A PRELIMINARY HABITAT SUITABILITY MODEL FOR OCEANIC WHITETIP SHARK IN THE WESTERN INDIAN OCEAN

Leire Lopetegui[1,2], Jan Jaap Poos[2], Haritz Arrizabalaga[1], Gency Guirhem[1], Hilario Murua[3], Nerea Lezama-Ochoa[4], Shane Griffiths[5], Jon Ruiz Gondra[6], Philippe S. Sabarros[7,8], Jose Carlos Baez[9], Maria Jose Juan-Jordá[1]

[1] AZTI, Marine Research, Basque Research and Technology Alliance (BRTA), Pasaia, Gipuzkoa, Spain
[2] Aquaculture and Fisheries Group, Wageningen University & Research, Wageningen, Netherlands
[3] International Sustainable Seafood Foundation, Washington, DC, USA
[4] Institute of Marine Sciences, University of California Santa Cruz, Santa Cruz, CA, USA
[5] Inter-American Tropical Tuna Commission, La Jolla, CA, USA
[6] AZTI, Marine Research, Basque Research and Technology Alliance (BRTA), Sukarrieta, Bizkaia, Spain
[7] MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Sète, France
[8] IRD, Ob7, Sète, France
[9] Instituto Español de Oceanografía, Centro Oceanográfico de Málaga, Fuengirola, Málaga, Spain

SUMMARY

Understanding the temporal, spatial and environmental factors influencing species distributions is essential to minimize the interactions of vulnerable species with fisheries and can be used to identify areas of high bycatch rates and their environmental conditions. Classified as critically endangered by the International Union for the Conservation of Nature, the oceanic whitetip shark (*Carcharhinus longimanus*) is the second main shark species incidentally caught by the tropical tuna purse seine fishery in the western Indian Ocean. In this study, we used the European Union purse seine fishery observer data (2010-2020) and generalized additive models to develop a habitat suitability model for juvenile oceanic whitetip shark in the western Indian Ocean. Sea surface temperature was the main environmental driver suggesting a higher probability of occurrence of this shark with decreasing temperatures. The type of fishing operation also was an important predictor explaining its occurrence, suggesting a higher probability of incidentally catching this species when using fish aggregating devices as set type. Moreover, predictive maps of habitat suitability suggested the area offshore of Kenya and Somalia are an important hotspot with higher probabilities of incidentally catching this species during the summer monsoon (June to September) when upwelling takes place. The habitat suitability models developed here could be used to inform the design and testing of potential time-area closures in the Kenya-Somalia basin with the objective of minimizing the bycatch of this critically endangered species with the least possible impact on fishing operations and fishery yields of target tunas.

KEYWORDS: Oceanic whitetip shark, Species Distribution Model, bycatch species, tropical tuna fishery, western Indian Ocean.

1. Introduction

The unintended catch of non-targeted species, i.e. bycatch, continues to be a key threat to sustainable fisheries globally. Fisheries targeting top predatory tuna and billfish species can have large impacts on non-targeted species including sharks, rays, sea turtles, seabirds and marine mammals, which are often less productive than target species (Clarke et al., 2014; M. Hall & M. Roman, 2013). In response to bycatch issues, tuna Regional Fisheries Management Organizations (RFMOs) in charge of managing and conserving tuna and billfish species in the Atlantic, Indian and Pacific Oceans have adopted wide range of measures to mitigate and reduce bycatch on vulnerable taxa. Yet they have achieved moderate progress in governing bycatch (Gilman, Passfield, & Nakamura, 2014; Juan-Jordá, Murua, Arrizabalaga, Dulvy, & Restrepo, 2018). Poor data collection, inadequate low observer coverage required in tuna fisheries for accurate assessments of bycatch, the large gaps in management measures for controlling the direct and indirect impacts on bycatch species and lack of compliance with existing measures have all contributed to low bycatch governance (Clarke et al., 2014; Ewell, Hocevar, Mitchell, Snowden, & Jacquet, 2020; Gilman et al., 2014; Maury et al., 2013). Furthermore, to date the existing management and conservation measures in tuna RFMOs have mostly focused on implementing changes in fishing gear and methods to reduce bycatch of vulnerable taxa and adopting best-practices for handling and releasing practices to increase their probability of post-release survival (Goñi et al., 2015; Grande et al., 2020; Poisson, Séret, Vernet, Goujon, & Dagorn, 2014). Measures limiting bycatch and requiring the implementation of time-area closures have only been adopted in tuna RFMOs to reduce bycatch of juveniles of commercially targeted tunas and swordfish (Hall, Gilman, Minami, Mituhasi, & Carruthers, 2017; IATTC, 2009), except for bycatch limits for dolphins in the eastern Pacific (IATTC, 1999). To what extent the use of time-area closures would be effective to reduce bycatch of vulnerable species and avoid high bycatch areas or biodiversity hotspots remains an important area of research in tuna RFMOs (Kaplan et al., 2014; Tolotti, Filmalter, et al., 2015).

Understanding the temporal, spatial and environmental factors influencing species distributions is essential to minimize the interactions of species with fisheries and can be used to identify areas of high bycatch rates and their environmental conditions (Deakos, Baker, & Bejder, 2011). To this effect, Species Distribution Models (SDMs), also known as niche models, are widely used to predict species distributions and environmental niche of species using species occurrence or abundance and environmental information (Elith & Leathwick, 2009), and are increasingly used to inform and support conservation planning and spatial management tools such as time-area closures (Marshall, Glegg, & Howell, 2014).

SDMs have been largely developed for commercial highly migratory pelagic fish species such as tunas (Erauskin-Extramiana et al., 2019; Setiawati, Sambah, Miura, Tanaka, & As-syakur, 2015), and billfishes (Rooker et al., 2012; Su, Sun, Punt, Yeh, & DiNardo, 2011). Applying SDM to highly migratory vulnerable species caught as bycatch in tuna and billfish fisheries has been more challenging in part due to the difficulty of collecting quality data in oceanic environments (McKinney, Hoffmayer, Wu, Fulford, & Hendon, 2012), the traditional low mandatory observer coverage rate implemented in most tuna fisheries (ICCAT, 2016; IOTC, 2014) and the difficulties of accessing national and observer datasets which often are not in the public domain (Ewell et al., 2020). In the last years, a 100% observer coverage all year round in tuna purse seine fisheries has become mandatory for purse seine fisheries in the eastern and western Pacific Ocean (Ewell et al., 2020; IATTC, 2019; WCPFC, 2018). The availability of observer data in the Inter-American Tropical Tuna Commission (IATTC) has resulted in an increase number of studies evaluating the environmental factors affecting the distributions of species bycaught in tuna fisheries such as for species of dolphinfish (Marín-Enríquez, Seoane, & Muhlia-Melo, 2018), sailfish (Martinez-Rincon, Ortega-Garcia, Vaca-Rodriguez, & Griffiths, 2015), wahoo (Martínez-Rincón, Ortega-García, & Vaca-Rodríguez, 2012), olive ridley sea turtle (Montero, Martinez-Rincon, Heppell, Hall, & Ewal, 2016), and spinetail devil ray (Lezama-Ochoa et al., 2019). In contrast, SDM studies for highly migratory vulnerable species have been relatively scarce in the Atlantic and Indian Ocean.

In this study, we take advantage of the high observer coverage in the European Union (EU) purse seine fishery operating in the tropical eastern Atlantic and western Indian Oceans to contribute to the understanding and predict distributions for vulnerable bycatch species in this fishery. Since the early 2000s the EU tuna purse seine fleet has been voluntarily increasing over time its observer coverage to currently 100% level all year round using a combination of human observers and Electronic Monitoring System (EMS) in the Atlantic and Indian Oceans (Escalle et al., 2016). This increased levels of observer coverage has created new opportunities to model habitat requirements for vulnerable species bycaught in this fishery (Lezama-Ochoa et al., 2020; Lopez, Alvarez-Berastegui, Soto, & Murua, 2020).

The EU tropical tuna purse seine fishery targets the three main tropical tuna species: Skipjack *Katsuwonus pelamis*, Yellowfin *Thunnus albacares* and Bigeye tuna *Thunnus obesus*, but also catches unintentionally non-target species (Amandè et al., 2012; Ruiz et al., 2018). This fishery operates using two types of fishing operation (set types): sets using drifting Fish Aggregating Devices (FAD) and sets associated with Free-swimming tuna Schools (FSC) (Marsac, 2017). FADs are composed by a floating structure (e.g. bamboo rafts with purse seiner corks) and an underwater part suspended below the floating object (e.g. nets, ropes, palm leaves) where pelagic species aggregate. Currently more than 80% of the tuna catches by the EU purse seine fishery are made in aggregated schools under FADs, while the reminder comes from FSC sets (Fonteneau, Pallares, & Pianet, 2000; Lennert-Cody & Hall, 2000; Marsac, 2017). The spatial extent and dynamics of FADs fisheries and understanding the spatio-temporal distributions of tuna and other pelagic species being attracted and aggregating around the FADs continues to be an area of research (Orue et al., 2019). Whereas FSC sets are set generally in association to monospecific schools of tuna, FAD sets attract tuna species and other pelagic fish and non-fish species, having 2.8 to 6.7 times higher catches of non-target species (Dagorn, Holland, Restrepo, & Moreno, 2013). Incidentally captured species in both FAD and FSC sets include sea turtles, seabirds, marine mammals, sharks, rays and other teleost (Gray & Kennelly, 2018). Due to their specific life-history traits (slow growth, late sexual maturity and, low fecundity), many species of sharks and rays have long generation times and low intrinsic population growth rates making them inherently susceptible to overexploitation (Frisk, Miller, & Fogarty, 2001). This study will focus on the critically endangered oceanic whitetip shark (*Carcharhinus longimanus*) as it is one of the main bycatch shark species in the tropical tuna purse seine fishery in the western Indian Ocean (Dagorn et al., 2013).

The oceanic whitetip shark is a large pelagic apex predator. As predatory sharks, they play a crucial regulatory role in the integrity of pelagic ecosystems, by maintaining balance and diversity in the species below them in the food web (Heithaus, Frid, Wirsing, & Worm, 2008; Pauly, Christensen, Dalsgaard, Froese, & Torres, 1998; Scheffer, Carpenter, & Young, 2005). This species has been described historically as one of the most abundant shark species in tropical waters worldwide (Compagno, 1984). However, over the last decades, the oceanic whitetip shark has experienced substantial population declines throughout the majority of its global range (Martin Hall & Marlon Roman, 2013; IOTC, 2015; Tremblay-Boyer, Carvalho, Neubauer, & Pilling, 2019; C. N. Young et al., 2017), due to overfishing and high demand and use in the international fin trade (C. N. Young et al., 2017) with unknown consequences on the resilience and integrity of marine ecosystems. Although it is a commonly caught bycatch species by a variety of pelagic fishing gears, such as tuna longlines, gillnets, and purse seines globally (Bonfil, Clarke, & Nakano, 2008), the oceanic whitetip shark has only recently received much attention in terms of regulatory and management protections (C. N. Young et al., 2017). In 2019, oceanic whitetip shark was classified as critically endangered globally by the International Union for the Conservation of Nature (IUCN; www.redlist.org), and it was included in Appendix II of the Convention on International Trade in Endangered Species (CITES; www.cites.org) which requires strict regulation of its international trade. As a highly migratory species, it is also listed on Annex I, Highly Migratory Species, of the United Nations Convention on the Law of the Sea (UNCLOS; www.un.org) which provides a detailed regime for the conservation and management of this species on the high sea areas beyond national jurisdiction. In line with these levels of protection, tuna RFMOs from all oceans have adopted a series of management and conservation measures to ban landings, storing, and selling of the oceanic whitetip shark caught in tuna fisheries (IATTC, 2011; ICCAT, 2010; IOTC, 2013; WCPFC, 2019). Despite these protective measures, there is no evidence yet that documented oceanic whitetip shark declines are halting (Pacoureau et al., 2021) and the effectiveness of the current management measures adopted by tuna RFMOs on oceanic whitetip sharks still needs to be evaluated in tuna RFMOs against measurable performance standards (Gilman et al., 2014).

Oceanic whitetip shark can be found in oceanic waters warmer than 18ºC, yet its thermal range of preference is between 20-28ºC (Andrzejaczek et al., 2018; Tolotti et al., 2017). Similar to other oceanic species, the abundance of this shark increases away from continental and insular shelves (Bonfil et al., 2008). Several studies indicate that oceanic whitetip sharks spend most of their time in the epipelagic zone, above 200 m depth of the water column (Andrzejaczek et al., 2018; Howey-Jordan et al., 2013; Musyl et al., 2011; Tolotti, Bach, Hazin, Travassos, & Dagorn, 2015; Tolotti et al., 2017). However, the species has been recorded conducting deep dives into the mesopelagic zone (> 200 m), appearing to tolerate colder waters down to 7.8ºC for short periods (Howey-Jordan et al., 2013; Howey et al., 2016; Musyl et al., 2011; Tolotti, Bach, et al., 2015; Tolotti et al., 2017). The reasons behind these deep dives have yet to be confirmed, but it may be a foraging or navigation strategy (Howey et al., 2016). Oceanic whitetip sharks are top predators that feed mostly on oceanic teleosts and cephalopods, corresponding to a trophic level of 4.2, similar to large pelagic teleosts such as tuna (Madigan et al., 2015). Sea surface temperature and mixed layer depth also appear to influence their vertical behaviors (Andrzejaczek et al., 2018; Tolotti et al., 2017). Thus, it could also be a thermoregulation strategy, as a sea surface temperature of 28ºC marked a distinct change in vertical movement (Andrzejaczek et al., 2018; Tolotti et al., 2017). Great distance migrations have been recorded in this species as well as some evidence of philopatry (i.e., site fidelity) (Filmalter et al., 2012; Howey-Jordan et al., 2013; Musyl et al., 2011; Tolotti, Bach, et al., 2015). In the Indian Ocean, oceanic whitetips have been documented exhibiting trans-equatorial migrations, up to 6,500 km (Filmalter et al., 2012). In the central Pacific, the largest recorded linear movement was 4,285 km over a period of 95 days (Musyl et al., 2011). In addition, two studies in the Bahamas and Northeast Brazil registered site fidelity behaviors (Howey-Jordan et al., 2013; Tolotti, Bach, et al., 2015). Despite the fact that a significant amount of research has been undertaken on this species in recent years, revealing new information on life history, movements and behavior, there is still a major knowledge gap in the relationship between the spatial distribution of this species and the environmental conditions at large spatial oceanic scales, such as the western Indian Ocean.

