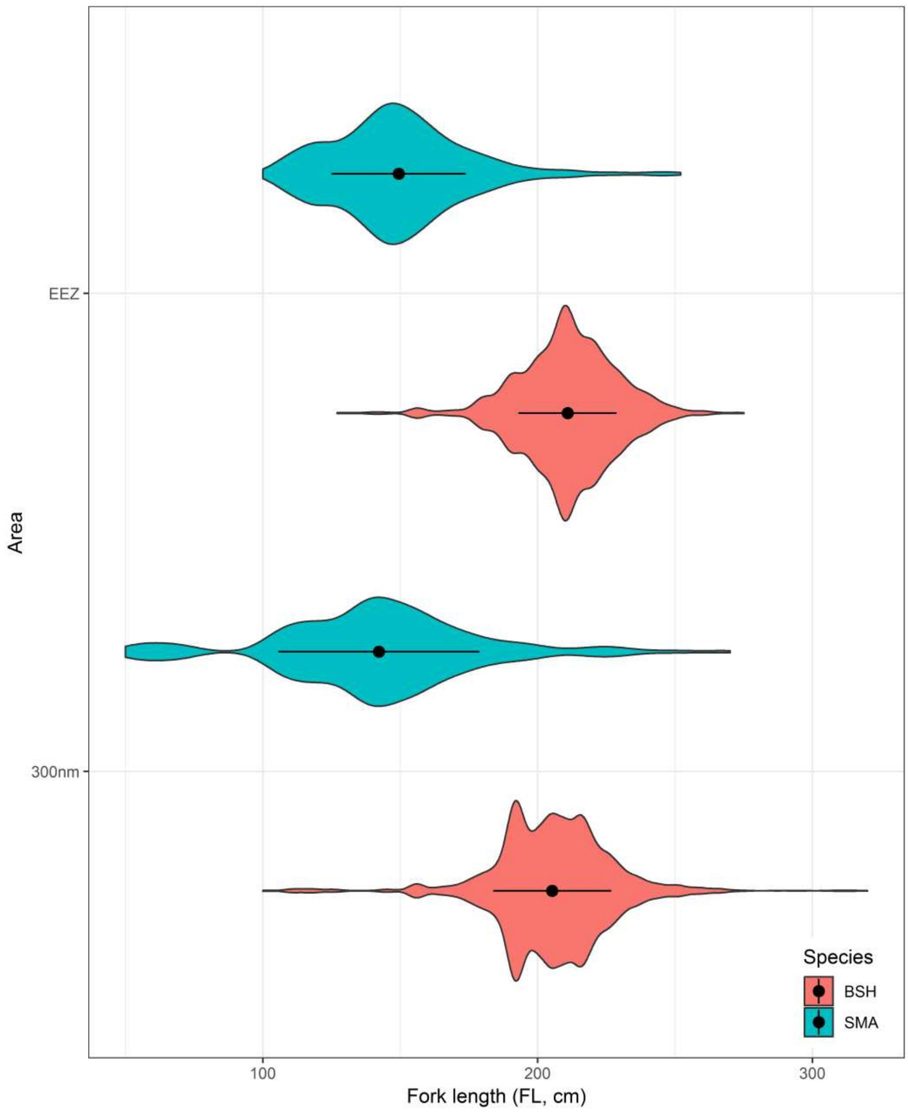


Figure 1. Size frequency distributions of the main shark species (BSH - blue shark and SMA - shortfin mako) in the Cabo Verde EEZ and 300 nm adjacent waters. The point and lines inside the plots represent the mean ± standard deviations. *(Note do editor: Color figure provided for the online version of the paper and a grayscale version is provided for the print version- this applies to all figures in the manuscript).*

In terms of seasonality, larger blue sharks were captured in the 1st, 3rd and 4th quarters of the year, while smaller specimens were caught mainly in the 2nd quarter (**Figure 2**), with those seasonal differences being statistically significant (K-Sample Asymptotic Permutation Test: Chi2 = 180.1, df = 3, p-value < 0.001).

For the shortfin mako the smaller size specimens were captured in the 1st and 2nd quarters), while larger specimens are captured later in the year, in the 3rd and 4th quarters (**Figure 2**). Those differences wee also statistically significant (K-Sample Asymptotic Permutation Test: Chi2 = 113.9, df = 3, p-value < 0.001).

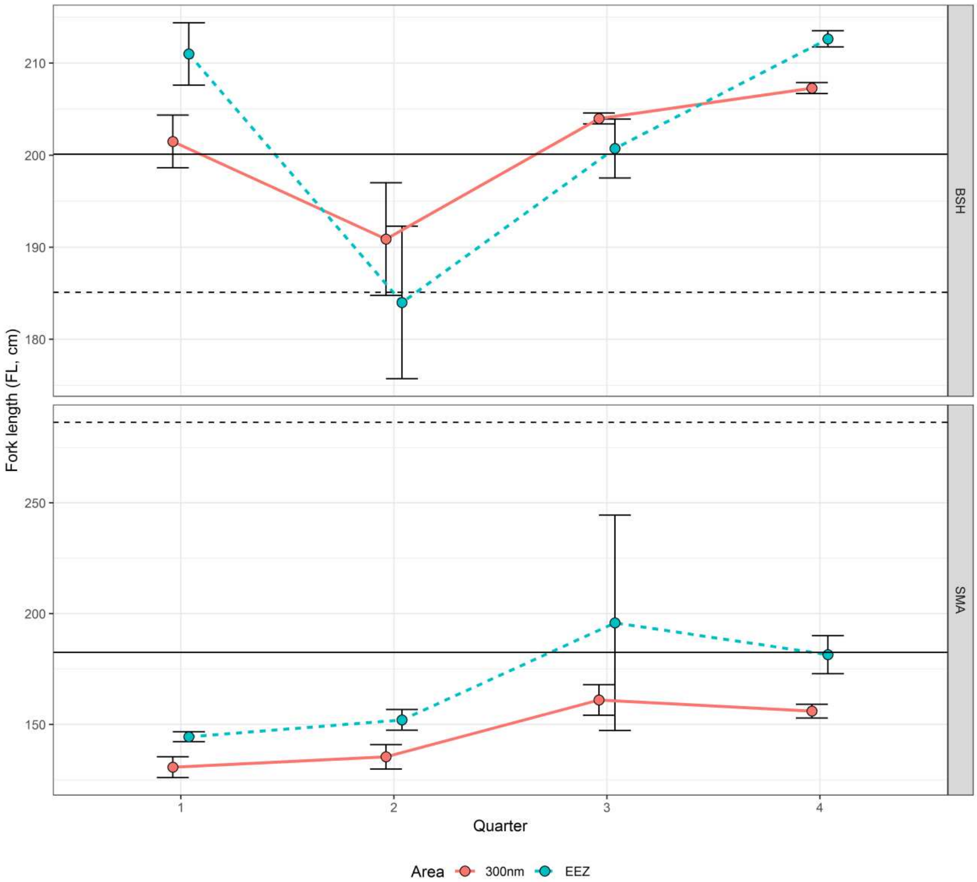


Figure 2. Seasonal mean sizes of the main shark species (BSH - blue shark and SMA - shortfin mako) in the Cabo Verde EEZ and 300 nm adjacent waters. The error bars refer to the 95% confidence intervals (CI). Mean sizes at first maturity (L_{50}) of each species are indicated for males (horizontal solid lines) and females (horizontal dashed lines) (Anon., 2014).

In terms of trends in the size distribution, blue shark mean size was relatively stable along the time series (**Figure 3**) in both areas, even though those relatively small differences were significant (K-Sample Asymptotic Permutation Test: Chi2 = 573.3, df = 7, p-value < 0.001). By contrast, there was a general decreasing trend in the mean size of shortfin mako during the study period, especially in the 300 nm adjacent waters, except in the most recent years (2014-2015) when mean sizes increased to similar levels of the initial years (**Figure 3**). The mean annual differences in the shortfin mako sizes were also statistically significant (K-Sample Asymptotic Permutation Test: Chi2 = 136.4, df = 8, p-value < 0.001).

