

MODELLING THE OCEANIC HABITATS OF SILKY SHARK (*CARCHARHINUS FALCIFORMIS*), IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

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Abstract

Investigating the relationship between abundance and environmental conditions is of primary importance for the correct management of marine species, especially highly migratory large pelagic species like silky sharks (*Carcharhinus falciformis*), a species that is currently ranked by the IUCN as near threatened or vulnerable, depending on the region. Tropical tuna purse seine vessels annually catch millions of tons of tuna worldwide. However, fishing may have implications on certain sensitive by-catch species, along with other potential impacts on the ecosystem. This work aims to provide the first insights into the environmental preferences of silky sharks by modelling their abundance from observer data with a set of biotic and abiotic oceanographic factors, spatial-temporal terms and fishing operation variables. This work considers Spanish observer data (IEO and AZTI database) from 2003 to 2015, and comprising ~7500 fishing sets for the Atlantic Ocean. Oceanographic data (SST, SST gradient, salinity, SSH, CHL, CHL gradient, oxygen, and current information such as speed, direction and kinetic energy) were downloaded and processed for the study period and area from the MyOcean-Copernicus EU consortium. Results provide information on the dynamics and hotspots of silky shark abundances as well as the most significant habitat preferences of the species. Models detected a significant relationship between seasonal upwelling events, mesoscale features and shark abundance and suggested strong interaction between productive systems and the spatial-temporal dynamics of sharks. The model also highlighted certain persistent areas of shark occurrence. This information could be used to assist t-RFMOs in the conservation and management of this vulnerable non-target species.

Keywords: Environmental preferences, *Carcharhinus falciformis*, Silky Shark, EBFM, By-catch

INTRODUCTION

According to the International Union for Conservation of Nature (IUCN), the silky shark (*Carcharhinus falciformis*) is near threatened or vulnerable, depending on the ocean. Whereas the silky shark population in the Indian and Western and Central Pacific Oceans seem to be near threatened, this species population appear to be vulnerable in the Atlantic and Eastern Pacific Oceans. Many fishing gears catch silky sharks, either as target or non-target species. In the case of the purse seine fishery targeting tropical tuna (Skipjack *Katsuwonus pelamis*, yellowfin *Thunnus albacares* and bigeye *Thunnus obesus*), this species is the most common shark species in the bycatch (Amandè et al. 2010). The catch rate appears particularly significant when fishing on fish aggregating devices (FADs) (Dagorn et al. 2012), which showed a high increase in the effort in the last decades (Fonteneau et al. 2013). Besides, the ghost fishing events produced by entangling drifting FADs may be of an important magnitude (Filmalter et al. 2013).

Because of the status of this species may be in decline, the principal tuna Regional Fisheries Management Organizations (t-RFMOs) have already launched pelagic shark investigation programs and some conservation and management measures (CMM) have been already adopted (e.g. Resolution 13/06 of IOTC, Recommendation 11-08 of ICCAT). In addition to this, other mitigation measures have been considered recently by scientist and industry, particularly those related to measures that can be applied before and after the set was conducted. For example, since 2013 EU fleets are almost exclusively implementing the use of non-entangling FADs (Franco et al. 2012; Goujon et al. 2012; Lopez et al. 2017) and new best releasing practices have been adopted in agreement with fishers (Goñi et al. 2015). Also recently, studies on the post-release mortality of silky sharks have been conducted, which provide very interesting and complementary information on the potential impact of certain fisheries on this species (Poisson et al. 2014). Other studies have investigated fine-scale movement behavior (Filmalter et al. 2015) and feeding ecology (Filmalter et al. 2016) of the species to improve the knowledge on their biological traits.

However, little is known on the silky shark habitat preferences (Amandè et al. 2008). Identifying the habitats of migratory marine species is key for both single species and ecosystem-based fisheries management, particularly when the distribution of these habitats vary temporally (Brodie et al. 2015). In that sense, species distribution models that include spatial-temporal, physical and biological environmental predictors can be used to achieve this goal. Identifying relationships between certain specific environmental conditions, locations, seasons and silky shark occurrences may lead to develop potential mitigation measures, such as silky shark seasonal prediction maps, and assist t-RFMOs in a better management and conservation of the species.

MATERIAL AND METHODS

Fisheries data

Spanish tropical tuna purse seine observer data for both AZTI and IEO research organizations were obtained from a consolidated fisheries observer program facilitated by the European program of data acquisition 'Data Collection Regulation' (DCR). These data consist of set-recorded locations of target and non-target fish captures. The data were spatially confined to the Eastern and Central Tropical Atlantic Ocean (20°S–23°N and 45°W–12°E; Fig. 1) and temporally limited from 2003 to 2015 to match the availability of the best quality observer data.

Information about fishing sets was collected by observers aboard 33 Spanish tropical tuna purse-seiners during 336 fishing trips. A total of 7296 fishing sets were observed, corresponding to 5253 fishing days. Observers collect data on the incidental mortality of non-target species and details of fishing operations. For each fishing set, the observer records the quantity in weight or number and average estimate of the bycatch in weight or length for each species. Additionally, these observers collect data on the local environment (i.e., sea surface temperature, SST), the rough amounts and species of tuna caught, and fishing-related activity. The number of silky sharks caught per set during the fishing trips was not always available because observers sometimes only recorded a total and/or an average weight of sharks caught. In such cases, data were converted into numbers using

published Length-Weight relationship $W = 2.10^3 * L^{3.23}$ (Froese and Pauly 2008). The term bycatch will be used herein in place of 'catch' to refer to the incidental mortalities of any non-target species.

For the 7296 fishing sets observed aboard Spanish purse seiners from 2003 to 2015, a total of 12705 silky sharks were recorded as bycatch. The silky sharks appeared in ~30% of the total sets (Fig. 2). The average numbers of silky shark per set were 1.74 and 6.38, for total sets and positive sets, respectively. The length frequency of the silky sharks ranged from 30 to 250 cm, but was dominated by the 90-130 cm individuals (Fig. 3) corresponding to immature individuals (Bonfil 2009). A very negligible part of the measured silky sharks (<0.5%) were above 240 cm (Fig. 3), which is the total length for first maturation in the Eastern Atlantic Ocean (Bonfil 2009). Thus, the model developed in this study should be considered almost exclusively for juveniles and pre-adults of silky sharks.

Environmental data

Physical and biological environmental covariates were collated for each fishing set location, sourced and extracted using python routines and motu-client from the MyOcean-Copernicus EU consortium (<http://marine.copernicus.eu/>) and are: (i) daily sea surface temperature (SST; °C; 1/4° spatial resolution); (ii) the SST gradient derived from daily SST analysis as the increase/decrease of temperature in each pixel over an 7-day period (SST grad; °C; 1/4° spatial resolution); (iii) daily sea level anomaly (SSH; m; 1/4° spatial resolution); (iv) daily eddy kinetic energy derived from altimetry (EKE; $m^2 s^{-2}$; 1/4° spatial resolution); (v) daily salinity (Sal; g/kg; 1/4° spatial resolution); (vi) daily u and v vectors of current (UV; m/s; 1/4° spatial resolution); (vii) daily heading and speed of current derived from UV (Head, Speed; °, m/s; 1/4° spatial resolution); (viii) monthly chlorophyll concentration (CHL; $mg m^{-3}$; 1/4° spatial resolution); (ix) the CHL gradient derived from monthly CHL analysis as the increase/decrease of CHL amount in each pixel over an 31-day period (CHL grad; $mg m^{-3}$; 1/4° spatial resolution); and (x) monthly oxygen concentration (O_2 ; mg/l; 1/4° spatial resolution). To account for potential community effect (i.e. silky sharks may show traits of social behavior when are juveniles), total by-catch of each fishing set, excluding sharks (in tons), were included in the analysis.

Some spatial-temporal variables were also considered as potential variables for the model, such as latitude, longitude, year, month, time of the day when the set was conducted, natural day (calendar day:1 to 366), quarter, etc. Although most of these variables are not directly related to environment, they may help identifying hidden mechanisms or processes occurring at different time and spatial scales in our study area.