In order to fill this knowledge gap, we modelled the habitat suitability of oceanic whitetip shark in the western Indian Ocean. The main objective of this study is to generate seasonal and yearly distribution prediction maps to investigate the spatio-temporal distributions of this species related to environmental conditions using the EU purse seine observer data. We used Generalized Additive Models (GAMs) to model the oceanic whitetip shark occurrence because these models are capable of capturing non-linear relationships by fitting smoothing functions to predictor variables (Montero et al., 2016). Because we used fisheries dependent data to identify relationships between environmental conditions and operational fishery characteristics and the oceanic whitetip shark occurrences, the habitat suitability predictions maps produced can assist in the identification and detection of hotspots or areas with high incidental bycatch probability. This type of work could assist the Indian Ocean Tuna Commission (IOTC) in the development of more effective management and conservation strategies involving spatial management tools such as time-area closures to prevent overfishing of this vulnerable shark species.

Based on previous research on the ecology of the oceanic whitetip shark, we hypothesize that the occurrence of oceanic whitetip shark is directly related to the oceanographic conditions of the western Indian Ocean and, specifically, with sea surface temperature, mixed layer depth and productivity (chlorophyll, phytoplankton, nitrate) environmental variables. The fishery-dependent variable describing the type of fishing operation (FAD or FSC sets) might also explain the occurrence of the sharks, as previous work suggest more sharks species, including oceanic whitetip shark are caught incidentally in greater quantities in FAD sets (Dagorn et al., 2013). Different spatial and temporal variables describing where and when the fishing operation takes place might also play an important role when explaining the distribution of the species as they are directly influenced by the oceanographic characteristics of this region driven by the monsoon regimes (Schott & McCreary, 2001).

2. Material and methods

2.1. Study area

The EU purse seine fishery targeting tropical tuna species in the Indian Ocean is primarily concentrated in the western side of the Indian Ocean (Figure S1). In the western Indian Ocean the ocean surface circulation is influenced by monsoon winds, affecting the production and seasonality of the area (Schott & McCreary, 2001). Two monsoon regimes are distinguished: winter monsoon from December to March (Northeast monsoon - NEM) and summer monsoon from June to September (Southwest monsoon - SWM), separated by spring intermonsoon (April and May) and autumn intermonsoon (October and November) transition regimes (Schott & McCreary, 2001). During the summer monsoon, a strong upwelling occurs in the western Indian Ocean (Schott & McCreary, 2001), where cold and highly saline productive waters are pumped up to the surface, producing an increase in primary production along the coast of Somalia (Hitchcock, Key, & Masters, 2000), spreading up to 500 km offshore (Wiggert, Murtugudde, & Christian, 2006). Besides coastal upwelling, other mesoscale processes that affect the productivity of the western Indian Ocean, such as eddies, filaments, fronts and whirls, play also an important role in the aggregation of top predators like tuna (Orue et al., 2019). The Seychelles-Chagos thermocline ridge (55°E-65°E; 5°S-12°S), that features a productive open-ocean upwelling area during the winter monsoon (Hermes & Reason, 2008), and the Mozambique Channel, which has a complex circulation influenced by mesoscale eddies (Schott, Xie, & McCreary Jr., 2009), are known to aggregate tuna and tuna-like species. These changes in circulation of surface currents affect the biophysical characteristic of the water column (i.e. chlorophyll, temperature, salinity, dissolved oxygen), which in turn affect the presence and abundance of pelagic species in the area (Orue et al., 2019) and the spatial dynamics of the fisheries targeting them (Marsac, 2017).

2.2. Data collection

2.2.1. Fisheries observer data

We used fishery-dependent observer data collected by human-observers and Electronic Monitoring System (EMS) onboard the EU purse seine fishery between 2010 and 2020 (Figure S2). The observer programs of the EU purse seine fleet are administered by two Spanish institutions, *AZTI* and *Instituto Español de Oceanografía* (IEO), and the French *Institut de Recherche pour le Développement* (IRD). A total of 26,523 sets have been observed between 2010 and 2020 (Figure S3). The 87.4% of the observed sets were sets using FAD and the rest (12.6%) FSC sets (Figure S3A). While the observer program started in 2003 in the Indian Ocean, the observer coverage decreased progressively during the first years owing to the high risk of piracy in the area. In 2010 the observer program was completely suspended. Sampling was resumed in 2011 and since 2014 the observed spatial coverage has progressively increased (Ruiz et al., 2018) (Figure S3B). Since 2015 the EMS have also been complementing the human observers in the task of collecting fishery data in this fishery. In the data set analyzed, 85.3% of sets observed were by human observers and 13.7% by the EMS (Figure S2).

The observer dataset contained operational set data including set location (longitude, latitude), date, GMT hours, type of fishing set (FAD or FSC) and vessel and observer code. For each fishing set, the total amount (in tonnes) and species-composition of the target tuna catch (Skipjack, Yellowfin and Bigeye tunas) and non-targeted species catch is recorded. The non-targeted catch can either be retained for its commercial value (e.g. small tunas *Auxis sp.*) or released back into the sea for its low commercial value or because it is prohibited to keep it on board (usually vulnerable taxa such as the oceanic whitetip shark) (Amandè et al., 2012; Ruiz et al., 2018). The non-targeted species retained or released are considered bycatch. The bycatch is comprised mainly of these major taxa groups (small tunas, billfishes, sharks, rays, and other bony fishes). For bycatch species, the numbers and mean size of the species by set is also recorded by the observers.

2.2.2. Environmental data

The environmental data were obtained at 1/4º spatial resolution and daily temporal resolution from EU Copernicus Marine Environment Monitoring Service (CMEMS) (https://marine.copernicus.eu/). We extracted 15 biological and physical variables for each position and date (between 2010-2020) of the fishing sets: chlorophyll (Chl), primary production of phytoplankton (NPPV), oxygen (O_2), nitrate (NO_3), phosphate (PO_4) and silicate (Si) concentrations, sea surface temperature (SST), sea surface height (SSH), mixed layer depth (MLD) and salinity (Sal) (Table 1). We also extracted the eastward (Uo) and northward (Vo) velocity vectors from CMEMS and used them to calculate the eddy kinetic energy (Ke), velocity (Vel), and heading of the current (Heading). We also calculated chlorophyll and sea surface temperature fronts based on previously extracted sea surface temperature and chlorophyll data using a front detection algorithm (Belkin & O'Reilly, 2009).

We chose these environmental variables as the initial predictor variables (Table 1) based on previous research. Previous studies describing oceanic whitetip shark habitat preferences have documented that these sharks are associated to waters between 20-28ºC of sea surface temperature (Andrzejaczek et al., 2018; Tolotti, Bach, et al., 2015) and confined to the MLD (Tolotti et al., 2017). Chlorophyll, primary production of phytoplankton, nitrate and phosphate have also been used as proxies of prey availability and accurate predictors of hotspots for pelagic species (Lam, Galuardi, & Lutcavage, 2014; Vacquié-Garcia et al., 2015). Oxygen concentrations may also limit sharks and their preys distribution (Nasby-Lucas, Dewar, Lam, Goldman, & Domeier, 2009). We also considered salinity as a predictor variable because it was found to be a significant variable to explain the habitat preferences in pelagic species such as tunas (Erauskin-Extramiana et al., 2019). Oceanic pelagic sharks often aggregate in mesoscale oceanographic features such as oceanographic fronts and eddies (Dewar et al., 2018; Lopez et al., 2020; Miller, Scales, Ingram, Southall, & Sims, 2015; Queiroz, Humphries, Noble, Santos, & Sims, 2012). Sea surface height, eddy kinetic energy, chlorophyll fronts and sea surface temperature fronts can also be considered as a proxies to describe mesoscale oceanographic features (Teo & Block, 2010; Zainuddin, Saitoh, & Saitoh, 2008). Therefore, we also selected them as potential predictor variables.

Table 1. Summary of the predictor environmental variables used in the analysis. All variables were extracted with a 1/4º spatial and daily temporal resolutions. Variable acronym and name, units, and source (Copernicus product number).

Variable acronym	Variable name	Units	Average	Min	Max	Source
Chl	Chlorophyll	mg.m-3	0.197	0.057	1.590	001_029
NPPV	Primary Production of Phytoplankton	mg.m-3	10.74	0.595	69.42	001_029
O_2	Oxygen	mmol.m-3	203.1	191.4	221.8	001_029
NO_3	Nitrate	mmol.m-3	0.158	0.0004	2.952	001_029
PO_4	Phosphate	mmol.m-3	0.102	0.00004	0.452	001_029
Si	Silicate	mmol.m-3	1.809	0.408	12.72	001_029
Chl fronts	Chlorophyll fronts	ratio	0.016	0.00001	1.329	Calculated
SST	Sea Surface Temperature	°C	28.57	22.94	31.68	001_30
SST fronts	Sea Surface Temperature fronts	°C.km-1	0.022	0.0003	0.096	Calculated
SSH	Sea Surface Height	m	0.372	0.0564	0.909	001_30
MLD	Mixed Layer Depth	m	18.47	9.783	104.5	001_30
Sal	Salinity	psu	35.31	33.12	37.05	001_30
Ke	Eddy kinetic energy	m/s	0.093	0.000001	1.444	Calculated
Vel	Velocity of the current	m/s	0.362	0.00106	1.987	Calculated
Heading	Heading of the current	degrees	178.52	0.00	359.98	Calculated

2.3. Statistical analysis

2.3.1. Modelling approach

We analyzed the relationships between the occurrences of oceanic whitetip shark and environmental, spatial and temporal variables using GAMs. GAMs are one of the most widely used statistical modelling tools to analyze relationships between the distributions of large marine species and their environment (Lezama-Ochoa et al., 2019; Lopez et al., 2020). This method is based on the use of non-parametric smoothing functions that allows a flexible description of complex species responses to the environment (Zuur, Ieno, & Smith, 2007). The general structure of the GAM is:

$$g(\mu i) = \alpha + f_1(X_{1i}) + f_2(X_{2i}) + f_3(X_{3i}) \ldots . + f_n(X_{ni})$$

where g is the link function (logit for binomial family), μi is the expected response variable (presence - absence in my case), α is the intercept, f_1 to f_n are smooth functions (thin plate or cyclic cubic regression splines), and X_{1i} to X_{ni} are the covariates (Guisan, Edwards, & Hastie, 2002).

We modelled the probability of occurrence of oceanic whitetip shark in an individual set. We modelled the occurrence and not the abundance of sharks in each specific set because only one oceanic whitetip shark was caught in most of the sets (Figure S4). Therefore, the incidental catch of oceanic whitetip sharks was transformed to the unit of presence/absence (1/0) and considered the dependent variable in the model.

The predictor variables considered in the modelling were: the environmental variables (Table 1), the operational information of the sets including the spatial variables (latitude and longitude), temporal variables (year, week, hours from sunrise), the type of purse seine set (FSC or FAD) and the species composition of the catch in each set (total catch and bycatch). The total catch and total bycatch of each fishing set, excluding oceanic whitetip sharks (TotalC and TotalBC; in tonnes) accounted for the potential effect of the community size, as sharks may show social behavior traits when they are juveniles (Jacoby, Croft, & Sims, 2012).

In addition, we also explored depth and distance to the nearest seamount as potential predictor variables. Bathymetry values were obtained from the ETOPO1 Global Relief Model from the National Oceanic and Atmospheric Administration (NOAA - https://www.ngdc.noaa.gov/mgg/global/) at 1/4º spatial resolution with the *marmap* package in R software (Pante & Simon-Bouhet, 2013). Considering that only seamounts shallower than 400 m depth showed significant aggregation effects in some marine predators, such as Skipjack *Katsuwonus pelamis* and Bigeye *Thunnus obesus* tunas (Morato et al., 2008), we extracted the coordinates of seamounts shallower than 400 m depth from the Global Distribution of Seamounts and Knolls (Yesson, Clark, Taylor, & Rogers, 2011). For each fishing set, distance to the nearest seamount (< 400 m depth), was calculated using the *geosphere* package in R software (Hijmans, 2011).

We also explored the mean size of oceanic whitetip sharks caught in the sets. The mean length of oceanic whitetip sharks by set was used to determine if catches were made by juveniles or adults of oceanic whitetip shark. Considering that oceanic whitetip sharks attain sexual maturity at 186 cm (C. N. Young & Carlson, 2020), we found that most of the sharks bycaught in the EU purse seine fishery are made of juvenile oceanic whitetip sharks. The mean length of the oceanic whitetip sharks ranged from 48 to 350 cm of total length but was dominated (90.2%) by juvenile individuals (< 186 cm) (Figure S5). Therefore, the habitat modelling is reflective of the habitat suitability for juvenile oceanic whitetip sharks.

In the GAMs, we restricted the degrees of freedom of the smooth functions for each predictor variable (Wood, 2006) to avoid over-fitting and to simplify interpretation of the results. We limited the maximum degrees of freedom (measured as number of knots, k) allowed to the smoothing functions to k = 6 for main effects and, k = 20 for interaction effects (Lezama-Ochoa et al., 2019). Each GAM was fitted using (i) thin plate regression splines for non-linear covariates, except for week and heading variation, where a cyclic cubic regression spline was used to account for a cyclical effect and (ii) a two-dimensional thin plate regression spline surface to account for spatial effects (latitude, longitude) of each fishing set (Wood, 2006). The *gam* function of the *mgcv* package was used to fit the model (Wood, 2014).

2.3.2. Correlation and multicollinearity of predictor variables

We used two measures to determine the correlation and multicollinearity between predictor variables in the GAM. First, all predictor variables were explored using Pearson's rank correlation (Wood, 2006). Pairs of variables with high correlation values (|r| > 0.6) were detected (Figure S6). Furthermore, multicollinearity between variables was examined conducting a Variance Factor Analysis (VIF) with a cut-off value of 5 (Lezama-Ochoa et al., 2019) using the *vifstep* function of the *usdm* package in R (Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014). This function deals with multicollinearity problems by excluding highly collinear variables from a set through a stepwise procedure. Based on the VIF test, the variables chlorophyll and velocity of the current were removed due to high collinearity with primary production of phytoplankton and kinetic energy (Table S1). According to the Pearson's rank correlation test, the pairs of (1) sea surface temperature - oxygen, (2) sea surface temperature - primary production of phytoplankton, (3) primary production of phytoplankton - nitrate and (4) salinity - latitude were highly correlated and thus we did not include them in the model at the same time (Figure S6).

2.3.3. Additional exploratory analysis

As an additional exploratory analysis, we fitted univariate binomial GAMs for each predictor variable considered (Figure S7). The univariate binomial GAMs provided information on the potential shape of each predictor variable on the response variable and on their raw likely contribution to the deviance explained of the model. From these univariate GAMs, we detected a similar temporal pattern between the variables heading of the current and week (Figure S8), as both variables seemed to describe seasonality in the response variable. We selected the variable week as a potential predictor variable over heading because of easier interpretation for predictions.