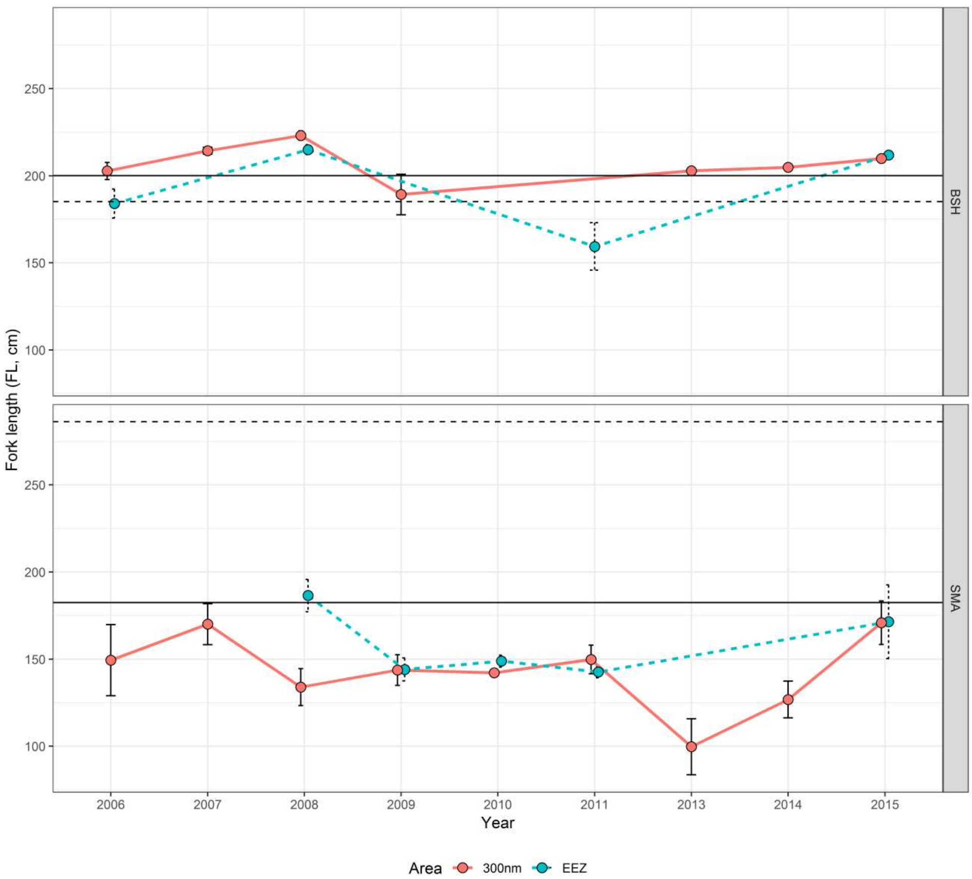


Figure 3. Time series trends of the mean sizes of the main shark species (BSH - blue shark and SMA - shortfin mako) in the Cabo Verde EEZ and 300 nm adjacent waters. The error bars refer to the 95% confidence intervals (CI). Mean sizes at first maturity (L_{50}) values are indicated for males (solid line) and females (dashed line) of each species (Anon., 2014).

3.1.3. Nominal catch per unit of effort (CPUE) distribution and trends

General increasing CPUE trends for both blue shark and shortfin mako were observed along the study period in both areas. More specifically, for blue shark there was a progressive increase between 2006 and 2015, while for shortfin mako there was an increase mainly in the earlier years, between 2006 and 2009, and then a more stable period between 2009 and 2015 (**Figure 4**).

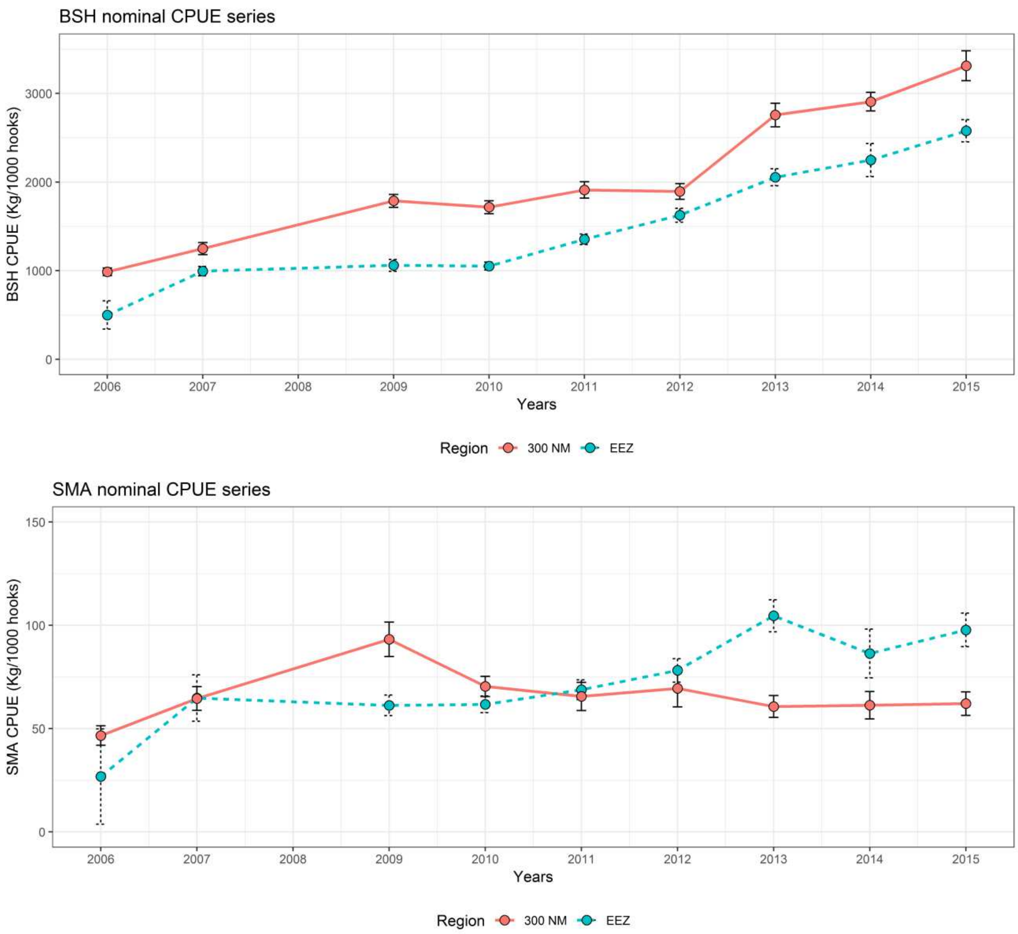


Figure 4. Time series of nominal catch per unit of effort (CPUE, biomass in Kg/1000 hooks) for blue shark (above) and shortfin mako (below) in each of the study areas, Cabo Verde EEZ and the 300 nm adjacent waters. The error bars refer to the 95% confidence intervals (CI).

In terms of the spatial CPUE distribution, higher blue shark catch rates occurred mainly outside the Cabo Verde EEZ, in the 300 nm adjacent waters, especially in the western area (**Figure 5**). For shortfin mako, higher CPUEs were also observed in the limits and outside the Cabo Verde EEZ, but mainly in the eastern areas towards the African western coast (**Figure 5**).

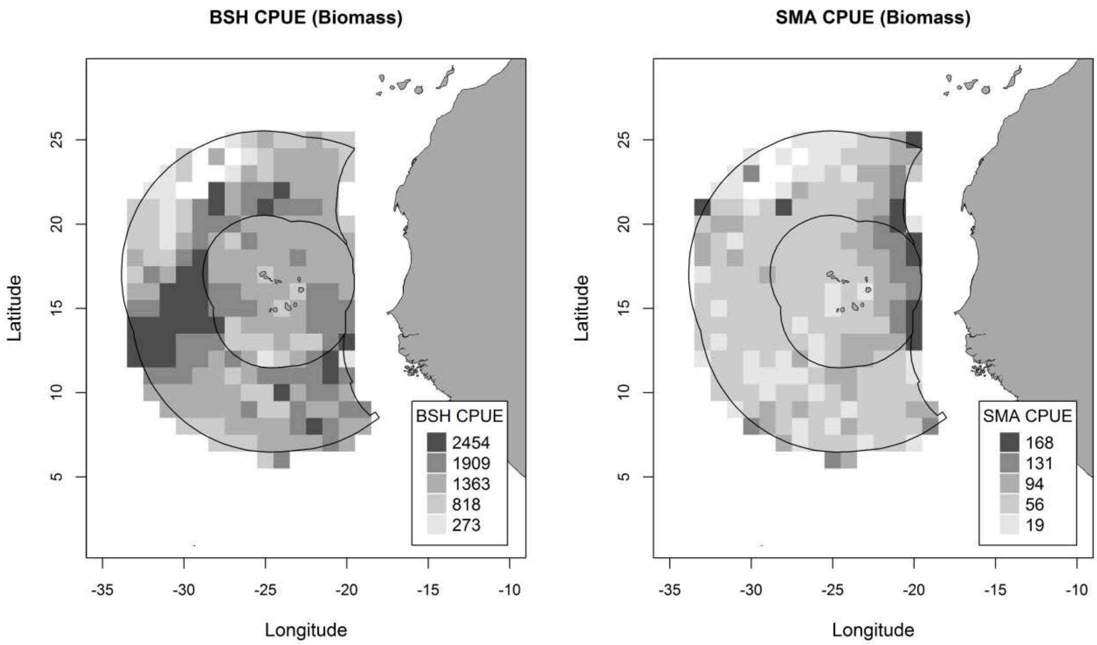


Figure 5. Spatial distribution (by 1°*1° squares) of catch per unit of effort (CPUE, biomass in kg/1000 hooks) in the Cabo Verde EEZ and 300 nm adjacent waters, for blue shark (left plot) and shortfin mako (right plot). Data was combined for the period 2006-2015.