Regime shifts identification

A first exploratory analysis of the spatial-temporal distribution of silky sharks showed that species occurrences appear to be variable in time and space (Fig. 4). Because natural quarters do not necessarily represent the more ecologically meaningful scenarios, we develop a new method based on statistical significance of changes of the most common oceanography variables. First, oceanographic variables were averaged for each day of the year using data from the study period (i.e. 2003-2015). Second, potential points of statistical changes were identified for each oceanographic variable, using the changepoint package (Killick and Eckley 2014). In a third step, obtained change point candidates were confirmed or rejected as change points using the package CausalImpact (Brodersen et al. 2015), a library using Bayesian procedures to investigate whether the origin of statistical changes is due to random effects or not.

The statistical tests performed in the current study identified three environmentally different seasons throughout the year, separated by the calendar days 155, 240, 290 (Fig. 5). The year dynamic is primarily dominated by a not very productive warm and stable season, going from late September (i.e. day 290) to early May (i.e. day 155) (stable season). From early May to the end of August (i.e. day 240), however, the environmental conditions and mechanisms appear to change and the system suffers a significant change. During this period, the productivity of the system increases, while decreasing the SST and increasing the amount of dissolved oxygen in the water (cooling season). A third period starting in the end of August (i.e. day 240) and

going until late September (i.e. day 290) completes the annual cycle and provides the system the opportunity to return to the predominant environmental situation, warming the sea surface and reducing the exceptional summer productivity (warming season). Thus, three seasons were identified by the analysis: stable, cooling and warming seasons. The identified oceanographic regimes will provide the best spatial-temporal windows to be used in the prediction part of the study.

Statistical model

As a preliminary exploration of the available covariates we used a recursive partitioning product, called Random Forest, available in the package PARTY (Hothorn et al. 2015) in the statistical language R (Team 2013). The aim was to explore the relative effect of covariates on the dependent variable (Dell et al. 2011). Predictor covariates were examined for correlation using pair plots and Pearson's rank correlations (Fig. 6). To avoid correlation, one covariate from covariate pairs with a correlation > 0.7 and < -0.7 was removed from the variable selection process (Dormann et al. 2013; Hassrick et al. 2016). As an additional measure to avoid collinearity, a variance inflation factor analysis (VIF), from the package usdm (Naimi 2015), was conducted using a cut-off value of 3 (Zuur et al. 2009). Based on obtained results, Quarter, Month, O_2 and speed were removed owing to correlation/collinearity with more ecologically important variables. All other covariates available for model selection had low cross-correlation and cross-collinearity scores.

In order to find the best distribution family to be used in the explanatory model, we carried out two statistical tests. An over dispersion test for our shark count data showed that over dispersion existed, and thus, the use of Negative Binomial distribution is recommended over a Poisson distribution (Wood 2006). Similarly, a zero-inflation test was conducted using function `vuong` of the package `pscl` (Jackman 2008), which showed that no excess of zeros was expected. These results confirmed that simple negative binomial distribution should be used in this particular study.

As an additional exploratory measure, univariate GAMs (Generalized Additive Models; Hastie and Tibshirani (1986)) were established for each covariate considered in the study. These informative models will provide knowledge on both the potential relationship of the response variable with each covariate and their raw likely contribution to the deviance explained.

Model covariates were selected using backward stepwise procedure (Wood 2006). To avoid over-fitting and to simplify the interpretation of the results, the maximum degrees of freedom (measured as number of knots k) allowed to the smoothing functions were limited to the main effects at $k = 6$ and, for the first-order interaction effects, at $k = 20$ (Giannoulaki et al. 2013; Jones et al. 2014). The model with the lowest Akaike information criterion (AIC, Akaike (1974)) was chosen as the final model. Calendar year (Year) was included in the model as a random effect spline smoother to account for inter-annual variability in shark abundance and fishing effort (Wood 2006; Brodie et al. 2015).

The final notation for the GAM model was:

$$\text{Abundance} \sim s(\text{Longitude, Latitude, } k=20) + s(\text{YearDay, } k=6) + s(\text{TotalBC, } k=6) + s(\text{SSH, } k=6) + \text{te}(\text{SST, SST grad, } k=20) + \text{te}(\text{CHL, CHL grad, } k=20) + \text{Year}_{\text{random}}$$

Where Abundance is the count of silky sharks in each fishing set, s represents a penalized regression spline type smoother based on generalized cross-validation (GCV), and te represents a tensor product smooth, a more satisfactory approach when both arguments of the same smooth are measured in fundamentally different units (Wood 2006).

The term $s(\text{Latitude, Longitude})$ measures the nonparametric spatial component of the shark abundance (Cortés-Avizanda et al. 2011). Although a preliminary analysis with a non-parametric spline correlogram (Bjørnstad and Falck 2001) suggested that the count data for silky sharks lack spatial autocorrelation, we included the spatial term in the model to check whether some spatial residual variation can be detected after estimating the covariate effects (Cortés-Avizanda et al. 2011).

All the models and analysis were conducted in the statistical language R (Team 2013).

Model validation and prediction

A jackknife procedure with 100 iterations was conducted to assess the consistency and robustness of the final model. In each repetition, 20% of the data was randomly left out and the model was fitted with the remaining 80%. Both AIC and deviance explained of the models were highly stable and converged fairly (quartiles of 25, 50, 75 for AIC 12832, 12901, 12989; and Dev. Expl: 31.9, 32.7, 33.3), suggesting that the model is independent to the data used and that performs reasonably well.

Averaged values of the environmental parameters included in the model per each calendar day were used to develop 366 predictions based on the final model (one per day). Density of sharks were averaged per each environmental regime identified previously (stable, cooling and warming seasons). Similarly, the standard deviation was also calculated for each regime.

RESULTS

Some environmental covariates were retained in the final model (Table 1), which suggested complex relationships between certain oceanographic conditions and silky shark abundance. The model achieved a 32% of deviance explained, which is a reasonably good score. Smoothing factors were retained in the final model for Latitude and Longitude interaction, Calendar day, total bycatch, SSH, SST and SST gradient interaction, and CHL and CHL gradient interaction. The model highlighted two main areas with higher shark abundance, the first located off Gabon and the second off Guinea. In addition to those potential hotspots areas for silky sharks, the model also identified the southern part of the central Atlantic Ocean as an area with higher abundance of silky sharks (Fig. 7). Calendar day had a strong influence on silky shark intensity, with the abundance peaking after ~250 days (Fig. 7). A positive pattern between shark abundance and the total bycatch occurred as well, with silky sharks showing a positive trend in abundance with increasing total bycatch (Fig. 7). The optimum SSH for silky shark abundance ranged between 0 and -0.1 m SSH (Fig. 7). Silky shark abundance peaked at relatively fast cooling waters of ~24-26 °C (waters that has decreased their temperature in about 3 °C in a week; Fig. 7). The CHL and CHL gradient interaction was strongly correlated with silky shark abundance, with an overall increase in shark abundance with waters significantly increasing their CHL concentration.

The predictions established by the model for the three different environmental regimes (stable, cooling, warming seasons) showed temporal variability in the shark intensity but also persistency in the spatial component (Fig. 8). The areas off Gabon and off Guinea were always locations of high shark abundance, being greater during warming and stable seasons than in the cooling period. It is interesting to note that the area of the southern part of the central Atlantic Ocean also predicted high intensity of shark abundance. However, this area also showed higher standard deviation values than other areas of the study (Fig. 8), suggesting that results may be a bit less confident in there, particularly off Brazil, where no observations were obtained from observer data.