2.3.4. Model selection

Considering the correlation and multicollinearity of covariates, we considered ten GAM candidate models (Table 2). We applied a forward step-wise variable selection procedure to build the models, which consists of building the null model (intercept only model) and then adding one new covariate at a time to check its contribution to the model (Venables & Dichmont, 2004). Covariate contributions were evaluated using model Akaike Information Criterion (AIC) and studying their significance (based on p-value). We only included significant covariates ($p < 0.05$) and those with large relative contributions to AIC ($\Delta AIC < 2$) in each step of the selection procedure. At the end, the best fit model was selected as the final model according to the lowest AIC value and the highest explained deviance (Akaike, 1974). We assessed the relative contribution of each predictor variable on the oceanic whitetip shark occurrence using partial effect plots. These plots show the effect of each predictor variable on the dependent variable (presence/absence of oceanic whitetip shark) after accounting for the average effect of all other variables in the model. Therefore, they provide an indication of how the presence/absence of oceanic whitetip shark depends on each predictor variable (Wood, 2006).

Table 2. Explored GAMs candidates with corresponded Akaike Information Criteria (AIC) and explained deviance (Dev. %) values and the variables selected for each model. *($p > 0.05$)

GAM	AIC	Dev. %	Variables
1	8875.680	9.15 %	Latitude x Longitude + SST + Year + Set type + Total catch + NO_3 + Chlfronts* + Ke* + Week
2	8903.221	8.74 %	Latitude x Longitude + Year + O_2 + Set type + Total catch + Ke* + Chlfronts* + NO_3*
3	8910.903	8.64 %	Latitude x Longitude + Year + NPPV + Set type + Total catch + Chlfronts*
4	8894.324	8.81 %	Latitude x Longitude + SST + s(Year) + Set type + Total catch + NO_3 + Chlfronts* + Ke*
5	8934.434	8.35 %	Latitude x Longitude + O_2 + s(Year) + Set type + Total catch + Chlfronts* + NO_3 + MLD
6	8939.333	8.23 %	Latitude x Longitude + NPPV + s(Year) + Set type + Total catch + Chlfronts*
7	8911.081	8.62 %	Latitude x Longitude + SST + Set type + NO_3 + Total catch + Chlfronts* + Salinity + Ke*
8	**8872.840**	**9.25 %**	Latitude x Longitude + SST + Year + Set type + Total catch + NO_3 + Chlfronts* + Sal* + Ke* + Week
9	8887.988	8.96 %	Latitude x Longitude + SST + Year + Set type + Total catch + Week + Salinity* + Chlfronts*
10	8978.062	8.18 %	SST x Latitude + Week + Set type + Year + Total catch + Salinity + Chlfronts* + SSH + MLD + NO_3

2.3.5. Model validation

We validated the final model using a cross-validation procedure (Elith & Leathwick, 2009). The dataset was randomly split into two sets: a training dataset to calibrate the model, and a testing dataset to evaluate the predictions. A k-fold cross-validation (k = 5) method was applied to split the training (80%) and testing (20%) data (Elith & Leathwick, 2009) using the *kfold* function from the *dismo* package in R software (Hijmans, Phillips, Leathwick, & Elith, 2020). Model performance was evaluated by computing a confusion matrix of the predicted and observed values using the *PresenceAbsence* R package (Freeman & Freeman, 2012). From the confusion matrix, we calculated the Area Under the receiver operating Curve (AUC), sensitivity (proportion of presences correctly predicted), specificity (proportion of absences correctly predicted), and the mean True Skill Statistic (TSS) validation indices (Pearson, 2010). The AUC is a threshold independent index that ranges from 0 to 1, and measures the ability of the model to correctly predict species presence or absence (Elith et al., 2006). An AUC value of 0.5 indicates that the prediction is as good as random, whereas 1 indicates perfect prediction (Fielding & Bell, 1997). Sensitivity measures the efficiency of the algorithm in correctly classifying positive cases, and specificity measures the efficiency of the algorithm in correctly classifying negative cases. The TSS index, which is calculated as sensitivity plus specificity minus 1, ranges from -1 to +1, where 0 indicates no predictive skill, +1 indicates perfect agreement, and values of zero or less indicate a performance no better than random (Brodie et al., 2015). The sensitivity, specificity and TSS indices are threshold dependent and thus, for these indices a selection of a threshold is necessary to transform the probabilities into binary predictions (presence or absence) (Jiménez-Valverde & Lobo, 2007). Different methods can be use in order to select this threshold probability value (Pearson, 2010). We used the Maximized Sum Threshold (MST) method to establish the threshold for the accuracy indices (Jiménez-Valverde & Lobo, 2007; Liu, Berry, Dawson, & Pearson, 2005). The MST method was selected because the low prevalence (number of presences) of the dataset, and because the MST method gives the most accurate predictions with low prevalence data while avoiding omission (false negative) errors. We repeated this procedure 5 times following the 5-fold cross-validation, and the performance scores' obtained were averaged over the different random sets to evaluate the predictive performance of the distribution model (Pearson et al., 2006).

2.3.6. Model habitat suitability predictions

We used the final model to predict the suitable habitat and distribution of oceanic whitetip shark, using the *predict.gam* function of the *mgcv* package (Wood, 2014). We obtained the environmental conditions of sea surface temperature and nitrate (the selected variables in the final model) present in each time period (each week x 11 years [2010-2020]) with the spatial resolution of 1º latitude x 1º longitude grid cell to predict the probability of oceanic whitetip shark occurrence, while the predictor variable of total catch was set to mean levels for each 1º x 1º grid cell. Then, we averaged the predicted probabilities (and the standard deviation calculated) to obtain an overall probability suitability habitat map (considering 11 years of weakly averages) and seasonal suitability habitat maps (for each monsoon regime: winter monsoon, spring intermonsoon, summer monsoon, and autumn intermonsoon). To assess temporal changes, we also estimated yearly predictions of suitable habitat for oceanic whitetip shark. On the one hand, we allowed to vary the year effect in the predictions to examine for potential interannual changes in shark abundance (using the year effect as a proxy of shark abundance). On the other hand, we fixed the year effect using the year 2010 as the baseline in the predictions to examine for interannual environmental changes. The ranges for the environmental variables in the environmental prediction dataset extended only 0.7% beyond the ranges observed in the environmental variables recorded in the observed sets.

3. Results

3.1. Spatial patterns of observed sets and occurrence of oceanic whitetip shark

The EU purse seine fishery responds to the high seasonal variability in the western Indian Ocean (Figure 1). During the winter monsoon (December - March), the fishery spreads around the equatorial region (southeast Seychelles and Chagos region) (Figure 1A). In spring intermonsoon, from March to May, the fleet fishes mainly in the Mozambique Channel and northwest Seychelles region using both fishing techniques (Figure 1B) (Marsac, 2017). From June to September, the fleet operates predominantly using FADs in the northwest Indian Ocean to the east of Somalia where a coastal upwelling takes place (Figure 1C) (Marsac, 2017). In November, as primary productivity levels fall and the catch rate on FADs decreases, the fleet moves into the equatorial Indian Ocean behind free-swimming schools of tunas (Figure 1D). At this time of the year, schools of yellowfin and bigeye tunas are spawning near the surface and thus are easier to find and catch with a lower need of FADs (Marsac, 2017). Hence, three main fishing grounds are identified in this area (Figure 1): the Somali basin, the equatorial region (southeast Seychelles and Chagos region) and the Mozambique Channel (Marsac, 2017). The fishery operates during all year around through these areas. However, in the last six years, the highest number of observed total sets per month was recorded during winter monsoon (Figure 2A).

For the total of 26,523 observed sets, oceanic whitetip shark was present in 4.5% of the observed sets. The occurrence of this shark was recorded throughout the year (Figure 1). Differences between monsoon regimes were apparent. During the winter monsoon, the occurrences of this shark are spread in almost all the area, from Mozambique Channel to Somali basin and equatorial region (Figure 1A). During spring intermonsoon, the recorded occurrences are also spread through the area but significantly lower than during the rest of the monsoon regimes (Figure 1B). During the summer monsoon and autumn intermonsoon the recorded occurrences are mainly concentrated in the Somali basin (Figure 1C & D). The highest number of occurrences of oceanic whitetip shark was recorded during summer monsoon months (Figure 2B). Moreover, of the sets where oceanic whitetip shark was present, the 93.7% used FAD for the fishing operation (presences in FAD by regimes: 84% winter, 82.3% spring, 88.7% summer and 95% autumn).

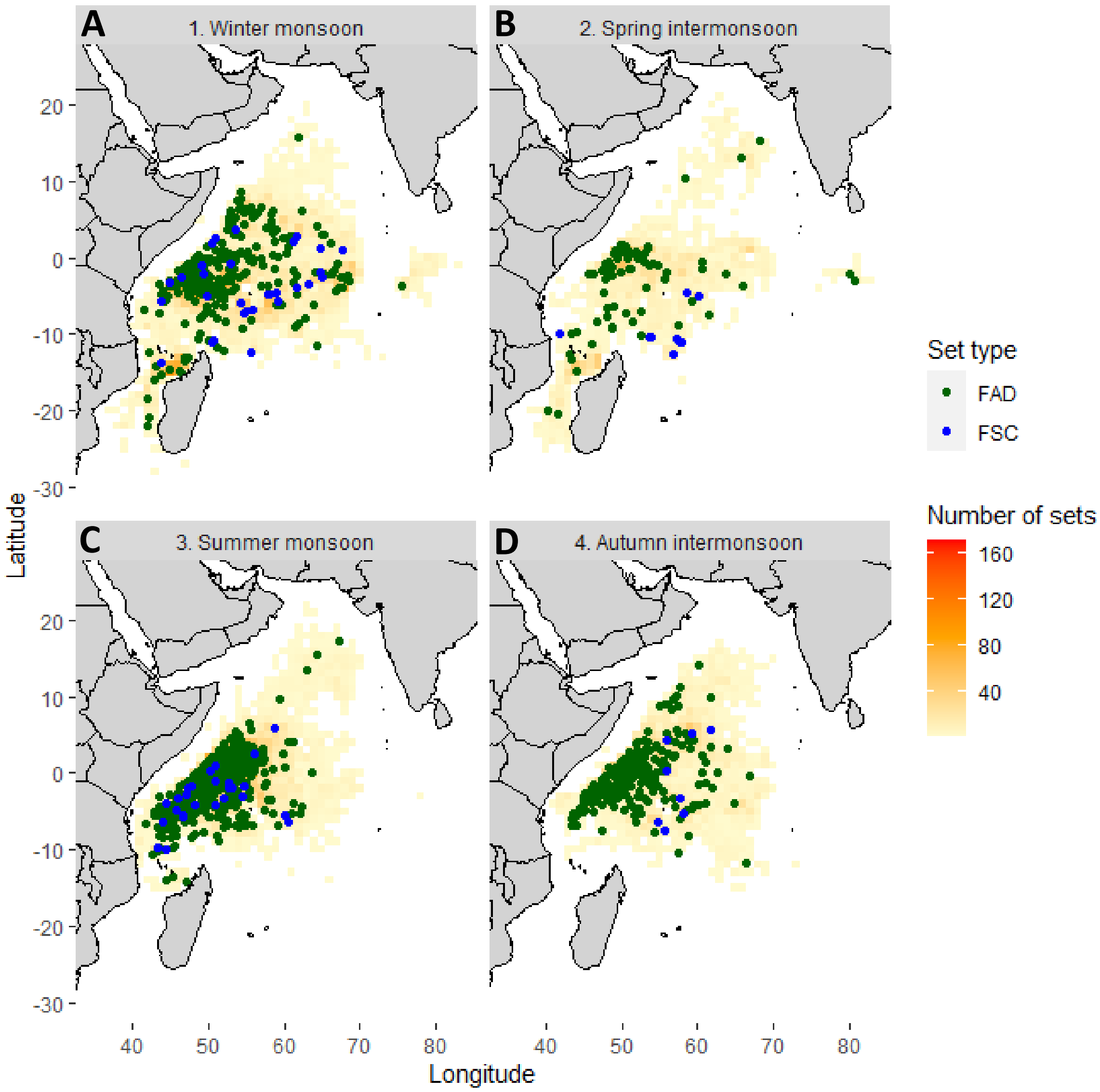

Figure 1. Spatial distribution of cumulative effort (observed sets) in the EU purse seine fishery from 2010-2020 by monsoon regimes (A: Winter monsoon, B: Spring intermonsoon, C: Summer monsoon and D: Autumn intermonsoon) and observed presences of oceanic whitetip shark (OCS) by set type (FAD or FSC). Check Figure S1 for a better appreciation of the cumulative effort.

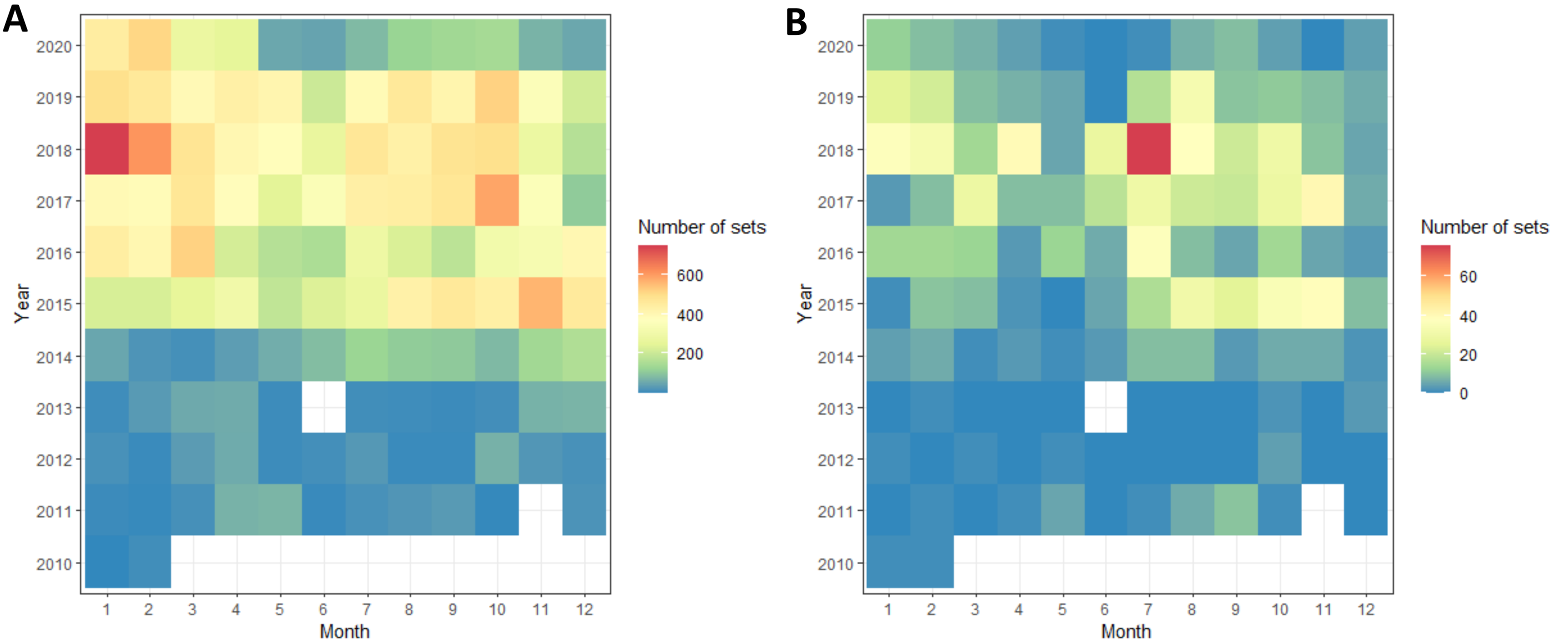

Figure 2. Temporal patterns of the EU purse seine fishing activity and the occurrence of oceanic whitetip shark recorded in the observer program. (A) Total number of observed sets in the fishery represented by years (2010-2020) on the y-axis and months (1-12) on the x-axis. (B) Total number of sets with presence of oceanic whitetip shark represented by years (2010-2020) and months (1-12).