3.1.4. CPUE standardization of blue shark

The percentage of fishing sets with zero catches of blue shark was low (2.9%). There was a slight decrease in the sets with zero catches in the earlier period until 2011, followed by a slight increase in the more recent years (**Figure S2** - Supplemental electronic material). In terms of data distribution, the nominal blue shark CPUEs were highly skewed to the right and became more normal distributed in the log-transformed scale (**Figure S3** - Supplemental electronic material).

Of the various models tested, the best fit was obtained with a lognormal GLMM model. All the explanatory variables tested for the CPUE standardization were significant and contributed significantly for explaining part of the model deviance, including the effects for year, quarter, area and targeting (**Table S2** - Supplemental electronic material). The interactions of quarter with targeting were also significant and included in the model as a fixed variable, as well as the interaction between year and quarter included as a random effect. On the final fitted model, the factors that contributed most for the deviance explanation were targeting, followed by year, quarter and area (**Table S2** - Supplemental electronic material). In terms of model validation, the residual analysis, including the residuals distribution along the fitted values, the QQ plots and the residuals histograms, showed a good model fit without major outliers or trends in the residuals (**Figure S4** - Supplemental electronic material).

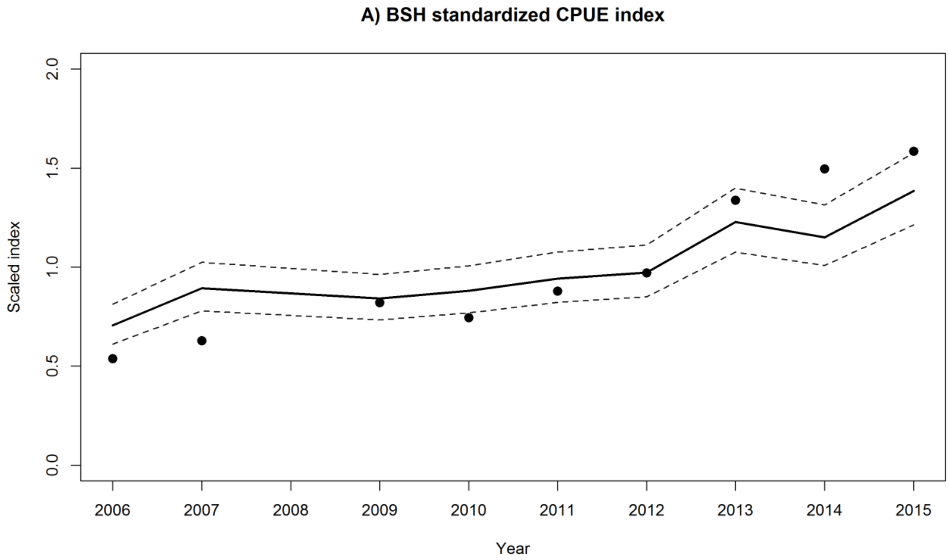
The final standardized index of abundance for the blue shark in the Cabo Verde EEZ between 2006 and 2015 shows an overall increase along the entire time series period, similar to what is observed in the nominal CPUE series (**Figure 6**).

3.1.5. CPUE standardization of shortfin mako

The overall percentage of fishing sets with zero catches of shortfin mako was 37.7%. Higher proportion of sets with zero shortfin mako catches were observed in the earlier years, and a progressive decrease for the most recent years (**Figure S5** - Supplemental electronic material). The CPUE distribution was also highly skewed to the right and became more normal distributed in the log-transformed scale (**Figure S6** - Supplemental electronic material).

Given the high percentage of zeros in the data and the shape of the distribution, the best fitted model was a tweedie GLM. All the explanatory variables tested were significant and contributed significantly for explaining part of the model deviance, including the effects for year, quarter, area and target (**Table S3** - Supplemental electronic material). The interactions of quarter with targeting were also significant and included in the model as a fixed effect. On the final fitted model, the factors that contributed most for the deviance explanation were the area, followed by quarter, year and targeting (**Table S3** - Supplemental electronic material). In terms of model validation, the residual analysis, including the residuals distribution along the fitted values, the QQ plots and the residuals histograms, showed a good model fit without major outliers or trends in the residuals (**Figure S7** - Supplemental electronic material).

The final standardized index of abundance for the shortfin mako shark in the Cabo Verde EEZ between 2006 and 2015 shows an increase in the earlier years until 2009, followed by a decrease in 2010, and then a slight increased again in the most recent years until 2015 (**Figure 6**).



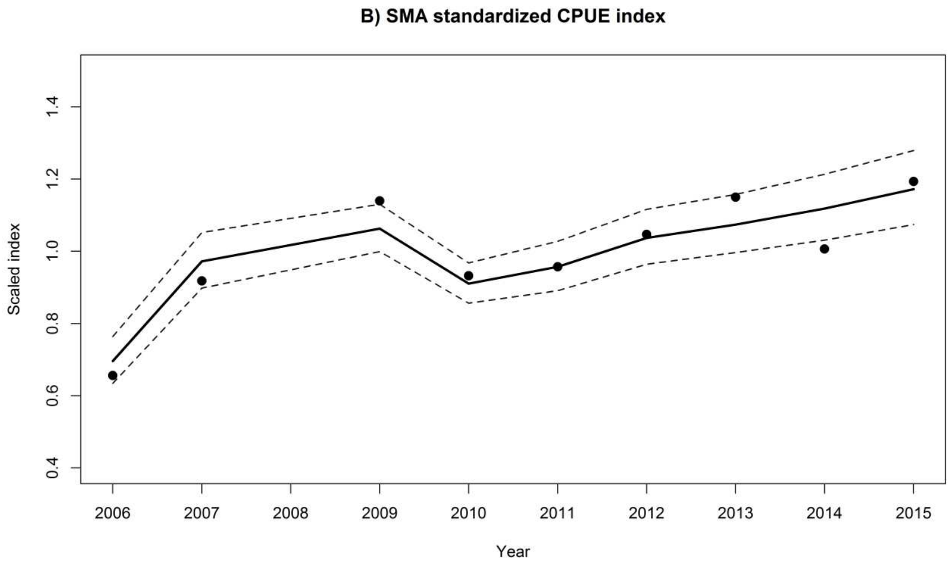


Figure 6. Standardized catch per unit effort (CPUE) series for blue shark (A - top) and shortfin mako (B - below) in the in the Cabo Verde region. The solid line represents the standardized CPUE, the dashed line represents the 95% confidence intervals of the standardized CPUE, and the black dots represent the nominal CPUE. Each series is scaled by the mean standardized CPUE

3.2. Satellite tagging

The SPOT tags (6 deployments) in blue shark had duration periods between 22 and 88 days, with 2 of the tagged specimens fished (recaptured) after 50 and 77 days at liberty. Overall, the deployed SPOT tags recorded data on 328 tracking days for the 6 blue shark specimens (**Table S4** - Supplemental electronic material).

Of the 25 deployed miniPAT tags (20 on blue shark and 5 on shortfin mako), 10 tags reached the full deployment period and popped-up on the expected date after 120 days (8 blue sharks and 2 shortfin makos), 10 specimens suffered post-release mortality (7 blue sharks and 3 shortfin makos) between 1 and 26 days at liberty, 1 blue shark was recaptured by a fishing vessel after 71 days at liberty, 2 blue sharks dived to the maximum tag depth (~1850m) after 56 and 76 days at liberty and the tags released automatically to avoid damage due to excessive pressure, 1 tag had premature release (shedding) after 12 days, and 1 tag failed to transmit. Overall, a total of 1,296 tracking days were recorded for blue sharks and 258 days for shortfin mako (**Table S4** - Supplemental electronic material).