DISCUSSION

The present work found relationship between silky sharks abundance and high productivity, which is in agreement with previous works that relate productivity features with large pelagic predators (Bakun 1996; McGlade et al. 2002; Humphries et al. 2010; Tew Kai and Marsac 2010; Marsac et al. 2014; Mugo et al. 2014; Potier et al. 2014; Young et al. 2014). Results showed that silky sharks may be strongly associated to areas of high productivity, likely produced by mesoscale features like eddies or seasonal or permanent upwelling events or domes. In fact, negative SSH anomalies are usually related to divergence areas and productive processes (Lopez-Calderon et al. 2006; Kahru et al. 2007; Tew Kai and Marsac 2010), and the interaction between SST and SST gradient, as well as the interaction between CHL and CHL gradient, showed that silky sharks are likely related to short term oceanographic mechanisms where water is cooling and gaining chlorophyll. Up to date, very few studies have tried to relate environmental conditions and silky shark abundance. Recently, a Maxent model has

been developed to better understand the potential impact of climate change on silky shark future distribution (Lezama Ochoa et al. 2016). Likewise, Lezama-Ochoa et al. (2015) analyzed the relationship between bycatch biodiversity of tropical tuna purse seine fishery in the Western Indian Ocean and certain environmental variables. The study found potential relationship between productive areas and higher biodiversity of the bycatch. The results of the current study may be in accordance with this idea as well. However, there is no specific mention to silky sharks in the work published by Lezama-Ochoa et al. (2015), as the study used different biodiversity index from the pelagic ecosystem as a whole for the analysis. Complementary species-specific analysis and distribution models should be conducted for the most representative and sensitive species and compared to previous results in the field, to gather and integrate information in a more holistic view towards an ecosystem-based fishery management (Pikitch et al. 2004).

Studies investigating the relationship between fronts and species distribution have been very helpful for the correct management and understanding of some large predators (Bigelow et al. 1999; Andrade 2003; Chassot et al. 2011; Belkin et al. 2014; Hobday and Hartog 2014; Mugo et al. 2014; Sagarminaga and Arrizabalaga 2014; Tseng et al. 2014; Nieto et al. 2015; Xu et al. 2015). In this work, we found relationship between silky sharks and certain oceanographic features of high productivity (likely translated in eddies, mesoscale features or seasonal upwelling events), as well as with some specific areas, but not particularly with fronts. Future analysis should include temperature and chlorophyll fronts in the models (intensity of the fronts, distance to the nearest front, etc.) and investigate this potential relationship in detail, as silky shark may be associated with fronts or areas with high front occurrences. Using specific algorithms developed to detect fronts, as the one developed by Cayula and Cornillon (1992), may provide interesting information that could complement current results for a better management of the species.

The model highlighted the vital importance of the areas off Gabon and off Guinea, as well as the southern part of the central Atlantic Ocean, for silky sharks. These hotspots, persistent at different scales throughout the year, seem to be key for juveniles of silky sharks. Other studies should conduct similar investigations for further life stages using data from observers or alternative fishery or non-fishery data sources. Results would be interesting to complement current results and obtain holistic models for the whole ontogeny of the species and would assist in the development of life stage-specific measures, if needed.

Although different methodologies and models such as the Bayesian-based zero-inflated Poisson (Amandè et al. 2008) and the zero-inflated negative binomial (Minami et al. 2007) have been used so far to model silky shark bycatch, the statistical tests performed in the current study showed that the best distribution model to be used with our particular dataset was the simple negative binomial. Moreover, these studies were not focused specifically on investigating the relationship between silky shark abundance and environmental conditions. Instead, they were primarily oriented to better understand the bycatch rate of this species in the tropical tuna purse seine fishery of the Western Indian Ocean (Amandè et al. 2008) and the Eastern Pacific Ocean (Minami et al. 2007). Investigating reasons potentially explaining bycatch rate of silky sharks in relation to fishing activity factors in the Atlantic Ocean may help producing offsets for future models, as well as provide complementary information to be used in the development of effective conservation and management measures. Indeed, combining both environmental studies and models explaining the bycatch rate in relation to fishing activity (i.e. time of the day when the set was conducted, size of the net, etc.) would be of primary importance to develop science-based CMMs and may efficiently contribute to mitigate the impact of the fishery on the species.

Because model has been validated, results appear to be consistent and promising and the methodology developed to identify regime shifts provides valuable progress in the field. Using the averaged values of the oceanographic parameters for the new regimes, this study provides the first prediction maps for each of the potential environmental scenario occurring all over the year, instead of providing maps for ecologically not-meaningful quarters. Similarly, and following the methodology and the idea suggested by Hobday et al. (2011), results of this study may also be used to produce monthly forecasting maps of potential future silky shark hotspots, which could be developed almost in real time to provide information in advance to assist management organizations and fishing industry on the best areas to avoid, if necessary.

Additionally, similar habitat models should be carried out for other target and non-target species, which would provide with very interesting and key information on the spatial-temporal distribution of important species. Combining models' information may provide maps of potential overlap of target and non-target species and may help developing predictions with potential ratios of target/non-target species.

Initiatives like the present work are highly necessary and may significantly help reducing the mortality of a species, improving selectivity by avoiding interaction between fishing gears and species. The outcomes of the present work should be discussed with t-RFMOs, managers and fishers during local and international workshops to better understand the applicability of the results and identify potential responses of the fleet and their dynamics in relation to it. These kinds of initiatives are very temporary and may significantly improve and complement ongoing initiatives like best releasing practices (Goñi et al. 2015) or the deployment of non-entangling FADs (Franco et al. 2012) that aims to reduce the mortality of this shark species.

Acknowledgments

The authors sincerely thank Dr. Maite Louzao and Igor Arregi for their useful comments, suggestion and assistance while developing the study.

References

- Akaike H (1974) A new look at the statistical model identification. *Automatic Control, IEEE Transactions on* 19: 716-723 doi 10.1109/tac.1974.1100705
- Amandè M, Chassot E, Chavance P, Pianet R (2008) Silky shark (*Carcharhinus falciformis*) bycatch in the French tuna purse-seine fishery of the Indian Ocean. *IOTC Proceedings IOTC-2008-WPEB-16*: 22p
- Amandè MJ, Ariz J, Chassot E, de Molina AD, Gaertner D, Murua H, Pianet R, Ruiz J, Chavance P (2010) Bycatch of the European purse seine tuna fishery in the Atlantic Ocean for the 2003–2007 period. *Aquatic Living Resources* 23: 353-362
- Andrade HA (2003) The relationship between the skipjack tuna (*Katsuwonus pelamis*) fishery and seasonal temperature variability in the south-western Atlantic. *Fisheries Oceanography* 12: 10-18 doi 10.1046/j.1365-2419.2003.00220.x
- Bakun A (1996) *Patterns in the ocean: ocean processes and marine population dynamics*. California Sea Grant College System/NOAA/Centro de Investigaciones Biologicas del Noroeste, La Paz, Mexico. 323 pp., ISBN 1-888691-01-8.
- Belkin IM, Hunt Jr GL, Hazen EL, Zamon JE, Schick RS, Prieto R, Brodziak J, Teo SLH, Thorne L, Bailey H, Itoh S, Munk P, Musyl MK, Willis JK, Zhang W (2014) Fronts, fish, and predators. *Deep Sea Research Part II: Topical Studies in Oceanography* 107: 1-2 doi <http://dx.doi.org/10.1016/j.dsr2.2014.07.009>
- Bigelow KA, Boggs CH, He XI (1999) Environmental effects on swordfish and blue shark catch rates in the US North Pacific longline fishery. *Fisheries Oceanography* 8: 178-198 doi 10.1046/j.1365-2419.1999.00105.x
- Bjørnstad ON, Falck W (2001) Nonparametric spatial covariance functions: Estimation and testing. *Environmental and Ecological Statistics* 8: 53-70 doi 10.1023/a:1009601932481
- Bonfil R (2009) *The Biology and Ecology of the Silky Shark, Carcharhinus Falciformis Sharks of the Open Ocean*. Blackwell Publishing Ltd., pp 114-127
- Brodersen KH, Gallusser F, Koehler J, Remy N, Scott SL (2015) Inferring causal impact using Bayesian structural time-series models. *The Annals of Applied Statistics* 9: 247-274
- Brodie S, Hobday AJ, Smith JA, Everett JD, Taylor MD, Gray CA, Suthers IM (2015) Modelling the oceanic habitats of two pelagic species using recreational fisheries data. *Fisheries Oceanography* 24: 463-477 doi 10.1111/fog.12122