3.2. Habitat suitability model

The final occurrence model explained 8.96% of the total deviance (the most parsimonious model based on the lowest AIC value, Table 2) and an adjusted r^2 of 0.043 (Table 3). The final model included (1) the environmental variables (sea surface temperature and nitrate), (2) the spatial variables (latitude-longitude interaction), (3) the temporal variables (year and week) and (4) fishery variables (type of fishing set and total catch) as predictor variables (Table S2).

Considering each of the predictor variables individually, the individual contribution of each variable to the model revealed the interaction between latitude and longitude (5.30%), sea surface temperature (3.55%) and nitrate (1.39%) were the most significant variables (Table S3).

We found a significant interaction between latitude and longitude highlighting the area off the coast of Kenya-Somalia as the main area with a higher oceanic whitetip shark probability of occurrence (Figure 3).

Table 3. Summary results for the parametric coefficients and smooth terms of the final GAM selected to model the occurrence of oceanic whitetip shark in the western Indian Ocean (2010-2020). Estimated degrees of freedom (e.d.f.).

Family	**Binomial**
Link function	Logit
Adjusted r^2	0.043
Deviance explained	8.96 %

Parametric coefficients

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept - 2010	-1.9269	0.7889	-2.443	0.0146
2011	-0.4082	0.8235	-0.496	0.6201
2012	-1.9723	0.8809	-2.239	0.0252
2013	-1.7935	0.8920	-2.011	0.0444
2014	-1.4074	0.8036	-1.752	0.0799
2015	-1.3963	0.7930	-1.761	0.0783
2016	-1.5965	0.7946	-2.009	0.0445
2017	-1.3446	0.7924	-1.697	0.0897
2018	-1.0706	0.7907	-1.354	0.1758
2019	-1.6768	0.7933	-2.114	0.0345
2020	-1.6228	0.7983	-2.033	0.0421
Set type (FSC)	-0.6712	0.1296	-5.179	< 0.001

Smooth terms

	e.d.f	**Ref. df**	**Chi.sq**	**p-value**
Latitude x Longitude	17.234	18.666	306.336	< 0.001
Sea surface temperature	1.405	1.716	91.136	< 0.001
Total catch	4.028	4.594	30.181	< 0.001
Nitrate	2.990	3.638	15.236	0.00383
Week	3.511	4.000	9.268	0.03069

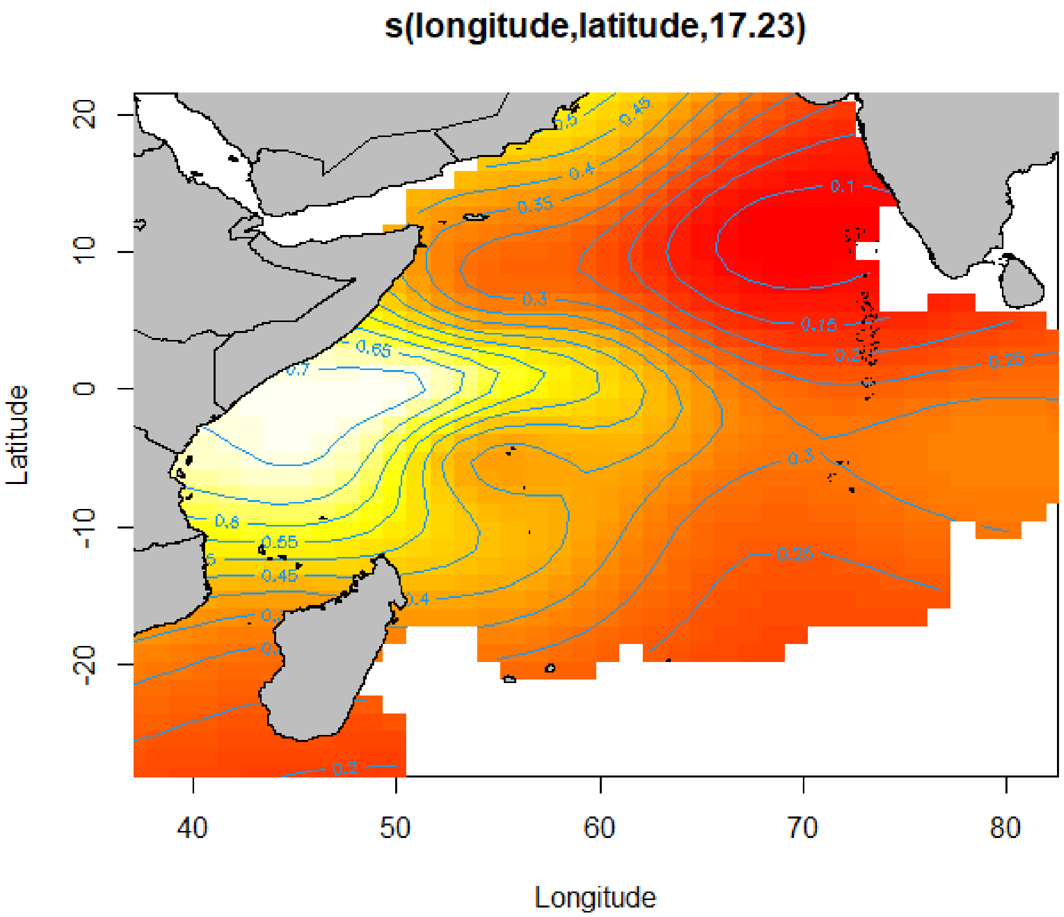

Figure 3. Latitude and longitude interaction effect on the probability of occurrence of the oceanic whitetip shark. Isoclines indicate probability of occurrence.

We also found an increase in the probability of occurrence with decreasing temperatures, with higher probabilities in areas with lower sea surface temperature (SST) (< 24ºC) relative to the range encountered by the fishery (24-32 ºC, Figure 4A). Higher probabilities of occurrence were also predicted in areas with low values of nitrate (NO_3) close to zero and intermediate values of nitrate (1.5-2.5 mmol.m-3), relative to the range encountered by the fishery (0-3.77 mmol.m-3, Figure 4B). There is also a relationship between the oceanic whitetip shark occurrence and the total catch in the set, with higher probabilities observed in sets with total catch of 270 tonnes relative to the rage of total catches in sets observed in the fishery (0.001-519.93 tonnes, Figure 4C). The time of the year also had a strong influence on the species' occurrence, with higher probabilities peaking around week 15 (April) and later on week 43 (October) (Figure 4D).

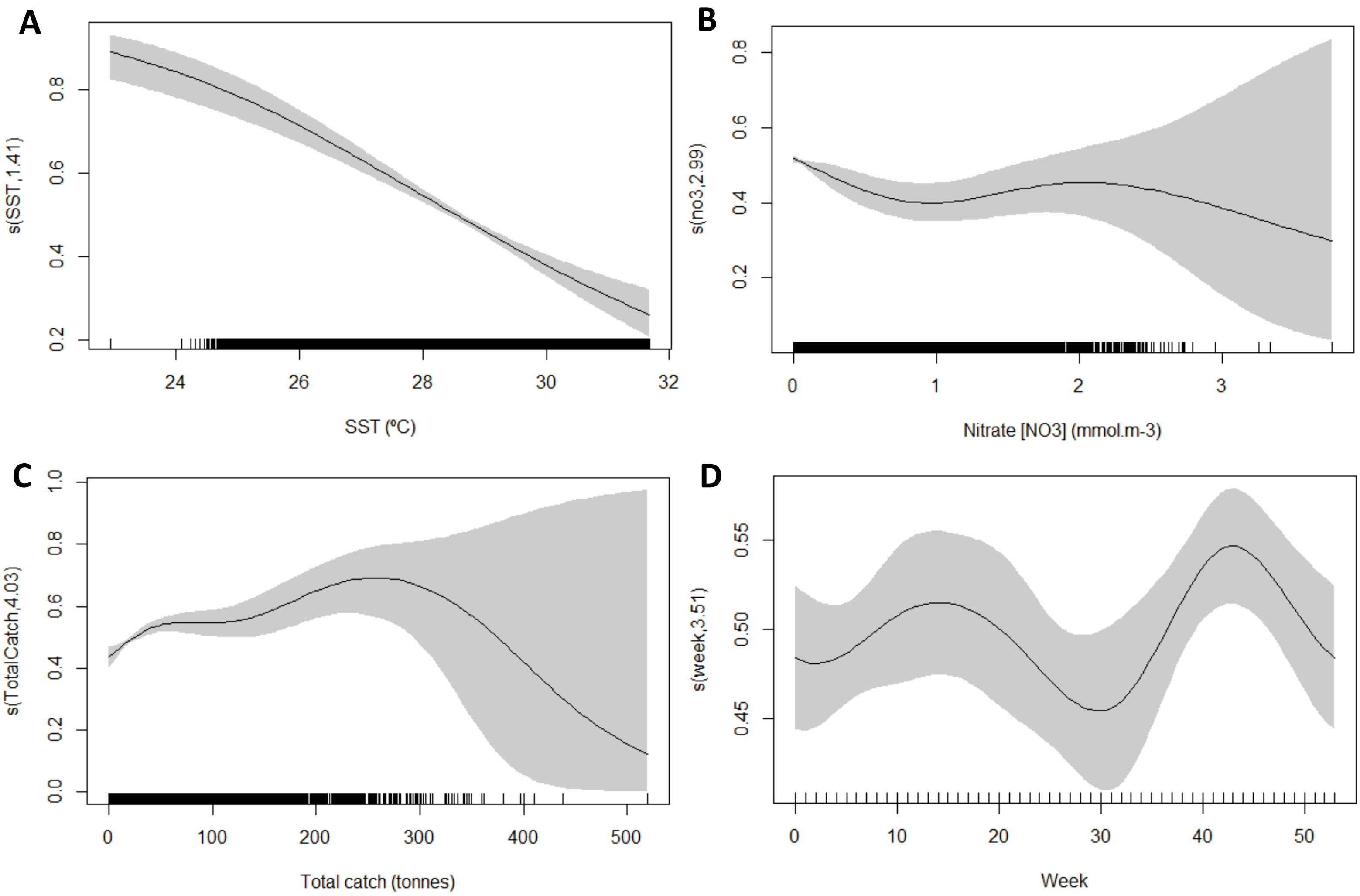

Figure 4. Smooth terms effect on the probability of occurrence of the oceanic whitetip shark. (A) Sea surface temperature (SST) (ºC), (B) nitrate (mmol.m-3), (C) total catch (tonnes) and (D) week.

Categorical variables (year and set type) also helped to explain the shark occurrence (Figure 5). Higher probabilities of occurrence were predicted at the beginning of the study period (year 2010 and 2011), followed by a decrease in 2012 and stabilization for the rest of the study period (Figure 5A). Finally, the type of purse seine fishery operation (set type) also affected the probability of occurrence of oceanic whitetip sharks, suggesting higher probabilities of oceanic whitetip shark occurrence when purse seine fishing operations were made with FADs (Figure 5B).

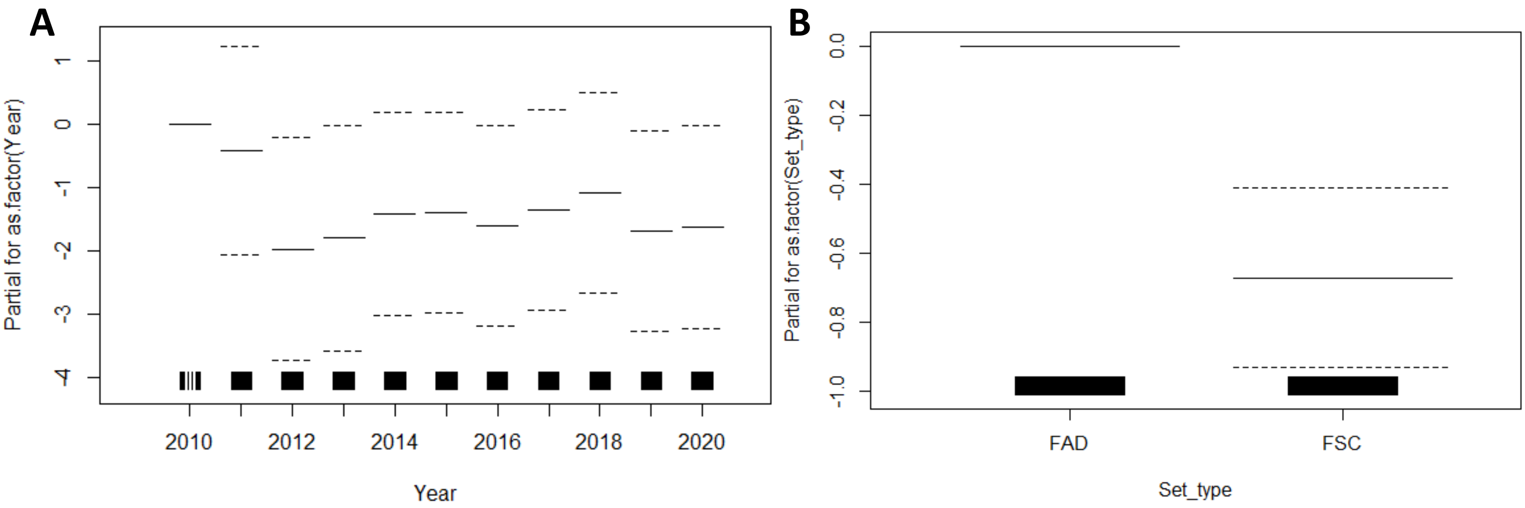

Figure 5. Fixed effect terms effect on the probability of occurrence of the oceanic whitetip shark. (A) Year, and (B) Set type (FAD or FSC).