From the miniPAT most likely estimated tracks, it was possible to see that most blue sharks moved substantial distances, on most cases to areas outside the EEZ (**Figure 7**). There was not a defined pattern in the movements, as there were cases of sharks moving towards the east, west, north and south. Particularly noteworthy was a blue shark that was tagged inside the Cabo Verde EEZ close to the Islands and that moved a significant distance towards the equatorial waters. Similar patterns were obtained with the GPS SPOT tags, showing blue sharks also moving outside the Cabo Verde EEZ, in this case mainly towards western and southeastern areas (**Figure 7**).

For the shortfin mako, most specimens also tended to move outside the Cabo Verde EEZ, but in this case mostly towards areas closer to the western African shelf, east of the Cabo Verde Islands. One particular specimen that was tagged inside the EEZ southeast of the Islands moved southeast, towards the region closer to the continental shelf at the latitude of the Bijagós Islands in Guiné Bissau (**Figure 7**).

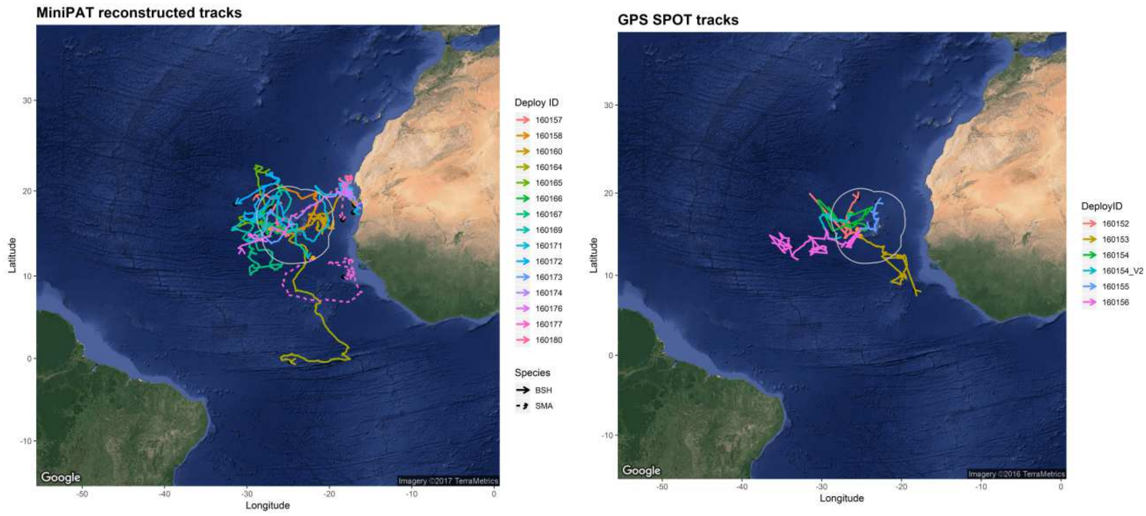


Figure 7. Reconstructed tracks for miniPAT (left panel) and GPS SPOT tags (right panel) for blue shark and shortfin mako. Only tags with tracking days > 26 days are shown, in order to exclude specimens that suffered post-release mortality after tagging and/or were fished (recaptured) very close to tagging location.

For blue shark there were differences in the spatial distribution of the satellite tagged sharks, when comparing between males and females. In general, males moved less and stayed closer to the islands, while females showed wider movement and traveled greater distances to other areas (**Figure 8**). When comparing maturity stages, there were also differences, with adults travelling greater distances than juveniles (**Figure 8)**.

For shortfin mako the probability of distributions was closer to the African continental shelf, mainly outside the Cabo Verde EEZ (**Figure 9**). For this species, as less specimens were tagged, the analysis was made jointly and not separated by sex or maturity stage.

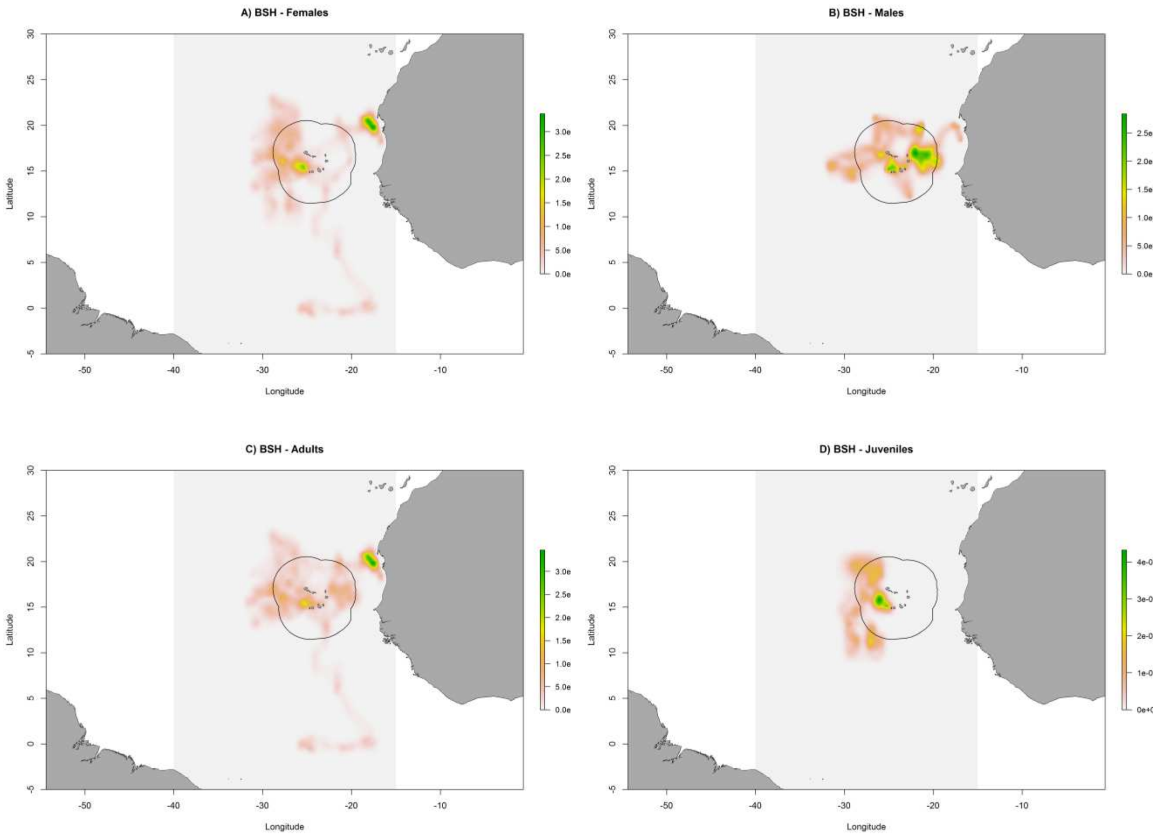


Figure 8. Probability surfaces of the spatial distribution of satellite tagged blue sharks (BSH) in the Cabo Verde region, tropical NE Atlantic. The plots represent females (A - top left), males (B - top right), adults (C - bottom left) and juveniles (D - bottom right). The colors in the legend refer to the distribution of the density of the specimens, ranging from red (lower density) to green (higher density).

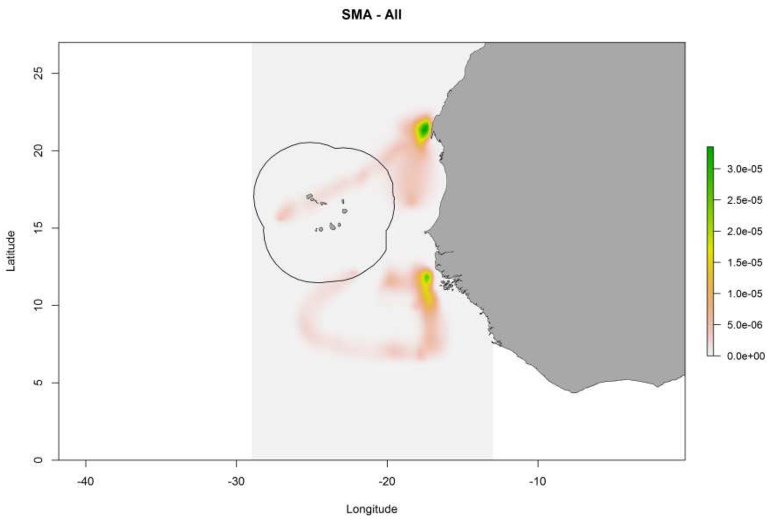


Figure 9. Probability surfaces of the spatial distribution of satellite tagged shortfin mako shark (SMA) in the Cabo Verde region, tropical NE Atlantic. The colors in the legend refer to the distribution of the density of the specimens, ranging from red (lower density) to green (higher density).