- Cayula J-F, Cornillon P (1992) Edge Detection Algorithm for SST Images. *Journal of Atmospheric and Oceanic Technology* 9: 67-80 doi 10.1175/1520-0426(1992)009<0067:edafsi>2.0.co;2
- Cortés-Avizanda A, Almaraz P, Carrete M, Sánchez-Zapata JA, Delgado A, Hiraldo F, Donázar JA (2011) Spatial Heterogeneity in Resource Distribution Promotes Facultative Sociality in Two Trans-Saharan Migratory Birds. *PLoS ONE* 6: e21016 doi 10.1371/journal.pone.0021016
- Chassot E, Bonhommeau S, Reygondeau G, Nieto K, Polovina JJ, Huret M, Dulvy NK, Demarcq H (2011) Satellite remote sensing for an ecosystem approach to fisheries management. *ICES Journal of Marine Science: Journal du Conseil* 68: 651-666 doi 10.1093/icesjms/fsq195
- Dagorn L, Holland KN, Restrepo V, Moreno G (2012) Is it good or bad to fish with FADs? What are the real impacts of the use of drifting FADs on pelagic marine ecosystems? *Fish and Fisheries*: n/a-n/a doi 10.1111/j.1467-2979.2012.00478.x
- Dell J, Wilcox C, Hobday AJ (2011) Estimation of yellowfin tuna (*Thunnus albacares*) habitat in waters adjacent to Australia's East Coast: making the most of commercial catch data. *Fisheries Oceanography* 20: 383-396 doi 10.1111/j.1365-2419.2011.00591.x
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36: 27-46 doi 10.1111/j.1600-0587.2012.07348.x
- Filmlalter JD, Capello M, Deneubourg J-L, Cowley PD, Dagorn L (2013) Looking behind the curtain: quantifying massive shark mortality in fish aggregating devices. *Frontiers in Ecology and the Environment* 11: 291-296 doi 10.1890/130045
- Filmlalter JD, Cowley PD, Forget F, Dagorn L (2015) Fine-scale 3-dimensional movement behaviour of silky sharks *Carcharhinus falciformis* associated with fish aggregating devices (FADs). *Marine Ecology Progress Series* 539: 207-223 doi 10.3354/meps11514
- Filmlalter JD, Cowley PD, Potier M, Ménard F, Smale MJ, Cherel Y, Dagorn L (2016) Feeding ecology of silky sharks *Carcharhinus falciformis* associated with floating objects in the western Indian Ocean. *Journal of Fish Biology*: n/a-n/a doi 10.1111/jfb.13241
- Fonteneau A, Chassot E, Bodin N (2013) Global spatio-temporal patterns in tropical tuna purse seine fisheries on drifting fish aggregating devices (DFADs): Taking a historical perspective to inform current challenges. *Aquatic Living Resources* 26: 37-48 doi doi:10.1051/alr/2013046
- Franco J, Moreno G, Lopez J, Sancristobal I (2012) TESTING NEW DESIGNS OF DRIFTING FISH AGGREGATING DEVICE (DFAD) IN THE EASTERN ATLANTIC TO REDUCE TURTLE AND SHARK MORTALITY. *Collect Vol Sci Pap ICCAT* 68: 1754-1762
- Froese R, Pauly D (2008) Fishbase 2008. Available from <http://www.fishbase.org>
- Giannoulaki M, Iglesias M, Tugores MP, Bonanno A, Patti B, De Felice A, Leonori I, Bigot JL, Tičina V, Pyrounaki MM, Tsagarakis K, Machias A, Somarakis S, Schismenou E, Quinci E, Basilone G, Cuttitta A, Campanella F, Miquel J, Oñate D, Roos D, Valavanis V (2013) Characterizing the potential habitat of European anchovy *Engraulis encrasicolus* in the Mediterranean Sea, at different life stages. *Fisheries Oceanography* 22: 69-89 doi 10.1111/fog.12005
- Goñi N, Ruiz J, Murua H, Santiago J, Krug I, Sotillo de Olano B, Gonzalez de Zarate A, Moreno G, Murua J (2015) System of verification of the code of good practices on board ANABAC and OPAGAC tuna purse seiners and preliminary results for the Atlantic Ocean. *IOTC–2015–WPEB11–INF09*
- Goujon M, Vernet AL, Dagorn L (2012) Preliminary results of the Orthongel program “eco-FAD” as June 30th 2012 *IOTC–2012–WPEB08–INF21*

- Hassrick JL, Henderson MJ, Huff DD, Sydeman WJ, Sabal MC, Harding JA, Ammann AJ, Crandall ED, Bjorkstedt EP, Garza JC, Hayes SA (2016) Early ocean distribution of juvenile Chinook salmon in an upwelling ecosystem. *Fisheries Oceanography* 25: 133-146 doi 10.1111/fog.12141
- Hastie T, Tibshirani R (1986) Generalized additive models. *Statistical science*: 297-310
- Hobday AJ, Hartog JR (2014) Derived Ocean Features for Dynamic Ocean Management. *Oceanography* 27: 134–145 doi <http://dx.doi.org/10.5670/oceanog.2014.92>
- Hobday AJ, Hartog JR, Spillman CM, Alves O (2011) Seasonal forecasting of tuna habitat for dynamic spatial management. *Canadian Journal of Fisheries and Aquatic Sciences* 68: 898-911 doi 10.1139/f2011-031
- Hothorn T, Hornik K, Strobl C, Zeileis A (2015) Party: a laboratory for recursive partitioning. . R package version 10-23
- Humphries NE, Queiroz N, Dyer JRM, Pade NG, Musyl MK, Schaefer KM, Fuller DW, Brunnschweiler JM, Doyle TK, Houghton JDR, Hays GC, Jones CS, Noble LR, Wearmouth VJ, Southall EJ, Sims DW (2010) Environmental context explains Lévy and Brownian movement patterns of marine predators. *Nature* 465: 1066-1069 doi http://www.nature.com/nature/journal/v465/n7301/supinfo/nature09116_S1.html
- Jackman S (2008) pscl: classes and methods for R developed in the political science computational laboratory. Stanford University. Department of Political Science, Stanford University, Stanford, California. R package version 0.95, URL <http://CRAN.R-project.org/package=pscl>
- Jones AR, Hosegood P, Wynn RB, De Boer MN, Butler-Cowdry S, Embling CB (2014) Fine-scale hydrodynamics influence the spatio-temporal distribution of harbour porpoises at a coastal hotspot. *Progress in Oceanography* 128: 30-48 doi <http://dx.doi.org/10.1016/j.pocean.2014.08.002>
- Kahru M, Fiedler PC, Gille ST, Manzano M, Mitchell BG (2007) Sea level anomalies control phytoplankton biomass in the Costa Rica Dome area. *Geophysical Research Letters* 34: L22601 doi 10.1029/2007gl031631
- Killick R, Eckley IA (2014) changepoint: An R Package for Changepoint Analysis. *Journal of Statistical Software* 58: 19 doi 10.18637/jss.v058.i03
- Lezama-Ochoa N, Murua H, Chust G, Ruiz J, Chavance P, Molina AD, Caballero A, Sancristobal I (2015) Biodiversity in the by-catch communities of the pelagic ecosystem in the Western Indian Ocean. *Biodivers Conserv* 24: 2647-2671 doi 10.1007/s10531-015-0951-3
- Lezama Ochoa N, Murua H, Chust G, Van Loon E, Ruiz J, Hall M, Chavance P, Delgado de Molina A, Villarino E (2016) Present and future potential habitat distribution of *Carcharhinus falciformis* and *Canthidermis maculata* by-catch species in the tropical tuna purse-seine fishery under climate change. *Frontiers in Marine Science* 3 doi 10.3389/fmars.2016.00034
- Lopez-Calderon J, Manzo-Monroy H, Santamaria-del-Angel E, Castro R, Gonzalez-Silvera A, Millan-Nunez R (2006) Mesoscale variability of the Mexican Tropical Pacific using TOPEX and SeaWiFS data. *Ciencias marinas* 32
- Lopez J, Goñi N, Arregi I, Ruiz J, Krug I, Murua H, Murua J, Santiago J (2017) Main results of the Spanish Best Practices program: evolution of the use of Non-entangling FADs, interaction with entangled animals, and fauna release operations. IOTC–2017–WGFAD01–11
- Marsac F, Barlow R, Ternon JF, Ménard F, Roberts M (2014) Ecosystem functioning in the Mozambique Channel: Synthesis and future research. *Deep Sea Research Part II: Topical Studies in Oceanography* 100: 212-220 doi <http://dx.doi.org/10.1016/j.dsr2.2013.10.028>
- McGlade JM, Cury P, Koranteng KA, Hardman-Mountford N (2002) The Gulf of Guinea Large Marine Ecosystem: environmental forcing and sustainable development of marine resources. *Newnes*