3.3. Model performance

The accuracy indices to evaluate the model performance showed low to moderate accuracy values (AUC: 0.72, Sensitivity: 0.65, Specificity: 0.71, TSS: 0.36, Table 4) suggesting a fair model accuracy. Despite the low prevalence of the species in the total observed sets, the model was able to predict oceanic whitetip shark presence - absence and identify the areas with the higher probabilities of occurrence for the species. Yet the modest values of the accuracy indices implies that the model might also over and under predict the observed cases.

Table 4. Accuracy indices to evaluate the predictive performance of the model: Area Under the receiver operating Curve (AUC), Sensitivity, Specificity and True Skill Statistic (TSS).

Interaction	AUC	Sensitivity	Specificity	TSS
1	0.71	0.59	0.76	0.35
2	0.73	0.67	0.69	0.36
3	0.74	0.69	0.69	0.38
4	0.71	0.65	0.70	0.35
5	0.72	0.67	0.70	0.37
Mean	0.72	0.65	0.71	0.36

3.4. Habitat suitability predictions

Predictions of oceanic whitetip shark's probability of occurrence highlighted the area offshore of Kenya-Somalia with the higher probability of oceanic whitetip shark occurrence (Figure 6 & S9). The higher probability of occurrence also occurred in sets around FADs (Figure 6 & S9) in the areas where there is higher density of FADs (Figure 1).

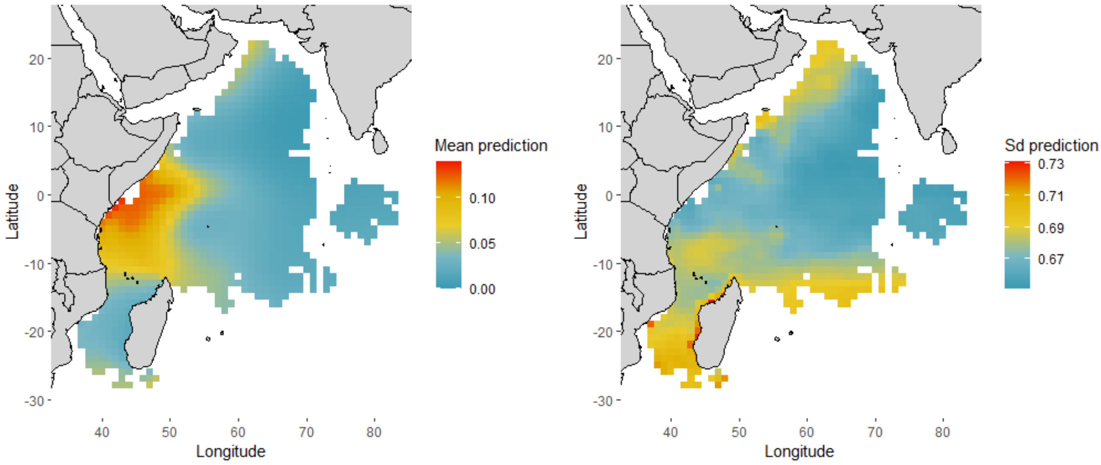

Figure 6. Mean prediction and standard deviation (Sd) of the probability of occurrence of oceanic whitetip shark bycatch from the tropical tuna purse seine fishery (2010-2020) per set in the western Indian Ocean, using FAD fishing technique as a baseline.

Predictions of oceanic whitetip shark probability of occurrence for each monsoon period indicated that the occurrence probability of oceanic whitetip shark varies seasonally (Figure 7 & S10). In all four regimes, the main area with higher probability of occurrence is concentrated in the Kenya-Somali basin (Figure 7 & S10). However, during the winter monsoon (December - March) the habitat suitability of the species around Oman shore was also predicted. During the summer monsoon (June - September), the probability of occurrence of this species was found to be the highest and in a wider area, spreading down until the Mozambique Channel (Figure 7 & S10).

The yearly prediction maps allowing the year effect to vary in combination with the environmental predictors showed the highest probability of occurrence in the Kenya-Somali basin at the beginning of the study period (year 2010 and 2011) and intermediate probability of occurrence in the year 2018 relative to the rest of the years (Figure 8A & S11A). When only the environmental predictor variables were allowed to vary and the year 2010 was used as the baseline year, the yearly prediction maps showed high consistency in the higher habitat suitability of this species for Kenya-Somali basin, yet some interannual variability in the habitat suitability was also observed (Figure 8B & S11B). The predicted habitat suitability around the Kenya-Somali basin in the year 2015, 2019 and 2020 appear to be lower relative to the other years driven by the warmer sea surface temperature reached (Figure 8B & S11B).

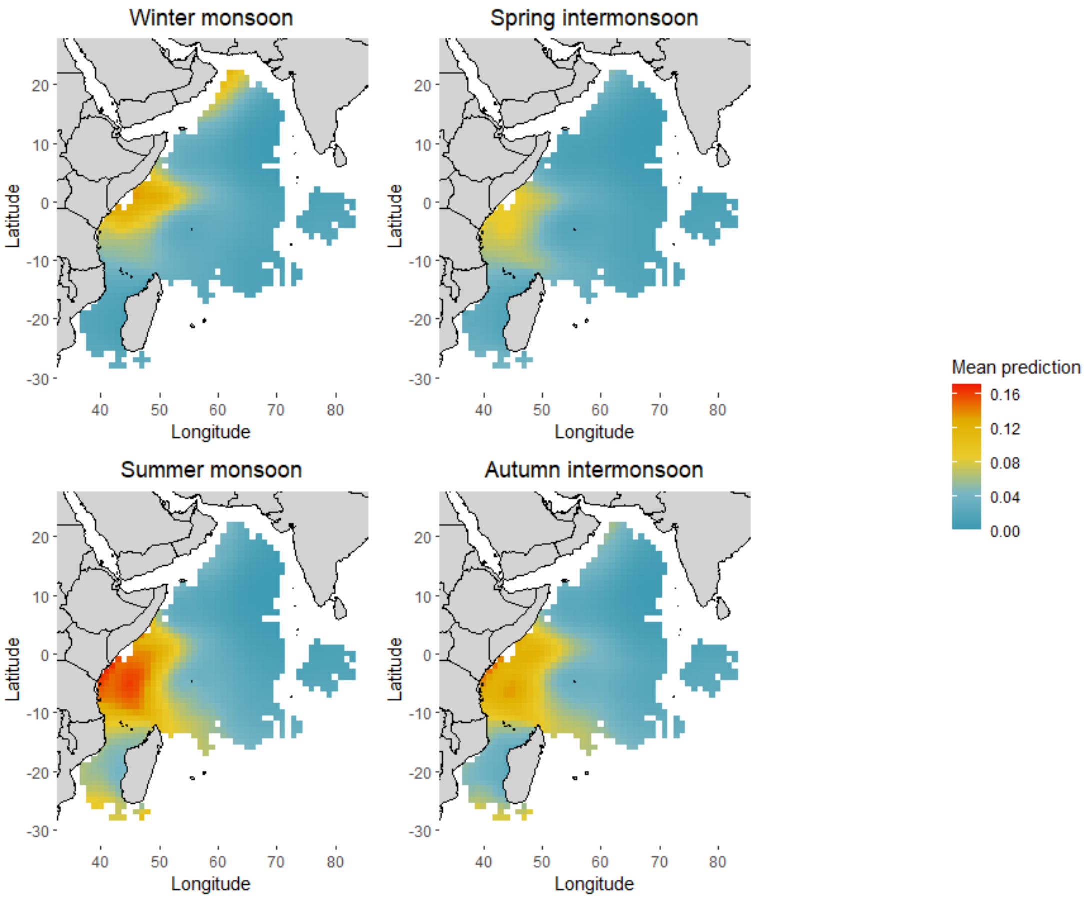

Figure 7. Mean prediction by monsoon regime (Winter: December-March; Spring: April-May; Summer: June-September; Autumn: October-November) of the presence of oceanic whitetip shark in the western Indian Ocean based on the FAD fishing technique.

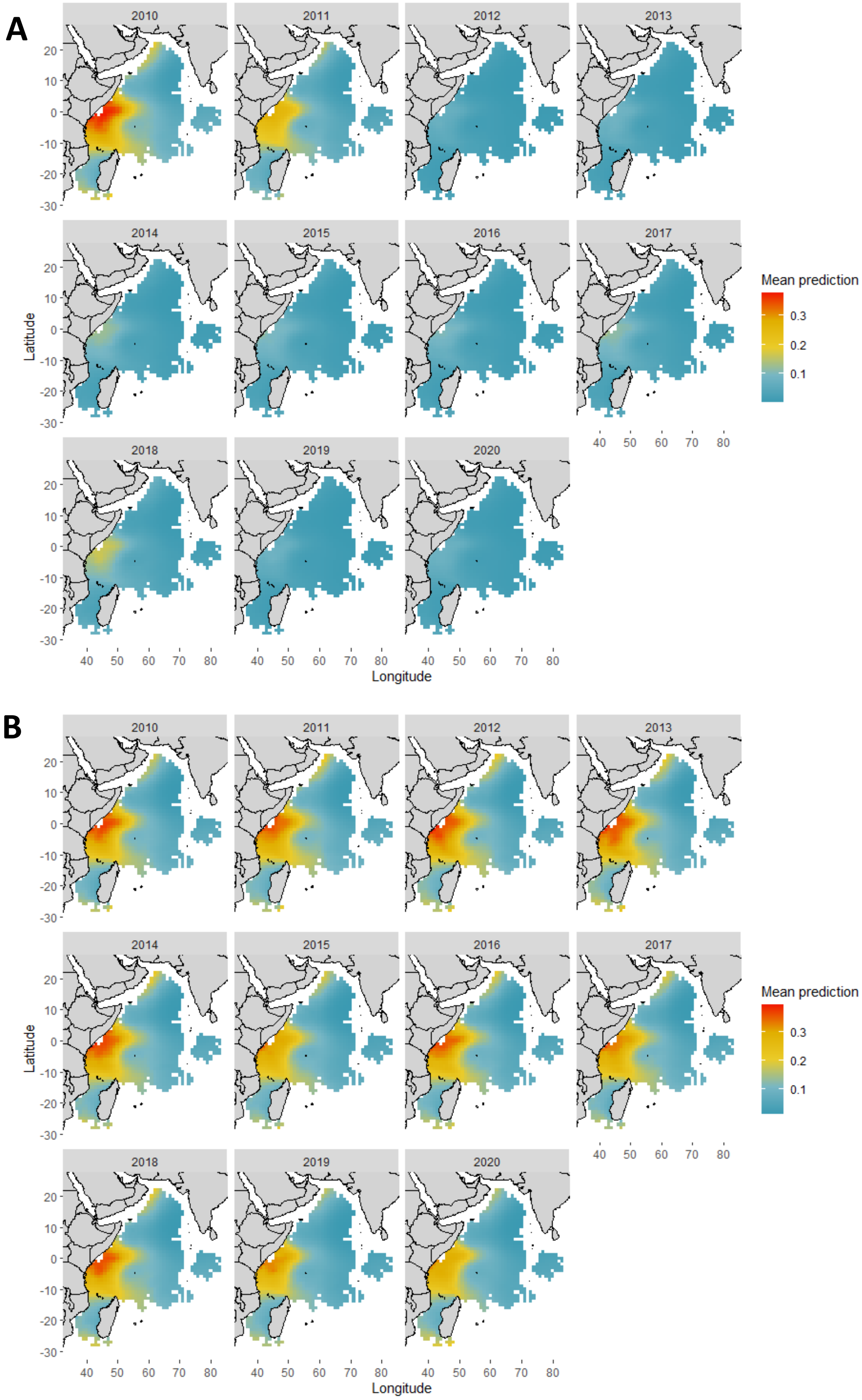

Figure 8. Mean prediction by years of the presence of oceanic whitetip shark in the western Indian Ocean based on the FAD fishing technique, (A) year effect included, (B) taking 2010 year as baseline.

4. Discussion

In this study we developed a habitat suitability model for juvenile oceanic whitetip shark in the western Indian Ocean using the EU purse seine fishery observer data. Different environmental, geographical, temporal and fishery dependent variables were selected to describe the habitat suitability of the oceanic whitetip shark in the study area. We found that sea surface temperature was the main environmental driver explaining the probability of occurrence of this shark, followed by nitrate concentration. The type of set used in the fishing operation also explained the probability of occurrence of the oceanic whitetip shark, with a higher probability of occurrence in FAD as set type. Moreover, the area offshore of Kenya-Somalia was observed as an important hotspot during the summer monsoon (June to September) with higher probabilities of occurrence for this pelagic species.

4.1. Predictor variables influencing the occurrence of oceanic whitetip shark

Sea surface temperature was the most important environmental predictor explaining the occurrences of the oceanic whitetip shark. We found a strong linear increase in the probability of oceanic whitetip shark occurrence with decreasing sea surface temperature. Due to the restricted range in sea surface temperature encountered by the fishery in the study area (24-32ºC), the model was not able to find a limited range of preferences and unimodal distribution of preferred temperatures as expected. However, our results are consistent with existing tagging studies that found out that the thermal range of preference of this shark is between 20-28ºC (Andrzejaczek et al., 2018; Musyl et al., 2011; Tolotti et al., 2017). Other studies in the Indian Ocean have also found out that sea surface temperature was the main environmental predictor explaining the distribution of top predators such as albacore (Chen, Lee, & Tzeng, 2005), bigeye (Lee, Chen, & Tzeng, 2005), yellowfin and skipjack tuna (Arrizabalaga et al., 2015).

The contribution of nitrate concentration to the model was minimal in comparison with the other selected variables. We expected to find increasing probabilities of occurrence of oceanic whitetip shark with increasing concentrations of nitrate, as nitrate is a limiting factor for phytoplankton growth (Dugdale, 1967) and thus, it can be considered as an indicative of primary production, which may attract top predatory species for feeding (J. Young et al., 2015). Instead, we found higher probabilities of occurrence in areas with low values of nitrate (close to zero) and intermediate values of nitrate. However, in practice the relationship between nitrate and the distribution of top predators might be hard to interpret as there might not be a direct link between them since they control different processes in the two extremes of the trophic chain. Moreover, the range of nitrate values found in our study area (0-3.77 mmol.m-3) was very low compared to other research studies modelling other migratory species, the spinetail devil ray (*Mobula mobular*) distributions in upwelling areas in the eastern Pacific Ocean where the nitrate concentrations were around 145.16 mmol.m-3 (Lezama-Ochoa et al., 2019). The oceanic regions in Indian Ocean are characterized by low concentrations of nitrate, in comparison to other oceanic regions in the Atlantic and Pacific Oceans (Pennington et al., 2006). These low concentrations might also make difficult the interpretation of the effect of nitrate in the oceanic whitetip shark probability of occurrence.