3.3. Spatial models

3.3.1. Modeling and predicting catch rates

There was considerable variability in the expected catch rates (CPUEs) of both blue shark and shortfin mako in the study area when taking into consideration the location (spatial effects) and quarter of the year (seasonal effects).

For blue shark, overall higher CPUEs were predicted outside the Cabo Verde EEZ, especially in the south and southwest regions, while lower CPUEs were expected both in the EEZ and also in the northern areas outside the EEZ (**Figure 10**). Higher CPUEs were predicted during the winter and autumn (quarters 1 and 4), while much lower overall CPUEs were predicted in late spring and summer, especially during quarter 2 (**Figure 10**).

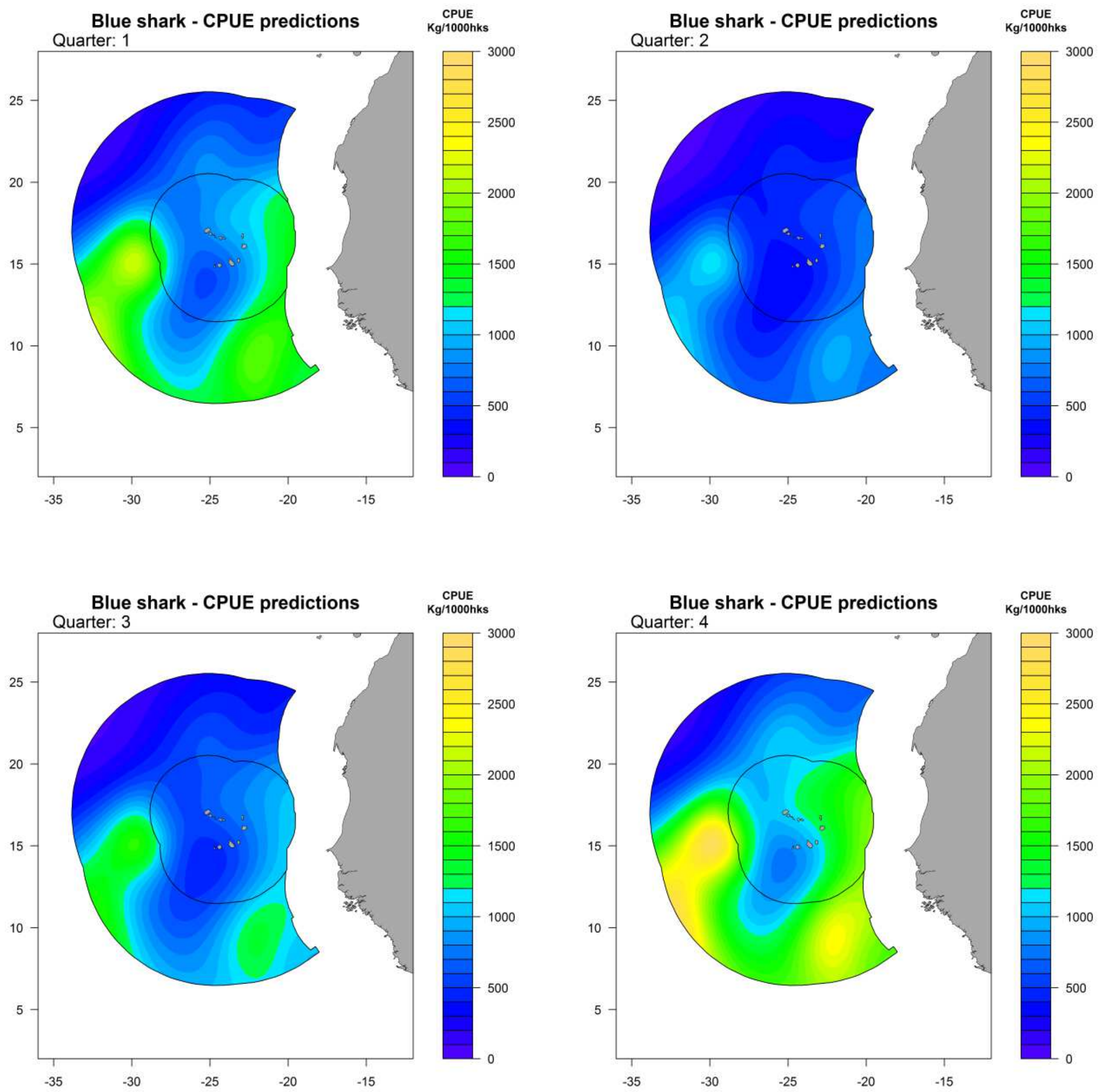


Figure 10. Seasonal prediction of the catch rates (CPUEs) of blue shark in the Cape Verde EEZ and 300nm adjacent waters. The predicted values are the result of a Generalized Additive Model (GAM) with lognormal distribution, taking into consideration the smooth terms of catch location estimated with thin plate regression splines and the quarter of the year used as a parametric term.

For shortfin mako very low CPUE along most of the study area was predicted, including both the Cabo Verde EEZ and most of the adjacent waters. The higher CPUEs for this species were predicted in the eastern areas, closer to the African continental shelf waters (**Figure 11**). The seasonal effects were not as noticeable as for the blue shark, with the overall trends mostly constant and low along all quarters of the year (**Figure 11**).