- Minami M, Lennert-Cody CE, Gao W, Román-Verdesoto M (2007) Modeling shark bycatch: The zero-inflated negative binomial regression model with smoothing. *Fisheries Research* 84: 210-221 doi <http://dx.doi.org/10.1016/j.fishres.2006.10.019>
- Mugo RM, Saitoh S-I, Takahashi F, Nihira A, Kuroyama T (2014) Evaluating the role of fronts in habitat overlaps between cold and warm water species in the western North Pacific: A proof of concept. *Deep Sea Research Part II: Topical Studies in Oceanography* 107: 29-39 doi <http://dx.doi.org/10.1016/j.dsr2.2013.11.005>
- Naimi B (2015) usdm: Uncertainty analysis for species distribution models, R package version 1.1-12
- Nieto K, Xu Y, Teo SLH, McClatchie S, Holmes J (2015) How important are coastal fronts to albacore tuna (*Thunnus alalunga*) habitat in the Northeast Pacific Ocean? *Progress in Oceanography* doi <http://dx.doi.org/10.1016/j.pocean.2015.05.004>
- Pikitch EK, Santora C, Babcock EA, Bakun A, Bonfil R, Conover DO, Dayton P, Doukakis P, Fluharty D, Heneman B, Houde ED, Link J, Livingston PA, Mangel M, McAllister MK, Pope J, Sainsbury KJ (2004) Ecosystem-Based Fishery Management. *Science* 305: 346-347 doi 10.1126/science.1098222
- Poisson F, Filmatler J-D, Vernet A-L, Laurent D (2014) Mortality rate of silky sharks (*Carcharhinus falciformis*) caught in the tropical tuna purse seine fishery in the Indian Ocean. *Canadian Journal of Fisheries and Aquatic Sciences* doi 10.1139/cjfas-2013-0561
- Potier M, Bach P, Ménard F, Marsac F (2014) Influence of mesoscale features on micronekton and large pelagic fish communities in the Mozambique Channel. *Deep Sea Research Part II: Topical Studies in Oceanography* 100: 184-199 doi <http://dx.doi.org/10.1016/j.dsr2.2013.10.026>
- Sagarminaga Y, Arrizabalaga H (2014) Relationship of Northeast Atlantic albacore juveniles with upper surface thermal and Chlorophyll-a fronts. *Deep Sea Research Part II: Topical Studies in Oceanography* doi <http://dx.doi.org/10.1016/j.dsr2.2013.11.006>
- Team RDC (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria ISBN 3-900051-07-0 <http://www.R-project.org> doi citeulike-article-id:2400517
- Tew Kai E, Marsac F (2010) Influence of mesoscale eddies on spatial structuring of top predators' communities in the Mozambique Channel. *Progress in Oceanography* 86: 214-223 doi <http://dx.doi.org/10.1016/j.pocean.2010.04.010>
- Tseng C-T, Sun C-L, Belkin IM, Yeh S-Z, Kuo C-L, Liu D-C (2014) Sea surface temperature fronts affect distribution of Pacific saury (*Cololabis saira*) in the Northwestern Pacific Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography* 107: 15-21 doi <http://dx.doi.org/10.1016/j.dsr2.2014.06.001>
- Wood S (2006) *Generalized additive models: an introduction with R*. Chapman & Hall/CRC
- Xu Y, Nieto K, Teo SLH, McClatchie S, Holmes J (2015) Influence of fronts on the spatial distribution of albacore tuna (*Thunnus alalunga*) in the Northeast Pacific over the past 30 years (1982–2011). *Progress in Oceanography* doi <http://dx.doi.org/10.1016/j.pocean.2015.04.013>
- Young JW, Hunt BPV, Cook TR, Llopiz JK, Hazen EL, Pethybridge HR, Ceccarelli D, Lorrain A, Olson RJ, Allain V, Menkes C, Patterson T, Nicol S, Lehodey P, Kloser RJ, Arrizabalaga H, Anela Choy C (2014) The trophodynamics of marine top predators: Current knowledge, recent advances and challenges. *Deep Sea Research Part II: Topical Studies in Oceanography* doi <http://dx.doi.org/10.1016/j.dsr2.2014.05.015>
- Zuur AF, Mira A, Carvalho F, Ieno EN, Saveliev AA, Smith GM, Walker NJ (2009) *Negative Binomial GAM and GAMM to Analyse Amphibian Roadkills Mixed effects models and extensions in ecology with R*. Springer New York, New York, NY, pp 383-397

Table 1. Multi variable-based GAM for silky shark.

Approximate significance of smooth terms:

	edf	p-value
s(Longitude,Latitude)	18.157	< 2e-16 ***
s(YearDay)	4.579	2.85e-16 ***
s(TotalBCW)	1.989	0.00533 **
s(SSH)	4.466	6.05e-14 ***
te(SST, difSST)	19.730	2.57e-08 ***
te(CHL,difCHL)	18.812	1.00e-09 ***
Year _{random}	10.753	< 2e-16 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.0847 Deviance explained = 32%
-REML = 8157.8 Scale est. = 1 n = 6653

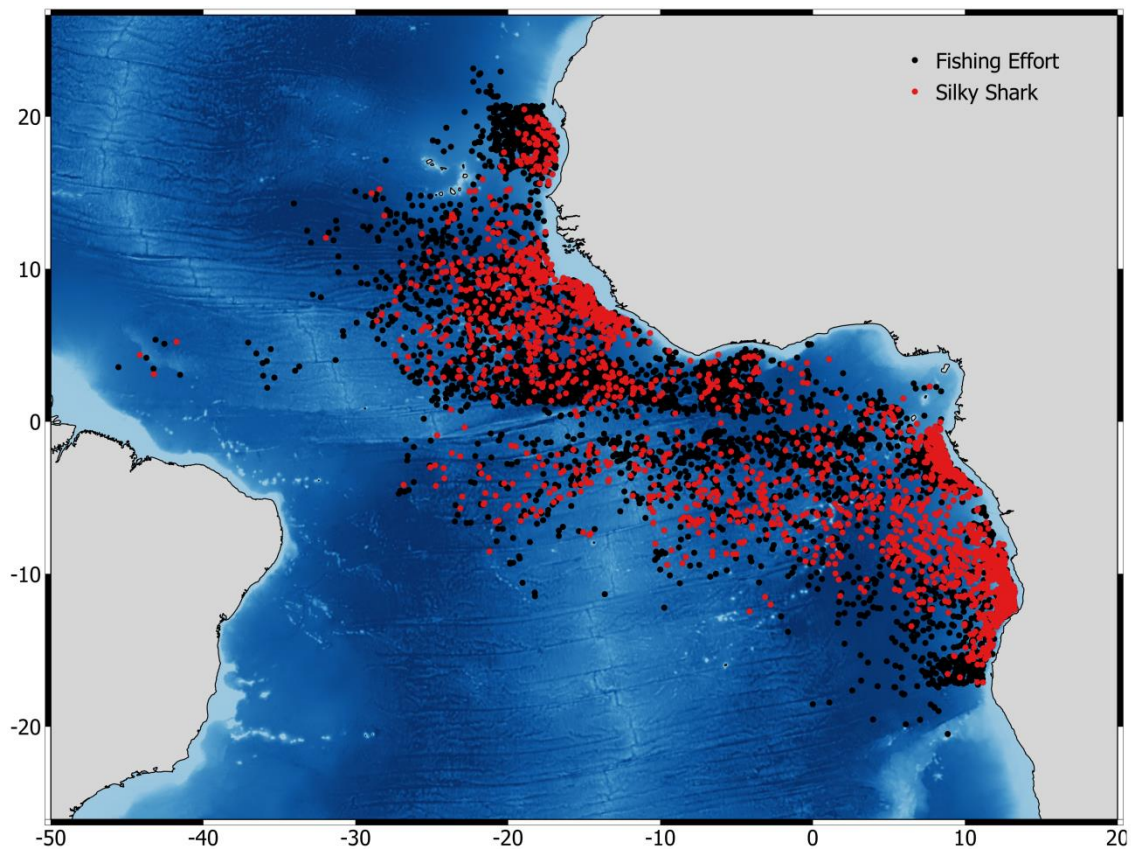


Figure 1. Spatial distribution of fishing effort (fishing sets, in black) as well as locations for sets where silky shark presence was detected (in red).