The spatial component selected in the final model as an interaction of latitude and longitude also significantly explained the occurrences of the oceanic whitetip shark. The model predicted a higher probability of occurrence offshore Kenya-Somalia coast suggesting this may be a hotspot area for these species with higher probability of catching oceanic whitetip shark in this area. Considering that most of the presences of oceanic whitetip shark through all the study area were juveniles (Figure S5), we can rule out that these upwelling areas may be used as reproductive areas for this species. Nevertheless, the seasonality of this hotspot can be associated to the upwelling seasonality in Kenya-Somali basin (Schott & McCreary, 2001). During the summer monsoon regime, when the upwelling takes place, sea surface temperature values decrease in Kenya-Somalia basin, and nitrate concentrations increase making this area potentially more suitable for oceanic whitetip shark. Other studies also found this area highly suitable for pelagic species such as silky sharks (Lezama-Ochoa et al., 2016) and skipjack tuna (Druon, Chassot, Murua, & Lopez, 2017).

We also found higher probabilities of occurrence when sets were made associated to FADs than when made associated to free schools of tunas. The probability of occurrence was observed to be higher in the area and time of the year with higher densities of FADs (Figure 1C) (Davies, Mees, & Milner-Gulland, 2014). Therefore, the high densities of FADs concentrated offshore the Kenya-Somalia coast might also be playing an important role when explaining the high probability of occurrence in Kenya-Somalia basin. However, we did not model explicitly for the spatial density of FADs as this type of information was not readily available to be taken into account the models. We hypothesize that FADs density might also be a factor determining the distribution of juvenile oceanic whitetip shark, as they may be acting as an ecological trap for these species (Dagorn et al., 2013). This hypothesis contends that deploying FADs in unnaturally large numbers could either entrain pelagic species in locations that they might normally leave or, conversely, take them to places to which they would not normally go (Hallier & Gaertner, 2008; Marsac, Fonteneau, & Ménard, 2000). In order to test this, future studies could consider the spatial density of FADs as an additional predictor variable in the model.

The temporal variable of week also was an important predictor of oceanic whitetip shark occurrence in the western Indian Ocean. A weekly temporal trend was observed peaking in week 15 (April) corresponding to spring intermonsoon and later in week 43 (October), right after summer monsoon. Seasonal changes in the probability of occurrence of oceanic whitetip shark can also be observed in the habitat suitability prediction maps by monsoon regimes. We found the highest probability of occurrence during the summer monsoon regime when the upwelling occurs (decreasing sea surface temperature and increasing nitrate concentration) and productivity increases attracting from small fishes to top predators. In line with this, past work suggest this area to be a feeding area for migratory species such as skipjack tuna (Druon et al., 2017), and blue whales (Charles, Branch, Alagiyawadu, Baldwin, & Marsac, 2012) during the summer monsoon.

Year modelled as fixed effect also explained the probability of occurrence of oceanic whitetip shark. Higher probabilities of occurrence were detected at the beginning of the study period (year 2010 and 2011), followed by a decrease in 2012 and stabilization for the rest of the study period. If the year effect is interpreted as an index of abundance, the results could be suggesting a decline and then a stabilization of the abundance of this species. This explanation cannot be completely rule out as over the past 20 years a substantial decline of oceanic whitetip shark has been reported in the Indian Ocean (IOTC, 2015). This can be the result of the increasing susceptibility to different fishing gears in the Indian Ocean and sensitive life history traits (low fecundity, slow-moderate growth rate, and late sexual maturity), making this shark species to be highly vulnerable to fisheries (C. N. Young & Carlson, 2020). Among all IOTC fisheries interacting with this species, the EU purse seine fishery might be an important contributor to observed declines, as the majority of the oceanic whitetip shark individuals incidentally caught are juveniles, and it is known that high juvenile mortality has a significant impact on population growth and status (Hutchinson, Itano, Muir, & Holland, 2015)

The probability of occurrence in oceanic whitetip shark also varied spatially among years. The habitat model tracked temporal changes in response to changes in sea surface temperature and nitrate when the year was fixed. For the years 2015, 2019 and 2020 the prediction maps show the habitat suitability contracts driven by the higher sea surface temperature values observed during these years. In 2015 and 2019, a positive Indian Ocean Dipole (IOD) event was registered (Shi & Wang, 2021; Zhang, Du, & Cai, 2018). This ocean-atmosphere phenomenon resulted in a higher sea surface temperature in the western side of the Indian Ocean as well as a less intense Somali upwelling that resulted in a reduced nitrate concentrations and thus of primary production in the western Indian Ocean (Yang et al., 2020). Therefore, these interannual climatic processes might be affecting the habitat suitability of this species. Considering the sea surface temperature effects on the habitat suitability of the oceanic whitetip shark and that climate change is increasing the positive IOD events (Cai, Sullivan, & Cowan, 2009), studying the effect of multiple climate change scenarios is necessary for this critically endangered species. As studied in other shark species, a considerable increase in sea surface temperature induced by climate change, could drive migrations of the sharks to southern waters (Lezama-Ochoa et al., 2016; Sequeira, Mellin, Fordham, Meekan, & Bradshaw, 2014) or produce vertical migrations to deeper waters (Andrzejaczek et al., 2018; Dulvy et al., 2008; Tolotti et al., 2017) resulting in a contraction of the habitat suitability in the study area.

Previous work investigating the relationships between ratio of bycatch to target catch across different set size classes in tuna purse seine fisheries, found bycatch ratios to be always highest when catches were small (Dagorn et al., 2012). These findings lead to the recommendations for tuna purse seine fisheries for targeting bigger schools, as the fishery improves its efficiency both through reductions in the ratio of bycatch to catch, as well as through an increase in the average set size (Dagorn et al., 2012). This is in line with our results as the model suggested a small increase in the probability of oceanic whitetip shark occurrence as the total catch in the set increases (Figure 4C).

4.2. Limitations of the study

The major limitation of this study is the use of fisheries-dependent data to describe the habitat suitability of this species because incidental catch probabilities are biased by the fishery behavior and limited to the fishing ground (Montero et al., 2016; Pennino et al., 2016). However, even if fishing fleets are commercially driven and are not operating randomly, the advantage of using fishery-dependent data for bycatch species is that fishing locations are not completely biased for these species as fishing behavior depends on target species (Pennino et al., 2016).

The habitat suitability model for oceanic whitetip shark explained a small proportion of total deviance (9%), and therefore results from this study should be taken with precaution. This low explained deviance is common when modeling bycatch species (Lezama-Ochoa et al., 2020; Lopez et al., 2017). Contrary to target species, that usually explain a higher percentage of total deviance than bycatch species in species distribution models (Erauskin-Extramiana et al., 2019; Su et al., 2011), probably due to a much higher prevalence of these species. Nevertheless, the habitat suitability model presented here for oceanic whitetip shark can still be useful as they provide new information about the preferential habitat of this data-poor bycatch species. Furthermore, based on the different calculated statistics indices (AUC, Sensitivity, Specificity and TSS), the model performance can still be considered good based on the available data and the previous knowledge about this species in the studied area, which can be confirmed and improved.

As mentioned before, future habitat suitability studies for oceanic whitetip shark could consider including the spatial density of FADs as a potential predictor variable, as the model was able to predict high oceanic whitetip shark occurrences along the Kenya-Somali basin where coincidentally greater densities of FADs are found. To account for previously mentioned potential biases in the fishery-dependent data source, future studies could also attempt to include additional data sources for modelling habitat suitability such as acoustic or satellite tag data or fisheries-independent surveys for model validation. Further tagging studies could also help to understand the habitat utilization of this shark species at three dimensions, as well as migrations and vertical movements. We used GAMs to model presence of oceanic whitetip shark, yet future studies could also model instead or in addition the abundance of oceanic whitetip sharks. Other techniques used in developing species distribution models, such as Bayesian Approaches and Random Forests, could also be applied in future studies to model presence and the abundance of the species.

4.3. Management implications

The habitat suitability model developed here could be used to inform analyses of time-area closures to mitigate the impacts of purse seine fisheries on juveniles of oceanic whitetip shark, as well as other fisheries also interacting with this species and contributing to the fishing mortality of oceanic whitetip shark. Based on the results of this study, a range of time-area closures could be explored for the area off the coast of Kenya-Somalia during the summer monsoon (June to September) to avoid the bycatch of this critically endangered species with the least possible impact on fishing operations. A time-area closure could also benefit tropical tuna stocks fished in the western Indian Ocean, as a meaningful amount of juveniles are also caught in this area in this time of the year by tuna purse seiners (Kaplan et al., 2014).

Long distance migrations (up to 6,500 Km) have been recorded by tagging studies in oceanic whitetip sharks in the Indian and central Pacific Oceans (Filmalter et al., 2012; Musyl et al., 2011). Understanding movement and connectivity of populations of highly mobile species is increasingly important in order to implement effective management measures (Heupel et al., 2015; Kaplan et al., 2014). Despite the growing number of tagging studies focusing on oceanic whitetip shark movements (Andrzejaczek et al., 2018; Filmalter et al., 2012; Howey-Jordan et al., 2013; Howey et al., 2016; Mejuto, García-Cortés, & Ramos-Cartelle, 2005; Musyl et al., 2011; Tolotti et al., 2017), the migrations patterns of the oceanic whitetip shark in the western Indian Ocean are not well understood. Therefore, testing the utility and effectiveness of time-area closures, whether static or dynamic, to reduce bycatch needs to be supported with further research to understand the migrations patterns and movements of oceanic whitetip shark in the western Indian Ocean to effectively implement spatial management tools.

Climate change effects are forcing species redistributions. A study evaluating the climate change effects on the future distribution of silky shark in the western Indian Ocean has suggested a loss of habitat suitability near the Somali coast, while it gained areas located farther south (mostly around 12ºS) by 2100 as a response to temperature warning (Lezama-Ochoa et al., 2016). A slight shift of suitable whale sharks habitat towards the poles have also been predicted in the Indian Ocean in response to changes in sea surface temperature (Sequeira et al., 2014). Taking these examples into account and considering the potential effect of sea surface temperature in the distributions of oceanic whitetip shark, climate change scenarios and their impact on the distribution of this species should also be tested when designing the time-area closures as the habitat suitability of this species can be changed by the warming oceans.

5. Conclusion

This study improves the understanding of the environmental characteristics associated with the occurrence of oceanic whitetip shark in the tropical western Indian Ocean, based on EU purse-seine fishery observer data and GAMs. Sea surface temperature was the main environmental driver explaining the occurrence of this shark. The type of fishing operation also was an important predictor explaining the occurrence of the oceanic whitetip shark, showing the probability of incidentally catching a shark is higher when using FAD as set type. Moreover, predictive maps suggested the area offshore of Kenya-Somalia to be an important hotspot with higher probabilities of incidentally catching this species during the summer monsoon (June to September). Based on this, the habitat models developed here could be used to inform analyses of potential time-area closures in the area off the coast of Kenya-Somalia during the summer monsoon with the objective of minimizing bycatch of this critically endangered species with the least possible impact on fishing operations and fishery yields of target tunas. Furthermore, further research on oceanic whitetip shark migrations, the effect of density of FADs on the species distributions, and the impact of climate change is also recommended in order to support and improve the design of effective spatial management measures to minimize bycatch of this species in tuna fisheries.

6. References

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control, 19*(6), 716-723. doi: 10.1109/tac.1974.1100705

Amandè, M. J., Chassot, E., Chavance, P., Murua, H., de Molina, A. D., & Bez, N. (2012). Precision in bycatch estimates: the case of tuna purse-seine fisheries in the Indian Ocean. *ICES Journal of Marine Science, 69*(8), 1501-1510. doi: 10.1093/icesjms/fss106

Andrzejaczek, S., Gleiss, A. C., Jordan, L. K. B., Pattiaratchi, C. B., Howey, L. A., Brooks, E. J., & Meekan, M. G. (2018). Temperature and the vertical movements of oceanic whitetip sharks, Carcharhinus longimanus. *Sci Rep, 8*(1), 8351. doi: 10.1038/s41598-018-26485-3

Arrizabalaga, H., Dufour, F., Kell, L., Merino, G., Ibaibarriaga, L., Chust, G., . . . Bonhomeau, S. (2015). Global habitat preferences of commercially valuable tuna. *Deep Sea Research Part II: Topical Studies in Oceanography, 113*, 102-112. doi: https://doi.org/10.1016/j.dsr2.2014.07.001

Belkin, I. M., & O'Reilly, J. E. (2009). An algorithm for oceanic front detection in chlorophyll and SST satellite imagery. *Journal of Marine Systems, 78*(3), 319-326. doi: https://doi.org/10.1016/j.jmarsys.2008.11.018

Bonfil, R., Clarke, S., & Nakano, H. (2008). The Biology and Ecology of the Oceanic Whitetip Shark, Carcharhinus Longimanus *Sharks of the Open Ocean* (pp. 128-139).

Brodie, S., Hobday, A. J., Smith, J. A., Everett, J. D., Taylor, M. D., Gray, C. A., & Suthers, I. M. (2015). Modelling the oceanic habitats of two pelagic species using recreational fisheries data. *Fisheries oceanography, 24*(5), 463—477.

Cai, W., Sullivan, A., & Cowan, T. (2009). Climate change contributes to more frequent consecutive positive Indian Ocean Dipole events. *Geophysical Research Letters, 36*(23). doi: https://doi.org/10.1029/2009GL040163

Clarke, S., Sato, M., Small, C., Sullivan, B., Inoue, Y., & Ochi, D. (2014). Bycatch in longline fisheries for tuna and tuna-like species: A global review of status and mitigation measures. *FAO Fisheries and Aquaculture Technical Paper No. 588*.

Compagno, L. J. V. (1984). FAO Species Catalogue. Vol. 4. Sharks of the World: An Annotated and Illustrated Catalogue of Shark Species Known to Date. Parts 1 and 2 *FAO Fisheries Synopsis No. 125*(FAO, Rome, Italy, 655 pp).

Charles, A., Branch, T. A., Alagiyawadu, A., Baldwin, R., & Marsac, F. (2012). Seasonal distribution, movements and taxonomic status of blue whales (Balaenoptera musculus) in the northern Indian Ocean. *Journal of Cetacean Resources and Management, 12*(2), 203-218.

Chen, I.-C., Lee, P.-F., & Tzeng, W.-N. (2005). Distribution of albacore (Thunnus alalunga) in the Indian Ocean and its relation to environmental factors. *Fisheries Oceanography, 14*(1), 71-80. doi: https://doi.org/10.1111/j.1365-2419.2004.00322.x

Dagorn, L., Filmalter, J., Forget, F., Amandè, M., Hall, M., Williams, P., . . . Bez, N. (2012). Targeting bigger schools can reduce ecosystem impacts of fisheries. *Canadian Journal of Fisheries and Aquatic Sciences, 69*, 1463-1467. doi: 10.1139/f2012-089

Dagorn, L., Holland, K. N., Restrepo, V., & Moreno, G. (2013). 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, 14*(3), 391-415. doi: https://doi.org/10.1111/j.1467-2979.2012.00478.x

Davies, T. K., Mees, C. C., & Milner-Gulland, E. J. (2014). The past, present and future use of drifting fish aggregating devices (FADs) in the Indian Ocean. *Marine Policy, 45*, 163-170. doi: 10.1016/j.marpol.2013.12.014

Deakos, M. H., Baker, J. D., & Bejder, L. (2011). Characteristics of a manta ray Manta alfredi -population off Maui, Hawaii, and implications for management. *Marine Ecology Progress Series, 429*, 245-260.