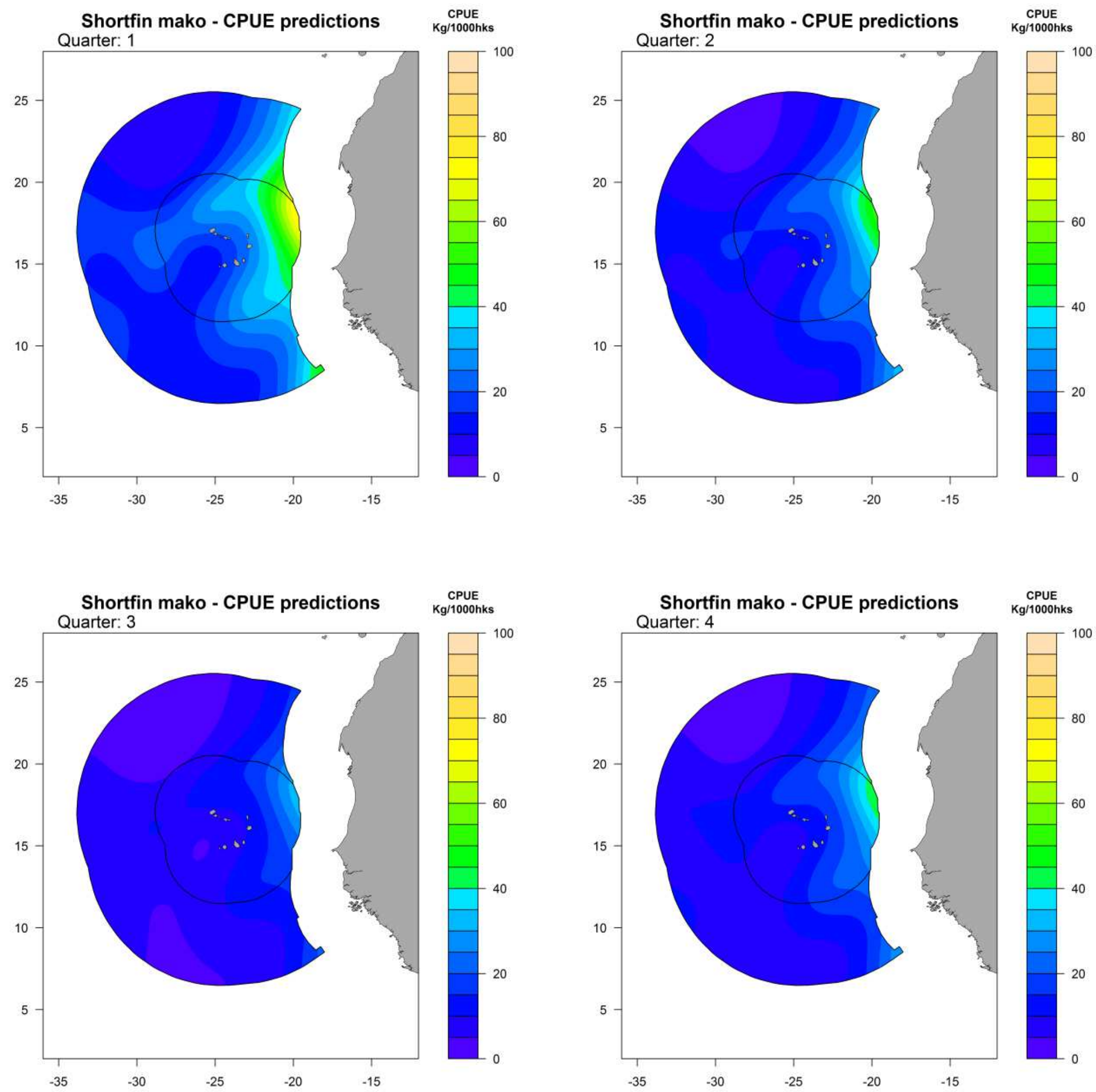


Figure 11. Seasonal prediction of the catch rates (CPUEs) of shortfin mako in the Cabo Verde EEZ and 300mn adjacent waters. The predicted values are the result of a Generalized Additive Model (GAM) with lognormal distribution, taking into consideration the smooth terms of catch location estimated with thin plate regression splines and the quarter of the year used as a parametric term.

3.3.2. Modeling and predicting catch sizes

For blue shark, smaller specimens were predicted both inside the Cabo Verde EEZ and the 300 nm adjacent waters, especially in the northeastern areas, as well as outside the study area towards the southwest. Seasonality was important in the blue shark predicted sizes, with overall smaller specimens expected during the spring months, in quarter 2 (**Figure 12**).

Nonetheless, it is important to note that the overall predicted blue shark sizes are relatively large for the species, given that blue sharks mature at 185.1 cm FL (females) and 200.1 cm FL (males). As such, most of the blue shark sizes predicted to occur in the study area along the entire year corresponds to large juveniles or sub-adults, and adults.

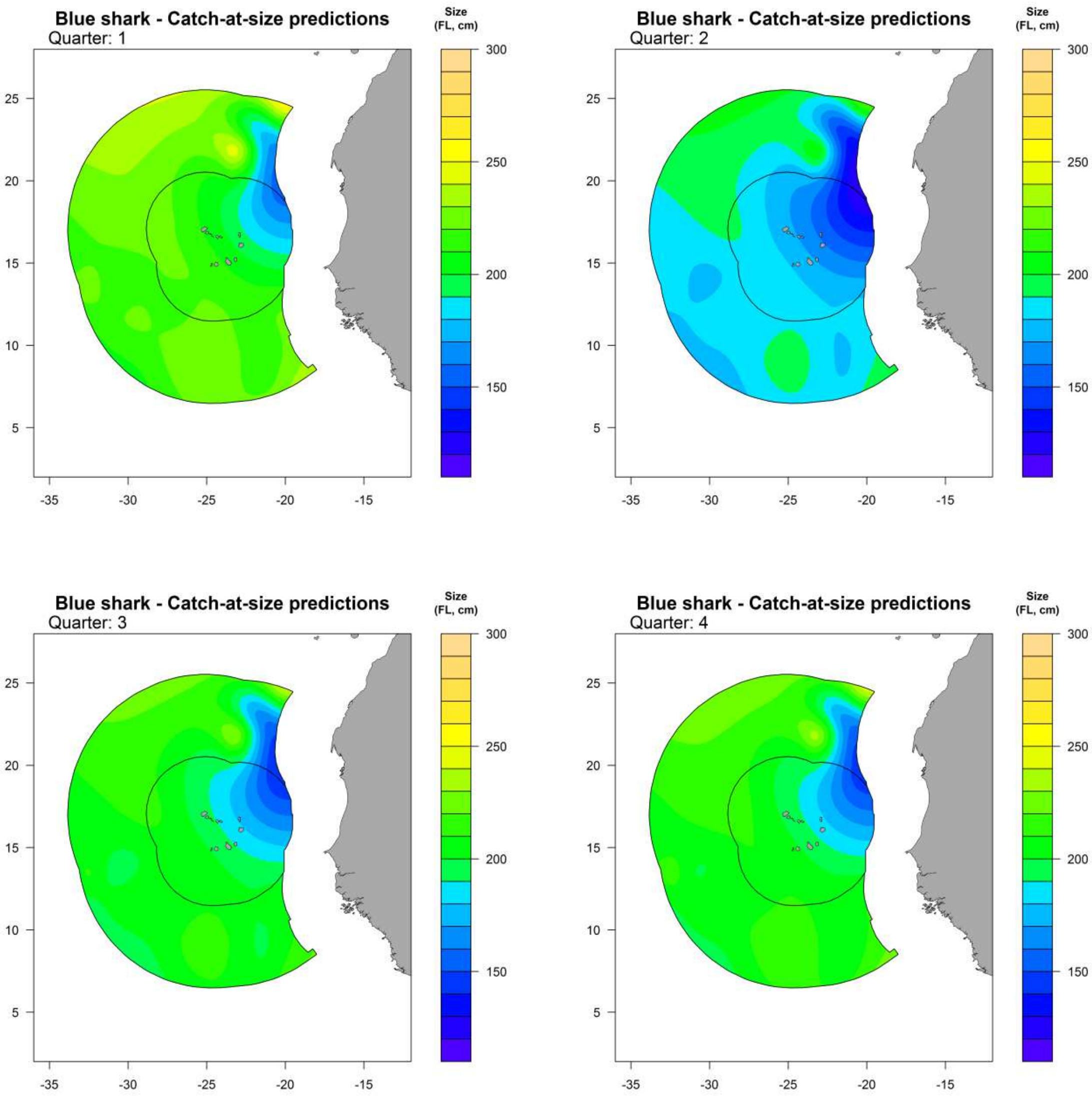


Figure 12. Seasonal prediction of the size distribution of blue shark in the Cabo Verde EEZ and adjacent waters (300 nm). The predicted values are the result of a Generalized Additive Model (GAM) with Gaussian distribution and identity link function, taking into consideration the smooth terms of catch location estimated with thin plate regression splines and the quarter of the year as a parametric term.

For shortfin mako, there were also marked spatial effects in the predicted size of the specimens, in this case with smaller specimens expected inside the study area, especially in the northeastern waters. Smaller specimens were expected to occur in quarters 1 and 2 and larger specimens were expected to occur mainly in the 2nd semester (**Figure 13**). Contrary to blue shark, for shortfin mako the overall expected specimen sizes corresponded mostly to small size specimens. As such, most of the shortfin mako specimens expected to occur in the study area along the entire year, particularly the females, correspond to juveniles.