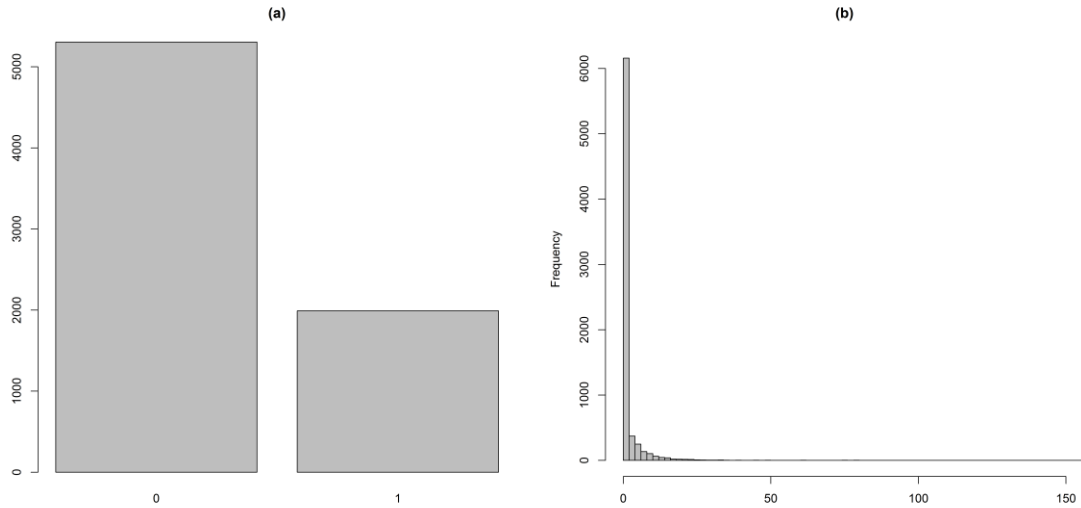


Figure 2. (a) Fishing set histogram of null and positive values of silky shark bycatch (b) Frequency histogram (in number) of silky shark bycatch

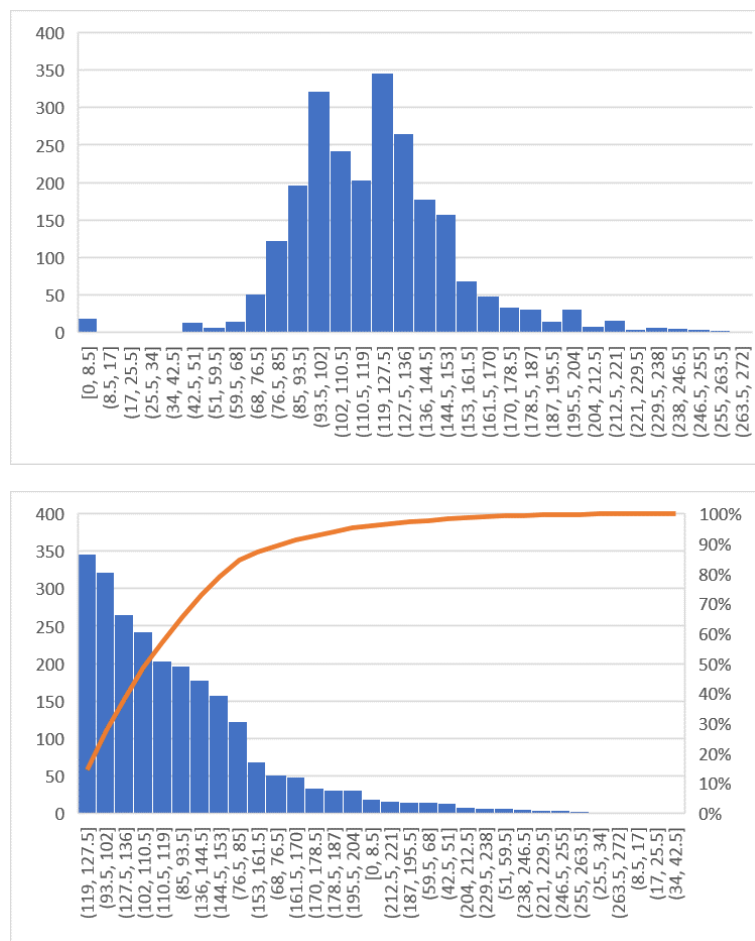


Figure 3. Histogram of size frequency (top) and accumulative histogram of size frequency (bottom) of the sharks investigated in this study.

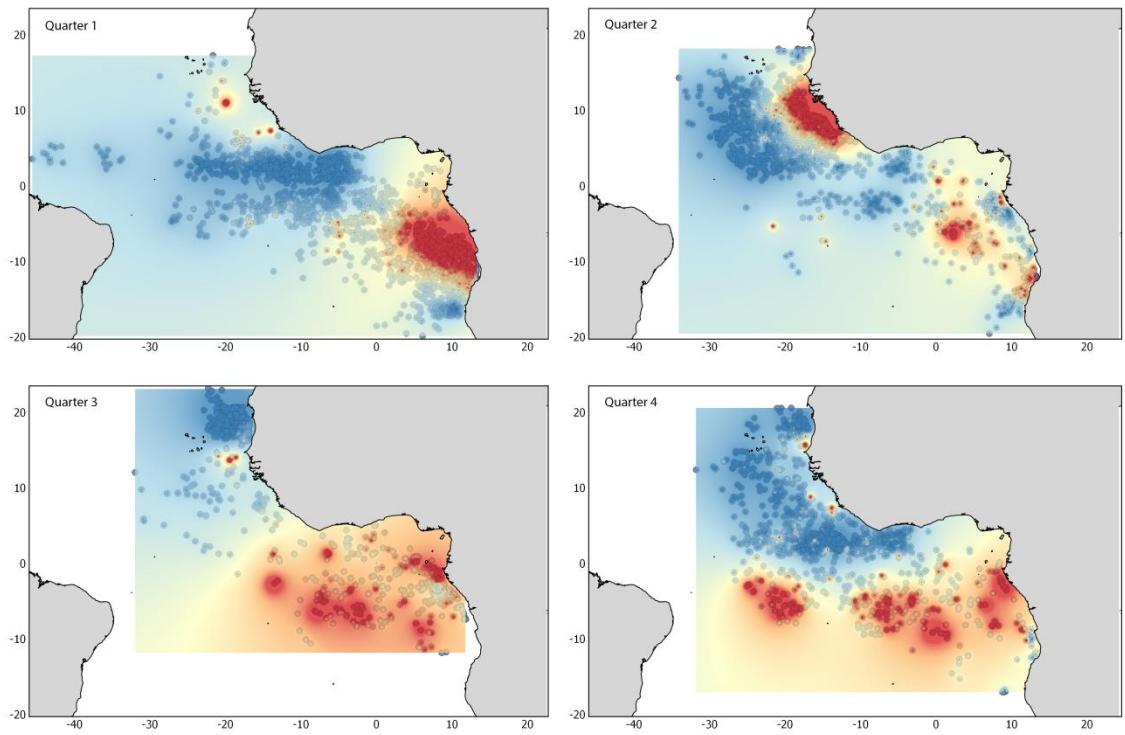


Figure 4. Heatmaps of the spatio-temporal distribution of silky sharks in the central and eastern tropical Atlantic Ocean. Shown, for information, the fishing effort and distribution of the sets used in the present study (blue dots).