Dewar, H., Wilson, S. G., Hyde, J. R., Snodgrass, O. E., Leising, A., Lam, C. H., . . . Kohin, S. (2018). Basking Shark (Cetorhinus maximus) Movements in the Eastern North Pacific Determined Using Satellite Telemetry. [Original Research]. *Frontiers in Marine Science, 5*(163). doi: 10.3389/fmars.2018.00163

Druon, J.-N., Chassot, E., Murua, H., & Lopez, J. (2017). Skipjack Tuna Availability for Purse Seine Fisheries Is Driven by Suitable Feeding Habitat Dynamics in the Atlantic and Indian Oceans. [Original Research]. *Frontiers in Marine Science, 4*(315). doi: 10.3389/fmars.2017.00315

Dugdale, R. C. (1967). Nutrient limitation in the sea: Dynamics, identification, and significance. *Limnology and Oceanography, 12(4)*, 685-695.

Dulvy, N. K., Rogers, S. I., Jennings, S., Stelzenmüller, V., Dye, S. R., & Skjoldal, H. R. (2008). Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology, 45*(4), 1029-1039. doi: https://doi.org/10.1111/j.1365-2664.2008.01488.x

Elith, J., Graham, C. H., Anderson, R. P., Dudík, M., Ferrier, S., Guisan, A., . . . Lehmann, A. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 129—151.

Elith, J., & Leathwick, J. (2009). Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution and Systematics, 40*, 677-697. doi: 10.1146/annurev.ecolsys.110308.120159

Erauskin-Extramiana, M., Arrizabalaga, H., Hobday, A. J., Cabré, A., Ibaibarriaga, L., Arregui, I., . . . Chust, G. (2019). Large-scale distribution of tuna species in a warming ocean. *Global Change Biology, 25*(6), 2043-2060. doi: https://doi.org/10.1111/gcb.14630

Escalle, L., Gaertner, D., Chavance, P., Delgado de Molina, A., Ariz, J., & Mérigot, B. (2016). Forecasted consequences of simulated FAD moratoria in the Atlantic and Indian Oceans on catches and bycatches. *ICES Journal of Marine Science, 74*(3), 780-792. doi: 10.1093/icesjms/fsw187

Ewell, C., Hocevar, J., Mitchell, E., Snowden, S., & Jacquet, J. (2020). An evaluation of Regional Fisheries Management Organization at-sea compliance monitoring and observer programs. *Marine Policy, 115*, 103842. doi: 10.1016/j.marpol.2020.103842

Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental conservation, 24*(01), 38—49.

Filmalter, J., Forget, F., Poisson, F., Vernet, A. L., Bach, P., & Dagorn, L. (2012). Vertical and horizontal behavior of silky, oceanic white tip and blue sharks in the western Indian Ocean. *IOTC-2012-WPEB08-23*.

Fonteneau, A., Pallares, P., & Pianet, R. (2000). A worldwide review of purse seine fisheries on FADs. *Pêche thonière et dispositifs de concentration de poissons, Caribbean-Martinique, 15-19 Oct 1999.*

Freeman, E., & Freeman, M. E. (2012). Package ‘PresenceAbsence’. *R Package Version, 1*(9).

Frisk, M. G., Miller, T. J., & Fogarty, M. J. (2001). Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. *Canadian Journal of Fisheries and Aquatic Sciences, 58*(5), 969-981. doi: 10.1139/f01-051

Gilman, E., Passfield, K., & Nakamura, K. (2014). Performance of regional fisheries management organizations: ecosystem-based governance of bycatch and discards. *Fish and Fisheries, 15*(2), 327-351. doi: https://doi.org/10.1111/faf.12021

Goñi, N., Ruiz, J., Murua, H., Santiago, J., Krug, I., de Olano, B. S., . . . 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. *System, 5*, 13.

Grande, M., Ruiz, J., Murua, H., Murua, J., Goñi, N., Arregi, I. K. I., . . . Santiago, J. (2020). Progress on the code of good practices on the tropical tuna purse seine fishery in the Atlantic Ocean. *Collect. Vol. Sci. Pap. ICCAT, 76*(9), 193—234.

Gray, C. A., & Kennelly, S. J. (2018). Bycatches of endangered, threatened and protected species in marine fisheries. *Reviews in Fish Biology and Fisheries, 28*(3), 521-541. doi: 10.1007/s11160-018-9520-7

Guisan, A., Edwards, T. C., & Hastie, T. (2002). Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling, 157*(2), 89-100. doi: https://doi.org/10.1016/S0304-3800(02)00204-1

Hall, M., Gilman, E., Minami, H., Mituhasi, T., & Carruthers, E. (2017). Mitigating bycatch in tuna fisheries. *Reviews in Fish Biology and Fisheries, 27*, 1-28. doi: 10.1007/s11160-017-9478-x

Hall, M., & Roman, M. (2013). Bycatch and non-tuna catch in the tropical tuna purse seine fisheries of the world. *FAO Fisheries and Aquaculture Technical Paper No. 568*.

Hall, M., & Roman, M. (2013). Bycatch and non-tuna catch in the tropical tuna purse seine fisheries of the world. *FAO fisheries and aquaculture technical paper*(568), I.

Hallier, J., & Gaertner, D. (2008). Drifting fish aggregation devices could act as an ecological trap for tropical tuna species. *Marine Ecology Progress Series, 353*, 255-264.

Heithaus, M. R., Frid, A., Wirsing, A. J., & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution, 23*(4), 202-210. doi: https://doi.org/10.1016/j.tree.2008.01.003

Hermes, J. C., & Reason, C. J. C. (2008). Annual cycle of the South Indian Ocean (Seychelles-Chagos) thermocline ridge in a regional ocean model. *Journal of Geophysical Research: Oceans, 113*(C4). doi: https://doi.org/10.1029/2007JC004363

Heupel, M. R., Simpfendorfer, C. A., Espinoza, M., Smoothey, A. F., Tobin, A., & Peddemors, V. (2015). Conservation challenges of sharks with continental scale migrations. [Original Research]. *Frontiers in Marine Science, 2*(12). doi: 10.3389/fmars.2015.00012

Hijmans, R. J. (2011). Introduction to the ”geosphere” package (Version 1.2-19).

Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2020). dismo: Species Distribution Modeling. R package version 1.3-3.

Hitchcock, G. L., Key, E. L., & Masters, J. (2000). The fate of upwelled waters in the Great Whirl, August 1995. *Deep Sea Research Part II: Topical Studies in Oceanography, 47*(7), 1605-1621. doi: https://doi.org/10.1016/S0967-0645(99)00156-3

Howey-Jordan, L. A., Brooks, E. J., Abercrombie, D. L., Jordan, L. K. B., Brooks, A., Williams, S., . . . Chapman, D. D. (2013). Complex Movements, Philopatry and Expanded Depth Range of a Severely Threatened Pelagic Shark, the Oceanic Whitetip (Carcharhinus longimanus) in the Western North Atlantic. *PLOS ONE, 8*(2), e56588. doi: 10.1371/journal.pone.0056588

Howey, L. A., Tolentino, E. R., Papastamatiou, Y. P., Brooks, E. J., Abercrombie, D. L., Watanabe, Y. Y., . . . Jordan, L. K. (2016). Into the deep: the functionality of mesopelagic excursions by an oceanic apex predator. *Ecol Evol, 6*(15), 5290-5304. doi: 10.1002/ece3.2260

Hutchinson, M. R., Itano, D. G., Muir, J. A., & Holland, K. N. (2015). Post-release survival of juvenile silky sharksÃ, Â captured in a tropical tuna purse seine fishery. *Marine Ecology Progress Series, 521*, 143-154.

IATTC. (1999). Agreement on the International Dolphin Conservation Program.

IATTC. (2009). Resolution C-09-01 on a multiannual program for the conservation of tuna in the eastern pacific ocean in 2009-2011

IATTC. (2011). Resolution C-11-10 on the conservation of oceanic whitetip sharks caught in association with fisheries in the antigua convention area.

IATTC. (2019). Resolution on scientific observers for longline vessels.

ICCAT. (2010). Recommendation 10-07 by ICCAT on the conservation of oceanic whitetip shark caught in association with fisheries in the ICCAT convention area.

ICCAT. (2016). Report of the 11th meeting of the working group on Integrated Monitoring Measures (IMM).

IOTC. (2013). Resolution 13/06 on a scientific and management framework on the conservation of sharks species caught in association with IOTC managed fisheries.

IOTC. (2014). Guidelines for the reporting of fisheries statistics to the IOTC.

IOTC. (2015). Status of the Indian Ocean oceanic whitetip shark (OCS: Carcharhinus longimanus). *IOTC–2015–SC18–ES18[E]*.

Jacoby, D. M. P., Croft, D. P., & Sims, D. W. (2012). Social behaviour in sharks and rays: analysis, patterns and implications for conservation. *Fish and Fisheries*, *13*(4), 399-417. doi: https://doi.org/10.1111/j.1467-2979.2011.00436.x

Jiménez-Valverde, A., & Lobo, J. M. (2007). Threshold criteria for conversion of probability of species presence to either–or presence–absence. *Acta Oecologica, 31*(3), 361-369. doi: https://doi.org/10.1016/j.actao.2007.02.001

Juan-Jordá, M. J., Murua, H., Arrizabalaga, H., Dulvy, N. K., & Restrepo, V. (2018). Report card on ecosystem-based fisheries management in tuna regional fisheries management organizations. *Fish and Fisheries, 19*(2), 321-339. doi: https://doi.org/10.1111/faf.12256

Kaplan, D. M., Chassot, E., Amandé, J. M., Dueri, S., Demarcq, H., Dagorn, L., & Fonteneau, A. (2014). Spatial management of Indian Ocean tropical tuna fisheries: potential and perspectives. *ICES Journal of Marine Science, 71*(7), 1728-1749. doi: 10.1093/icesjms/fst233

Lam, C. H., Galuardi, B., & Lutcavage, M. E. (2014). Movements and oceanographic associations of bigeye tuna (Thunnus obesus) in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences, 71*(10), 1529-1543. doi: 10.1139/cjfas-2013-0511

Lee, P.-F., Chen, I., & Tzeng, W. (2005). Spatial and Temporal Distribution Patterns of Bigeye Tuna (Thunnus obesus) in the Indian Ocean. *Zoological Studies, 44*, 260-270.

Lennert-Cody, C., & Hall, M. (2000). The development of the purse seine fishery on drifting Fish Aggregating devices in the Eastern Pacific Ocean: 1992-1998. *Pêche thonière et dispositifs de concentration de poissons, Caribbean-Martinique, 15-19 Oct 1999 15-19 octobre 1999.*

Lezama-Ochoa, N., Hall, M. A., Pennino, M. G., Stewart, J. D., López, J., & Murua, H. (2019). Environmental characteristics associated with the presence of the Spinetail devil ray (Mobula mobular) in the eastern tropical Pacific. *PLOS ONE, 14*(8), e0220854. doi: 10.1371/journal.pone.0220854

Lezama-Ochoa, N., Lopez, J., Hall, M., Bach, P., Abascal, F., & Murua, H. (2020). Spatio-temporal distribution of the spinetail devil ray Mobula mobular in the eastern tropical Atlantic Ocean. *Endangered Species Research, 43*, 447-460.

Lezama-Ochoa, N., Murua, H., Chust, G., Van Loon, E., Ruiz, J., Hall, M., . . . 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. [Original Research]. *Frontiers in Marine Science, 3*(34). doi: 10.3389/fmars.2016.00034

Liu, C., Berry, P. M., Dawson, T. P., & Pearson, R. G. (2005). Selecting thresholds of occurrence in the prediction of species distributions. *Ecography, 28*(3), 385-393. doi: https://doi.org/10.1111/j.0906-7590.2005.03957.x

Lopez, J., Alvarez-Berastegui, D., Soto, M., & Murua, H. (2020). Using fisheries data to model the oceanic habitats of juvenile silky shark (Carcharhinus falciformis) in the tropical eastern Atlantic Ocean. *Biodiversity and Conservation, 29*(7), 2377-2397. doi: 10.1007/s10531-020-01979-7

Lopez, J., Moreno, G., Lennert-Cody, C., Maunder, M., Sancristobal, I., Caballero, A., & Dagorn, L. (2017). Environmental preferences of tuna and non-tuna species associated with drifting fish aggregating devices (DFADs) in the Atlantic Ocean, ascertained through fishers' echo-sounder buoys. *Deep Sea Res. Part II Top. Stud. Oceanogr., 140*, 127-138.

Madigan, D. J., Brooks, E. J., Bond, M. E., Gelsleichter, J., Howey, L. A., Abercrombie, D. L., . . . Chapman, D. D. (2015). Diet shift and site-fidelity of oceanic whitetip sharks Carcharhinus longimanus along the Great Bahama Bank. *Marine Ecology Progress Series, 529*, 185-197. doi: 10.3354/meps11302

Marín-Enríquez, E., Seoane, J., & Muhlia-Melo, A. (2018). Environmental modeling of occurrence of dolphinfish (Coryphaena spp.) in the Pacific Ocean off Mexico reveals seasonality in abundance, hot spots and migration patterns. *Fisheries Oceanography*, *27*(1), 28-40. doi: https://doi.org/10.1111/fog.12231

Marsac, F. (2017). The Seychelles Tuna Fishery and Climate Change *Climate Change Impacts on Fisheries and Aquaculture* (pp. 523-568).

Marsac, F., Fonteneau, A., & Ménard, F. (2000). *Drifting FADs used in tuna fisheries: an ecological trap?* Paper presented at the Pêche thonière et dispositifs de concentration de poissons, Caribbean-Martinique, 15-19 Oct 1999.