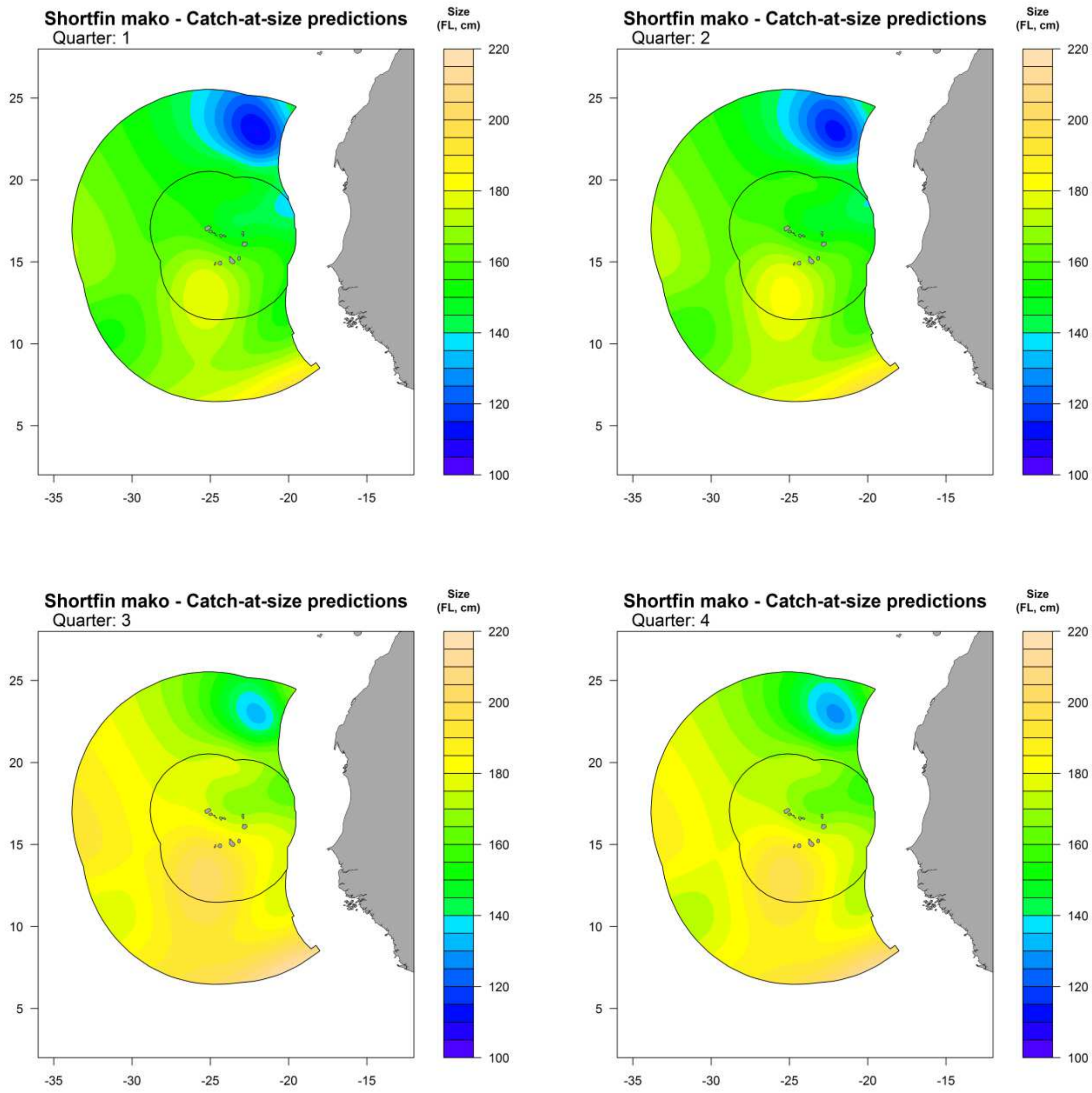


Figure 13. Seasonal prediction of the size distribution of shortfin mako shark in the Cabo Verde EEZ and 300 nm adjacent waters. The predicted values are the result of a Generalized Additive Model (GAM) with Gaussian distribution and identity link function, taking into consideration the smooth terms of catch location estimated with thin plate regression splines and the quarter of the year used as a parametric term.

4. Discussion

4.1. Shark indicators in the regional (NE Atlantic) context

In the region of the Cabo Verde EEZ and adjacent waters, the elasmobranch catch composition from pelagic fisheries is largely composed by blue shark, followed by shortfin mako. This is common in pelagic longline fisheries operating in other regions of the Atlantic Ocean (e.g., Mejuto et al., 2009; Coelho et al., 2012; Frédou et al., 2015). However, other less frequently captured elasmobranch species, which include threshers, silky shark, longfin mako, oceanic whitetip, hammerheads and the crocodile shark, were also recorded in similar proportions in pelagic longlines operating in other Atlantic regions (e.g., Coelho et al., 2012).

A CPUE standardization procedure was carried out for the two main shark species using statistical models, specifically Generalized Linear Models (GLMs) and Generalized Linear Mixed Models (GLMMs). Such standardization procedure was carried out to remove the fishery-dependent effects of the nominal CPUE data (i.e., spatial, seasonal and targeting effects), which allows the estimation of relative indexes of abundance that can then be used as population status indicators (Hilborn and Walters, 1992). The value of such standardization lies in the improvement in the proportionality between the derived index and true abundance (Ye and Dennis, 2009). Standardized CPUE series are also often used in stock assessment models by most RFMOs (Regional Fisheries Management Organizations). In this case the results from the CPUE standardization process showed an increase for the blue shark index of abundance over the entire time series, between 2006 and 2015. For the shortfin mako the abundance index was more variable, showing an increase in the earlier years of 2006-2009, followed by a decrease in 2010, and then an overall slight increase in the more recent period until 2015.

In terms of targeting effects, the differences in fishing strategy used in the models reflect the increased economic importance of sharks among the EU pelagic longline fleets, which traditionally targeted swordfish almost exclusively. These changes in target species were incorporated into the model by a proxy based on the ratio of the swordfish catch and the combined swordfish and blue shark catches by set. This ratio is in general considered a good proxy indicator of target criteria more clearly directed at swordfish *versus* a more diffuse fishing strategy aimed at the two main species (i.e., swordfish and sharks). Moreover, this methodology has been consistently applied to both EU fleets (Portuguese and Spanish) that have a similar method of operation, including applications to the Atlantic and Indian Oceans (e.g., Mejuto et al., 2013; Coelho et al., 2014). Other approaches for including targeting effects into the CPUE standardization process have been tested in the past. Specifically, for the Portuguese pelagic longline fishery, Coelho et al. (2015a) tested a cluster analysis based on the catch composition of the 10 major species or species-groups, in an analysis, as suggested by He et al. (1997), that has been successfully applied for CPUE standardization of other fleets (e.g. Wang and Nishida, 2014; Hoyle at al., 2018). However, Coelho et al. (2015a) demonstrated that for the Portuguese pelagic longline fleet (and EU fleets in general), given that the catches are largely dominated by the two major species (i.e., swordfish and blue shark) the use of ratios or clusters resulted in very similar results.

Size distribution trends can also be used as stock status indicators (Tu et al., 2018) and it was observed that the catch of blue shark in the Cabo Verde region is mainly composed of relatively large adult specimens. There were no major variations in the time series trends, with the mean sizes relatively stable along the time period, both in the Cabo Verde EEZ and adjacent waters. This further suggests that there are no signs of population declines. Both the CPUE and size indicators for blue shark seem to indicate an apparently stable population in the region.

The catches of shortfin mako were mainly composed of small juvenile specimens, and there was a general decreasing trend in the mean catch size during the time period. This catch composed mainly of juvenile specimens and the general decreasing trend in mean sizes might be an indicator of overfishing for this species in the region. The relatively large catch rates of juvenile shortfin mako may also indicate that the Cabo Verde region and West African continental shelf is functioning as an aggregation area for juvenile specimens, that become vulnerable to the fisheries taking place in the region. Thus, fisheries indicators for shortfin mako should be closely monitored, preferably based on fishery observer programs.

One important aspect of this study is that it used detailed data exclusively from the EU fleets that operate in the Cabo Verde region (Portugal and Spain) but it should be noted that other fleets from other countries also operate in the region (e.g. Asian fleets). As such, the results presented here should be interpreted as representative only of the EU fleet component, while the effects of other fleets operating in the region were not considered. Although it should be noted that the Asian fleets traditionally target albacore and tropical tunas, setting their gear in deeper water and thus having lower catch rates of pelagic sharks.

It is important to put these results and conclusions within a wider Atlantic perspective. For the blue shark, the Ecological Risk Assessments carried out both in the Atlantic (Cortés et al., 2010; Cortés et al., 2015) and Indian Oceans (Murua et al., 2013, 2018) showed that this species is one of the most productive of all pelagic shark species and therefore capable of sustaining relatively high levels of fishing mortality. Still, the overall vulnerability status was determined to be intermediate, mainly due to the also relatively large susceptibility of blue shark to pelagic fisheries, predominately pelagic longlines. The latest Atlantic blue shark stock assessments carried out by ICCAT in 2015 showed that for the north Atlantic the stock was unlikely to be overfished or subject to overfishing, even though there were high levels of uncertainty (Anon., 2015). This contrasts with the South Atlantic stock where it was not possible to discount that in recent years the stock may have been at levels near B_{MSY} and that fishing mortality has been approaching F_{MSY}, implying that future increases in fishing mortality in the southern stock could push the stock to an overfished state (Anon., 2015). The standardized CPUE increasing trends observed in this study for the blue shark in the Cabo Verde region are in line with the trends from the other fleets used in the last stock assessment by ICCAT. Specifically, for a number of fleets that operate in the North Atlantic, including both eastern and western regions (Portugal, Spain, Japan, US, Chinese-Taipei, Venezuela and Ireland). This general increasing trend has also been registered since the mid-2000s.