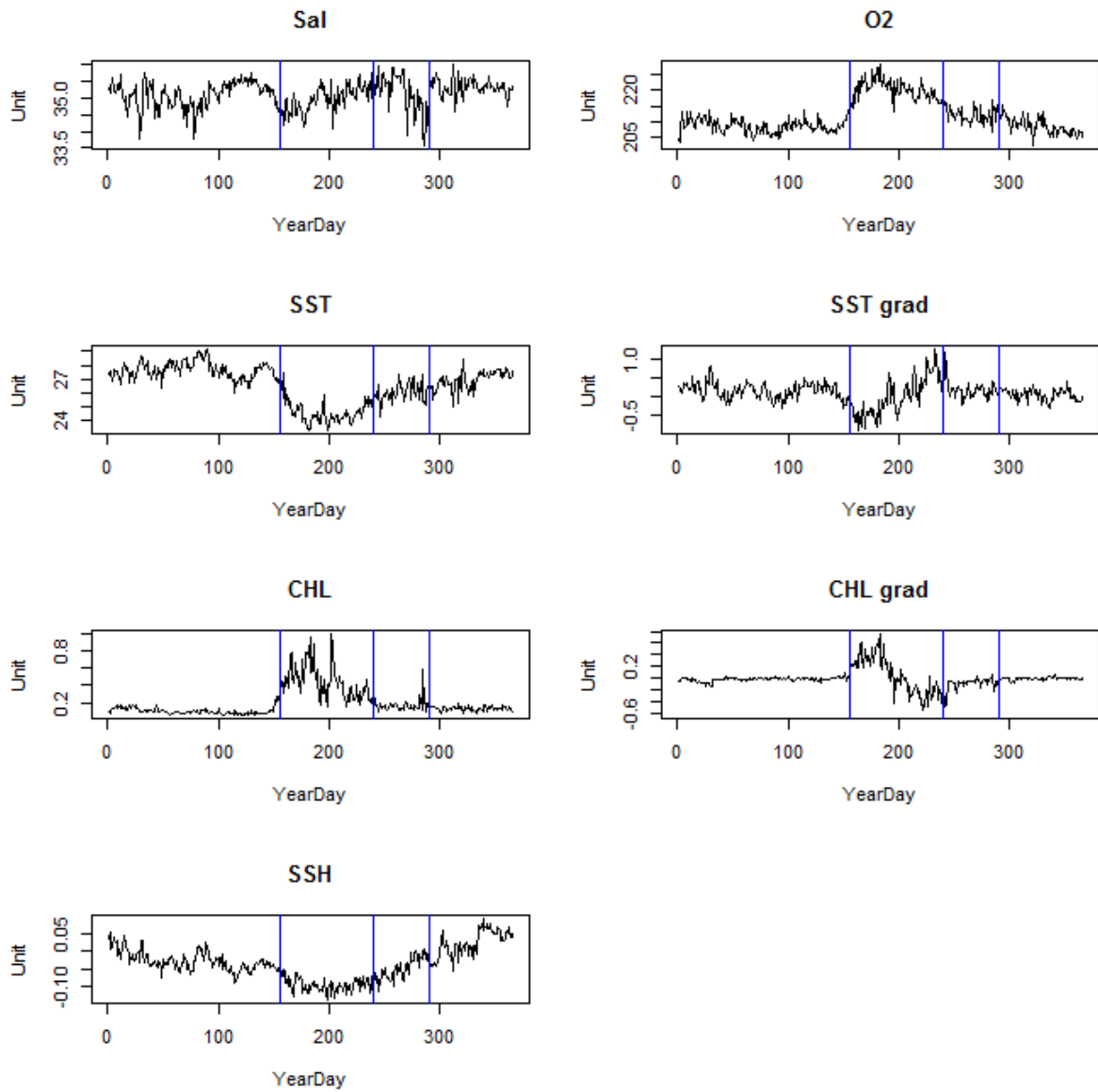


Figure 3. Annual averages for each of the oceanographic variable used in the regime shift identification analysis and their corresponding statistical change points (vertical blue lines).

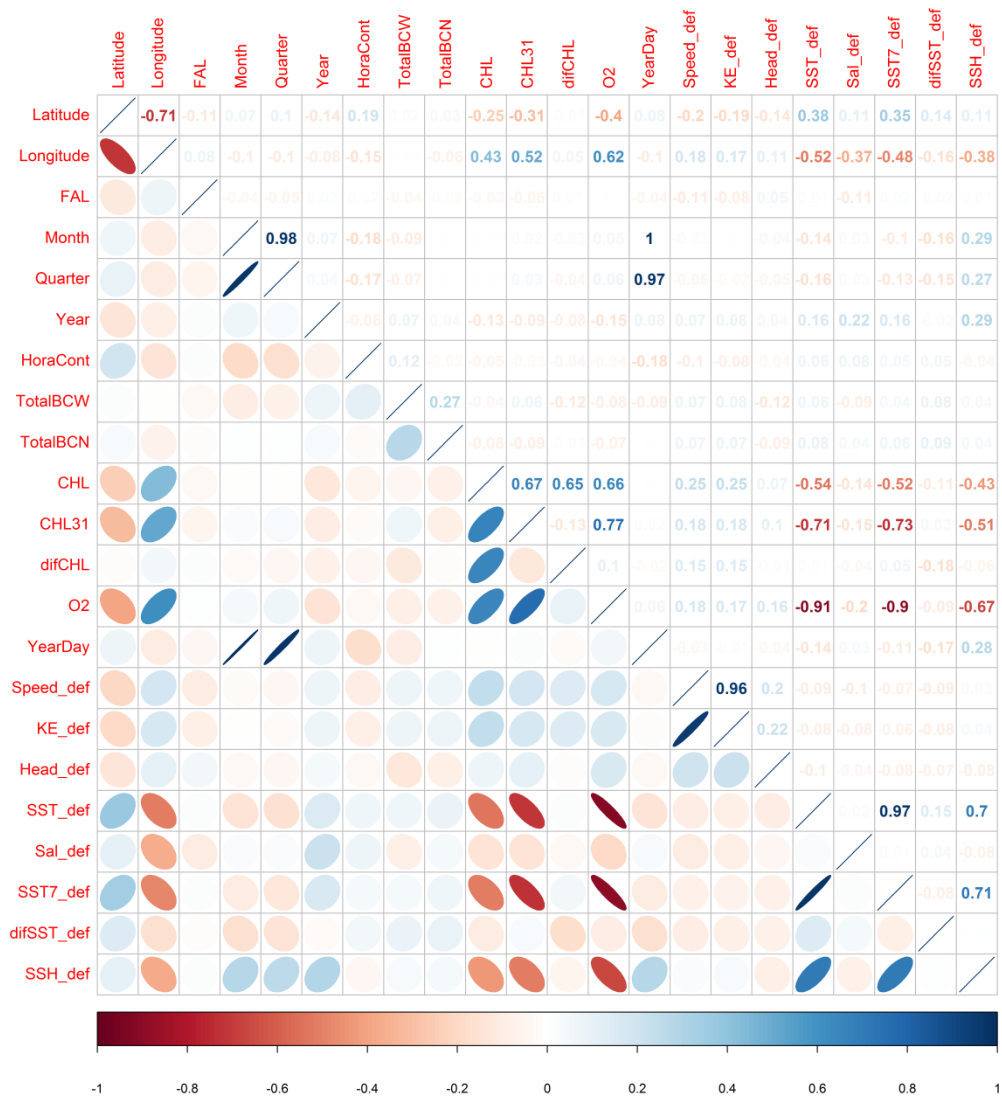


Figure 6. Pearson correlation figures and scores among all the covariates considered in the present study.