For shortfin mako the Ecological Risk Assessments carried out in the Atlantic (Cortés et al., 2010; Cortés et al., 2015) and Indian Ocean (Murua et al., 2013, 2018) ranked the species as one of the most vulnerable of all pelagic sharks, mainly due to its very low productivity and high susceptibility to fisheries, especially pelagic longlines. In the latest shortfin mako stock assessment carried out by ICCAT in 2017 (Anon., 2017), the results indicated that there were high probabilities that the North Atlantic stock was overfished and experiencing overfishing (Anon, 2017). In terms of the CPUE indexes used on that assessment, most fleets showed increases in stock abundance between 2000 and 2009, followed by reductions since then. These results have been recently updated by ICCAT (Anon., 2019), which again highlighted the poor stock condition of the North Atlantic stock. This is contrary to the results obtained in our study, where the series between 2006 and 2015 was mostly stable or showing an increasing trend. The reasons for the differences obtained might be related with the location of the fisheries, as the series used for the stock assessment were coming from other fleets operating mostly in different regions of the North Atlantic. As such, it is possible to hypothesize that even though the shortfin mako biomass in the North Atlantic has experienced overall reductions due to overfishing, the fraction of the population in the tropical NE Atlantic still seems to be relatively stable in terms of biomass. This could be either because it is still in better condition and/or because the region is a core area for the species in the Atlantic, where specimens tend to aggregate and therefore signals in population declines might take longer time to be detected.

4.2. Satellite tagging

During this study, tagged blue shark and shortfin mako showed considerable movement in the region. Specifically the tagged blue sharks (tagged inside the Cabo Verde EEZ) showed very variable movements in all directions, with sharks moving both inside and outside the EEZ. It was noteworthy that for blue sharks, the females and adults tended to move further away from the islands, while on the contrary the males and juvenile blue sharks tended to aggregate more around the Cabo Verde islands.

As regards shortfin mako, a clearer pattern of movements was observed, with the sharks tagged in the Cabo Verde EEZ tending to move mostly towards the West African continental shelf. This corroborated the observations from the catches and the prediction models using data from the commercial fisheries, where higher catch rates were also predicted for the eastern parts of the study area. For shortfin mako, therefore, it seems that areas closer to the African continental shelf, outside the Cabo Verde EEZ but in the EEZ of other African continental countries, are of particular importance.

Other pelagic shark species are also present in the region. While those other species, such as oceanic whitetip, silky shark, bigeye thresher, hammerheads and crocodile shark are not as common in the region, they are also accidentally by-caught in pelagic longline fisheries, though most of these species are now discarded due to ICCAT prohibition of retention and CITES regulations. Some previous studies have focused on satellite tagging and habitat use for the less common species, such as Coelho et al. (2015b) for the bigeye thresher and Santos and Coelho (2018) for the smooth hammerhead. Still, the knowledge on those more rare species is substantially lower than for the main shark species and therefore more effort should be put into continued tagging for those species in the future.

4.3. Spatial models and predictions

Higher catch rates (in weight) were predicted outside the Cabo Verde EEZ for both blue and shortfin mako. For shortfin mako, in particular, considerably higher CPUEs are predicted along the African continental shelf, in areas outside the Cabo Verde EEZ but inside the EEZ of other

West African countries. As noted in section 4.2 above, this was corroborated with the satellite tagging data that also showed that those areas along the West African shelf are of particular importance for this species. These results show that even though the shortfin mako is an oceanic and pelagic species, it seems to have a strong relation with continental shelf areas, especially the juveniles. A recent study using satellite telemetry to map the movements of shortfin mako shark in the West Atlantic (US and Mexico) concluded that shortfin mako displayed very region-specific movements, with little distributional overlap between the Gulf of Mexico/Caribbean Sea and the western North Atlantic (Vaudo et al., 2017). In the eastern Atlantic, our study now seems to have reached similar conclusions and a comparable situation might be occurring off West Africa, with shortfin makos showing the same type of region-specific movements mainly along the West African continental shelf area.

There was considerable variability in the expected mean size for both species taking into account spatial and seasonal effects. One important note, however, is that even though those spatial and seasonal effects are important, in general the overall size of blue sharks was expected to be composed mainly of relatively large adult individuals; whereas the overall size of shortfin makos was expected to be mainly composed of relatively small juveniles. This was consistent over the entire region and throughout the year. Both the spatial and seasonal effects were influential in the expected mean size, in the case of the blue shark with the smaller specimens occurring in the area mainly during spring months (quarter 2), while) and in the case of shortfin makos the smaller specimens are expected to occur mainly in the 1st semester during the winter and spring months.

When comparing those results within an Atlantic wide perspective, it is important to note that, although there is some information available for blue shark, there is little information available on the shortfin mako and for other pelagic shark species. Blue shark shows a strong size latitudinal stratification pattern in all oceans, with a tendency for the larger adult specimens to occur in warmer equatorial and tropical regions and the smaller juveniles occurring in colder temperate waters (Coelho et al., 2018). However, for some other species the opposite pattern has been found, as for example for the bigeye thresher in the Atlantic, where smaller and younger sharks tend to concentrate predominantly in the tropical regions, while the larger specimens seem to prefer temperate areas of the northern and southern Atlantic (Fernandez-Carvalho et al., 2015b).

5. Conclusions and recommendations

As a final conclusion, the Cabo Verde region appears to be part of the Atlantic wide distributional cycle where those shark species move through their life cycles. The blue shark shows widespread and large scale movements in and out of the Cabo Verde EEZ as well as into wider regions. The presence of the large adults in the Cabo Verde region corroborates the previously hypothesized distributional patterns in the North Atlantic, with the large adult specimens occurring mainly in warmer tropical waters (Coelho et al., 2018). In the case of the shortfin mako, although the entire region appears to be an aggregation area for juveniles, the region closer to the African continental shelf seems to be of particular importance to this species, with large aggregations of small juvenile specimens.

The following are the main conclusions and recommendations from this study:

- Blue shark and shortfin mako are the main shark species captured in the pelagic longlines, both in Cabo Verde archipelago EEZ as well as in other regions; this is the same case of most oceanic-wide waters fished by pelagic longline gears;
- For both species the estimated indices of abundance for the Cabo Verde region showed overall increases over the time series period (2006-2015);
- Blue sharks captured in the region are mainly large adults and there were no major trends in mean sizes over time. By contrast, the shortfin makos caught in the region are relatively small juveniles, and there were some indications of possible declines in the mean sizes over time;
- Considering the abundance indexes, local depletion effects do not seem to be occurring for those two shark species in the region as there are no signs of decreasing local abundance (biomass). However, for the shortfin mako there are signs of a decreasing trend in the mean sizes that can indicate overfishing on this species;
- The satellite tagged sharks showed high mobility of the specimens with movements both inside and outside the Cabo Verde EEZ. In some cases, the sharks moved considerable distances over the tagged periods, especially in the case of blue shark;
- The shortfin mako sharks seem to have marked region-specific movements and habitat use, mainly along the West African continental shelf. This type of region-specific movements has also been recently hypothesized for this species in the West Atlantic;
- The presence of the large adult blue shark in the Cabo Verde region corroborates the hypothesis of the distributional patterns of this species in the North Atlantic, with large adult specimens occurring mainly in warmer tropical waters and juveniles in colder temperate and more coastal waters;

- For the shortfin mako the areas closer to the African continental shelf seem to be of particularly importance, with large aggregations of small juvenile specimens. Such areas should be of priority focus for the species conservation.

6. Acknowledgements

This study was part of Project EU/MARE/2012/21: "*Scientific advice for fisheries beyond EU waters*", specifically within Specific Contract Nº 7: "*The provision of advice on the conservation of pelagic sharks associated to fishing activity under EU Sustainable Fisheries Partnership Agreements in the Atlantic Ocean*". The information reported in this paper are those of the authors and do not necessarily reflect the official opinion of EASME or the EU Commission. Neither EASME nor the EU Commission can guarantee the accuracy of the data included in this study. Neither EASME nor the EU Commission or any person acting on their behalf may be held responsible for the use which may be made of the information contained therein.

The authors are grateful to all fishery observers and longline vessel skippers and crews that have contributed with data, including data voluntarily provided as self-sampling as well as data regularly collected with logbooks and by onboard fishery observers (collected within EU/DCF: *Data Collection Framework*). R. Coelho is supported by an Investigador-FCT contract (Ref: IF/00253/2014) from FCT, the Portuguese Foundation for Science and Technology. D. Rosa and C.C. Santos are supported by PhD grants from FCT (Refs: SFRH/BD/136074/2018 and SFRH/BD/139187/2018, respectively). This paper is contribution number 948 from AZTI Tecnalia (Marine Research Division).

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