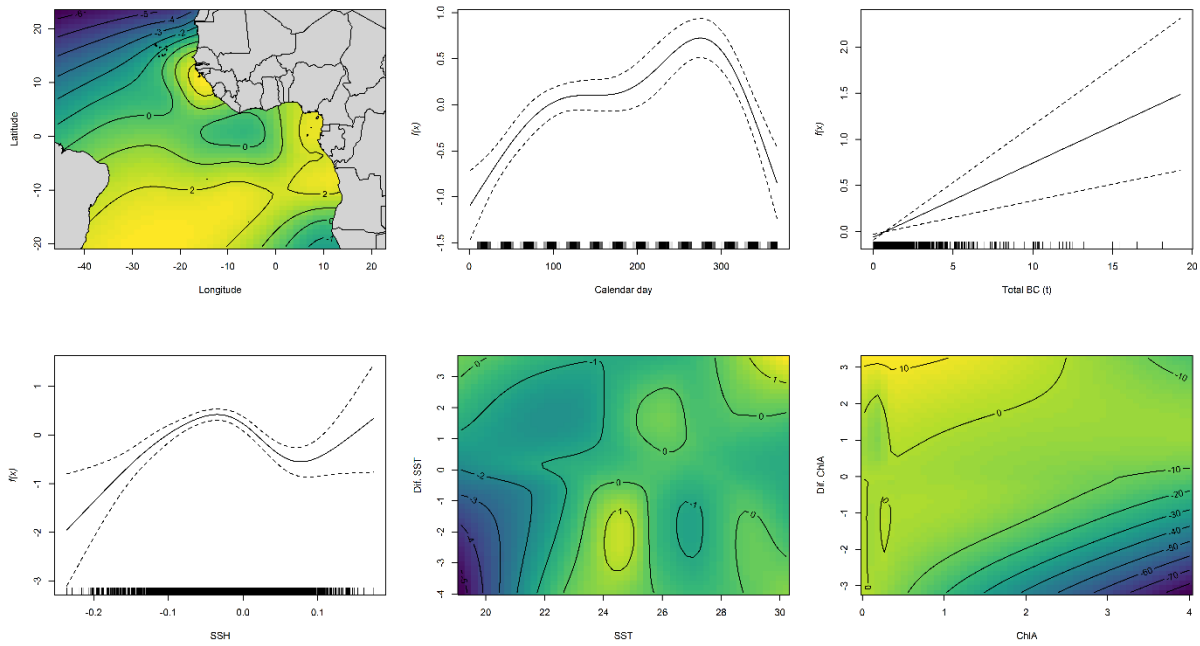


Figure 4. The partial effects of each individual covariate (Calendar Day, Total BC, SSH) are plotted as smoothed fits. Broken lines correspond to 2 standard errors, above and below the estimate of the smooth being plotted. Short vertical lines located on the x-axes of each plot indicate the values at which observations were made. The partial effect of the two-dimensional terms (latitude and longitude; SST and SST gradient; CHL and CHL gradient) are represented in surface plots.

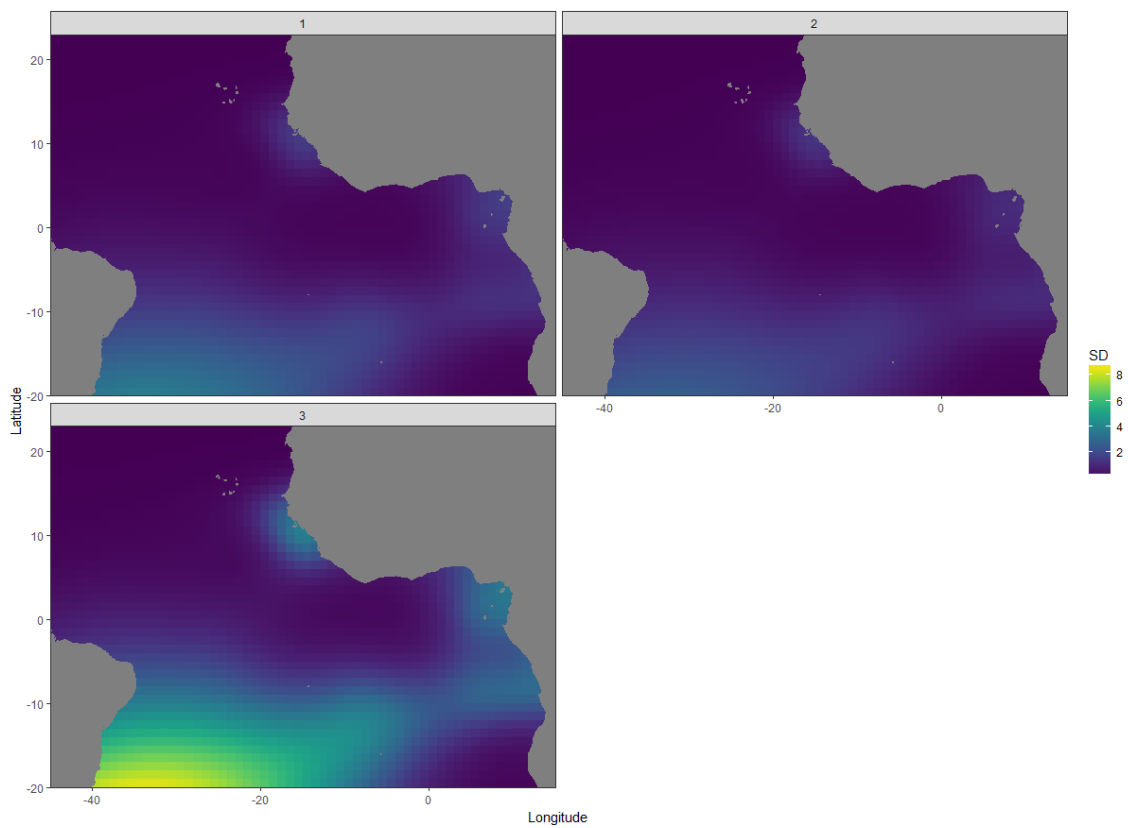
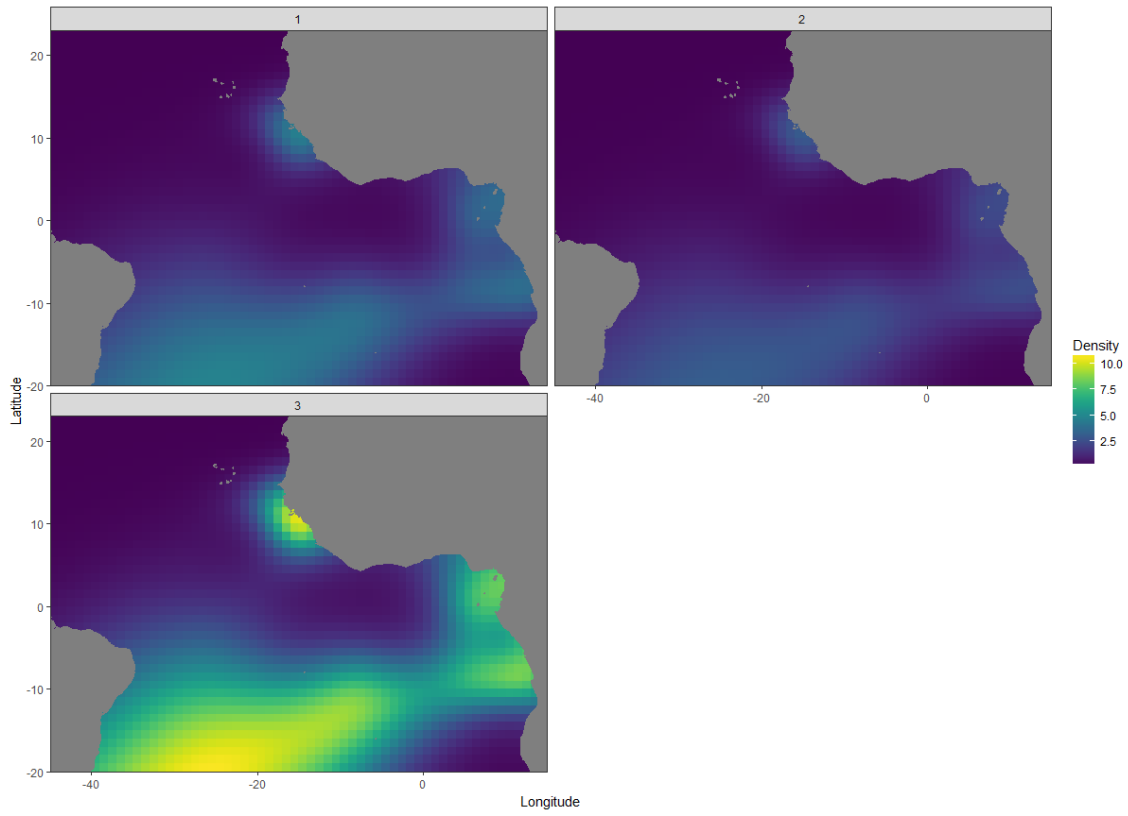


Figure 5. Averaged predictions of shark density (top) and standard deviation (bottom) for the three environmental regimes identified in this study: stable (1), cooling (2) and warming (3) periods.