Marshall, C. E., Glegg, G. A., & Howell, K. L. (2014). Species distribution modelling to support marine conservation planning: The next steps. *Marine Policy, 45*, 330-332. doi: https://doi.org/10.1016/j.marpol.2013.09.003

Martínez-Rincón, R. O., Ortega-García, S., & Vaca-Rodríguez, J. G. (2012). Comparative performance of generalized additive models and boosted regression trees for statistical modeling of incidental catch of wahoo (Acanthocybium solandri) in the Mexican tuna purse-seine fishery. *Ecological Modelling, 233*, 20-25. doi: https://doi.org/10.1016/j.ecolmodel.2012.03.006

Martinez-Rincon, R. O., Ortega-Garcia, S., Vaca-Rodriguez, J. G., & Griffiths, S. P. (2015). Development of habitat prediction models to reduce by-catch of sailfish (<i>Istiophorus platypterus</i>) within the purse-seine fishery in the eastern Pacific Ocean. *Marine and Freshwater Research, 66*(7), 644-653. doi: https://doi.org/10.1071/MF14062

Maury, O., Miller, K., Campling, L., Arrizabalaga, H., Aumont, O., Bodin, Ö., . . . Murtugudde, R. (2013). A global science–policy partnership for progress toward sustainability of oceanic ecosystems and fisheries. *Current Opinion in Environmental Sustainability, 5*(3), 314-319. doi: https://doi.org/10.1016/j.cosust.2013.05.008

McKinney, J. A., Hoffmayer, E. R., Wu, W., Fulford, R., & Hendon, J. (2012). Feeding habitat of the whale shark Rhincodon typus in the northern Gulf of Mexico determined using species distribution modelling. *Marine Ecology Progress Series, 458*, 199-211.

Mejuto, J., García-Cortés, B., & Ramos-Cartelle, A. (2005). Tagging-recapture activities of large pelagic sharks carried out by Spain or in collaboration with the tagging programs of other countries. *ICCAT Coll Vol Sci Pap, 58*, 974-1000.

Miller, P. I., Scales, K. L., Ingram, S. N., Southall, E. J., & Sims, D. W. (2015). Basking sharks and oceanographic fronts: quantifying associations in the north-east Atlantic. *Functional Ecology, 29*(8), 1099-1109. doi: https://doi.org/10.1111/1365-2435.12423

Montero, J. T., Martinez-Rincon, R. O., Heppell, S. S., Hall, M., & Ewal, M. (2016). Characterizing environmental and spatial variables associated with the incidental catch of olive ridley (Lepidochelys olivacea) in the Eastern Tropical Pacific purse-seine fishery. *Fisheries Oceanography, 25*(1), 1-14. doi: https://doi.org/10.1111/fog.12130

Morato, T., Varkey, D. A., Damaso, C., Machete, M., Santos, M., Prieto, R., . . . Santos, R. S. (2008). Evidence of a seamount effect on aggregating visitors. *Marine Ecology Progress Series, 357*, 23-32.

Musyl, M. K., Brill, R. W., Curran, D. S., Fragoso, N. M., McNaughton, L. M., Nielsen, A., . . . Moyes, C. D. (2011). Postrelease survival, vertical and horizontal movements, and thermal habitats of five species of pelagic sharks in the central Pacific Ocean. *Fishery Bulletin, 109*(4), 341-368.

Naimi, B., Hamm, N., Groen, T., Skidmore, A., & Toxopeus, A. (2014). Where is positional uncertainty a problem for species distribution modelling. *Ecography, 37*, 191-203. doi: 10.1111/j.1600-0587.2013.00205.x.

Nasby-Lucas, N., Dewar, H., Lam, C. H., Goldman, K. J., & Domeier, M. L. (2009). White Shark Offshore Habitat: A Behavioral and Environmental Characterization of the Eastern Pacific Shared Offshore Foraging Area. *PLOS ONE, 4*(12), e8163. doi: 10.1371/journal.pone.0008163

Orue, B., Lopez, J., Moreno, G., Santiago, J., Soto, M., & Murua, H. (2019). Aggregation process of drifting fish aggregating devices (DFADs) in the Western Indian Ocean: Who arrives first, tuna or non-tuna species? *PLOS ONE, 14*(1), e0210435. doi: 10.1371/journal.pone.0210435

Pacoureau, N., Rigby, C. L., Kyne, P. M., Sherley, R. B., Winker, H., Carlson, J. K., . . . Dulvy, N. K. (2021). Half a century of global decline in oceanic sharks and rays. *Nature, 589*(7843), 567-571. doi: 10.1038/s41586-020-03173-9

Pante, E., & Simon-Bouhet, B. (2013). marmap: A Package for Importing, Plotting and Analyzing Bathymetric and Topographic Data in R. *PLOS ONE, 8*(9), e73051. doi: 10.1371/journal.pone.0073051

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., & Torres, F. (1998). Fishing Down Marine Food Webs. *Science, 279*(5352), 860. doi: 10.1126/science.279.5352.860

Pearson, R. G. (2010). *Species Distribution Modeling for Conservation Educators and Practitioners*.

Pearson, R. G., Thuiller, W., Araújo, M. B., Martinez-Meyer, E., Brotons, L., McClean, C., . . . Lees, D. C. (2006). Model-based uncertainty in species range prediction. *Journal of Biogeography, 33*(10), 1704-1711. doi: https://doi.org/10.1111/j.1365-2699.2006.01460.x

Pennington, J. T., Mahoney, K. L., Kuwahara, V. S., Kolber, D. D., Calienes, R., & Chavez, F. P. (2006). Primary production in the eastern tropical Pacific: A review. *Progress in Oceanography, 69*(2), 285-317. doi: https://doi.org/10.1016/j.pocean.2006.03.012

Pennino, M. G., Conesa, D., López-Quílez, A., Muñoz, F., Fernández, A., & Bellido, J. M. (2016). Fishery-dependent and -independent data lead to consistent estimations of essential habitats. *ICES Journal of Marine Science, 73*(9), 2302-2310. doi: 10.1093/icesjms/fsw062

Poisson, F., Séret, B., Vernet, A.-L., Goujon, M., & Dagorn, L. (2014). Collaborative research: Development of a manual on elasmobranch handling and release best practices in tropical tuna purse-seine fisheries. *Marine Policy, 44*, 312—320.

Queiroz, N., Humphries, N. E., Noble, L. R., Santos, A. M., & Sims, D. W. (2012). Spatial Dynamics and Expanded Vertical Niche of Blue Sharks in Oceanographic Fronts Reveal Habitat Targets for Conservation. *PLOS ONE, 7*(2), e32374. doi: 10.1371/journal.pone.0032374

Rooker, J. R., Simms, J. R., Wells, R. J. D., Holt, S. A., Holt, G. J., Graves, J. E., & Furey, N. B. (2012). Distribution and Habitat Associations of Billfish and Swordfish Larvae across Mesoscale Features in the Gulf of Mexico. *PLOS ONE, 7*(4), e34180. doi: 10.1371/journal.pone.0034180

Ruiz, J., Abascal, F. J., Bach, P., Baez, J. C., Cauquil, P., Grande, M., . . . Sabarros, P. S. (2018). Bycatch of the European, and Associated Flag, Purse-Seine Tuna Fishery in the Indian Ocean for the Period 2008-2017. *IOTC-2018-WPEB14-15*.

Scheffer, M., Carpenter, S., & Young, B. d. (2005). Cascading effects of overfishing marine systems. *Trends in Ecology & Evolution, 20*(11), 579-581. doi: https://doi.org/10.1016/j.tree.2005.08.018

Schott, F. A., & McCreary, J. P. (2001). The monsoon circulation of the Indian Ocean. *Progress in Oceanography, 51*(1), 1-123. doi: https://doi.org/10.1016/S0079-6611(01)00083-0

Schott, F. A., Xie, S.-P., & McCreary Jr., J. P. (2009). Indian Ocean circulation and climate variability. *Reviews of Geophysics, 47*(1). doi: https://doi.org/10.1029/2007RG000245

Sequeira, A. M. M., Mellin, C., Fordham, D. A., Meekan, M. G., & Bradshaw, C. J. A. (2014). Predicting current and future global distributions of whale sharks. *Global Change Biology, 20*(3), 778-789. doi: https://doi.org/10.1111/gcb.12343

Setiawati, M., Sambah, A., Miura, F., Tanaka, T., & As-syakur, A. R. (2015). Characterization of bigeye tuna habitat in the Southern Waters off Java–Bali using remote sensing data. *Advances in Space Research, 55*. doi: 10.1016/j.asr.2014.10.007

Shi, W., & Wang, M. (2021). A biological Indian Ocean Dipole event in 2019. *Scientific Reports, 11*(1), 2452. doi: 10.1038/s41598-021-81410-5

Su, N.-J., Sun, C.-L., Punt, A. E., Yeh, S.-Z., & DiNardo, G. (2011). Modelling the impacts of environmental variation on the distribution of blue marlin, Makaira nigricans, in the Pacific Ocean. *ICES Journal of Marine Science, 68*(6), 1072-1080. doi: 10.1093/icesjms/fsr028

Teo, S. L. H., & Block, B. A. (2010). Comparative Influence of Ocean Conditions on Yellowfin and Atlantic Bluefin Tuna Catch from Longlines in the Gulf of Mexico. *PLOS ONE, 5*(5), e10756. doi: 10.1371/journal.pone.0010756

Tolotti, M. T., Bach, P., Hazin, F., Travassos, P., & Dagorn, L. (2015). Vulnerability of the Oceanic Whitetip Shark to Pelagic Longline Fisheries. [Research Support, Non-U.S. Gov't]. *PLoS One, 10*(10), e0141396. doi: 10.1371/journal.pone.0141396

Tolotti, M. T., Bauer, R., Forget, F., Bach, P., Dagorn, L., & Travassos, P. (2017). Fine-scale vertical movements of oceanic whitetip sharks (Carcharhinus longimanus). *Fishery Bulletin, 115*(3), 380-395. doi: 10.7755/fb.115.3.8

Tolotti, M. T., Filmalter, J. D., Bach, P., Travassos, P., Seret, B., & Dagorn, L. (2015). Banning is not enough: The complexities of oceanic shark management by tuna regional fisheries management organizations. *Global Ecology and Conservation, 4*, 1-7. doi: https://doi.org/10.1016/j.gecco.2015.05.003

Tremblay-Boyer, L., Carvalho, F., Neubauer, P., & Pilling, G. (2019). Stock assessment for oceanic whitetip shark in the Western and Central Pacific Ocean: WCPFC-SC15-2019/SA-WP-06. Report to the WCPFC Scientific Committee ….

Vacquié-Garcia, J., Guinet, C., Dragon, A. C., Viviant, M., El Ksabi, N., & Bailleul, F. (2015). Predicting prey capture rates of southern elephant seals from track and dive parameters. *Marine Ecology Progress Series, 541*, 265-277.

Venables, W. N., & Dichmont, C. M. (2004). GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. *Fisheries Research, 70*(2), 319-337. doi: https://doi.org/10.1016/j.fishres.2004.08.011

WCPFC. (2018). Implementation Programme for the Regional Observer Programme. *Handbook of Conservation Management Measures & Resolutions For WCPFC Regional Observer Programmes*.

WCPFC. (2019). Conservation and management measure for sharks (2019-04).

Wiggert, J. D., Murtugudde, R. G., & Christian, J. R. (2006). Annual ecosystem variability in the tropical Indian Ocean: Results of a coupled bio-physical ocean general circulation model. *Deep Sea Research Part II: Topical Studies in Oceanography, 53*(5), 644-676. doi: https://doi.org/10.1016/j.dsr2.2006.01.027

Wood, S. (2006). *Generalized Additive Models: An Introduction With R* (Vol. 66).

Wood, S. (2014). Package 'mgcv'. *R package version1.7-29*.

Yang, K., Cai, W., Huang, G., Wang, G., Ng, B., & Li, S. (2020). Oceanic Processes in Ocean Temperature Products Key to a Realistic Presentation of Positive Indian Ocean Dipole Nonlinearity. *Geophysical Research Letters, 47*(16), e2020GL089396. doi: https://doi.org/10.1029/2020GL089396

Yesson, C., Clark, M. R., Taylor, M. L., & Rogers, A. D. (2011). The global distribution of seamounts based on 30 arc seconds bathymetry data. *Deep Sea Research Part I: Oceanographic Research Papers, 58*(4), 442-453. doi: https://doi.org/10.1016/j.dsr.2011.02.004

Young, C. N., & Carlson, J. K. (2020). The biology and conservation status of the oceanic whitetip shark (Carcharhinus longimanus) and future directions for recovery. *Reviews in Fish Biology and Fisheries, 30*(2), 293-312. doi: 10.1007/s11160-020-09601-3

Young, C. N., Carlson, J. K., Hutchinson, M., Hutt, C., Kobayashi, D., McCandless, C. T., & Wraith, J. (2017). Status review report: oceanic whitetip shark (*Carcharhinius longimanus*). *Final Report to the National Marine Fisheries Service, Office of Protected Resources*.

Young, J., Hunt, B., Cook, T., Llopiz, J., Hazen, E., Pethybridge, H., . . . Choy, A. (2015). The trophodynamics of marine top predators: Current knowledge, recent advances and challenges. *Deep Sea Research Part II Topical Studies in Oceanography, 113*. doi: 10.1016/j.dsr2.2014.05.015

Zainuddin, M., Saitoh, K., & Saitoh, S.-i. (2008). Albacore (Thunnus alalunga) fishing ground in relation to oceanographic conditions in the western North Pacific Ocean using remotely sensed satellite data. *Fisheries Oceanography, 17*(2), 61-73. doi: https://doi.org/10.1111/j.1365-2419.2008.00461.x

Zhang, L., Du, Y., & Cai, W. (2018). Low-Frequency Variability and the Unusual Indian Ocean Dipole Events in 2015 and 2016. *Geophysical Research Letters, 45*(2), 1040-1048. doi: https://doi.org/10.1002/2017GL076003

Zuur, A., Ieno, E., & Smith, G. (2007). *Analysing Ecological Data* (Vol. 75).

7. Supplement material

Table S1. Variance Inflation Factor (VIF) for each variable.

Variable	VIF
Latitude	4.016102
Longitude	1.917046
Total catch	1.107843
Total bycatch	1.112823
Year	2.186625
Week	1.373110
Hours from sunrise	1.045314
Chlfronts	1.185016
NO_3	2.320101
NPPV	3.128955
O_2	3.118725
PO_4	3.664145
Si	2.888167
MLD	1.309311
Salinity	2.791832
SST	3.467685
SSH	1.539950
SSTfronts	1.031010
Ke	1.161193
Heading	1.066023
Depth	1.553515
Distance to seamount	1.042348

Table S2. The piece-wise construction of the **best model** with each new variable improving the AIC value.

Variables	AIC
Latitude x Longitude	9199.364
Latitude x Longitude + SST	9043.117
Latitude x Longitude + SST + Year	8969.637
Latitude x Longitude + SST + Year + Set type	8933.439
Latitude x Longitude + SST + Year + Set type + Total catch	8907.759
Latitude x Longitude + SST + Year + Set type + Total catch + NO_3	8895.298
Latitude x Longitude + SST + Year + Set type + Total catch + NO_3 + Week	8891.513

Table S3. Individual contribution of each variable (Explained deviance) running the model separately.

Variable	Explained deviance
Latitude x Longitude	5.30 %
Year	1.19 %
Week	1.21 %
Set type	0.55 %
Total catch	0.69 %
Sea surface temperature	3.55 %
Nitrate	1.39 %

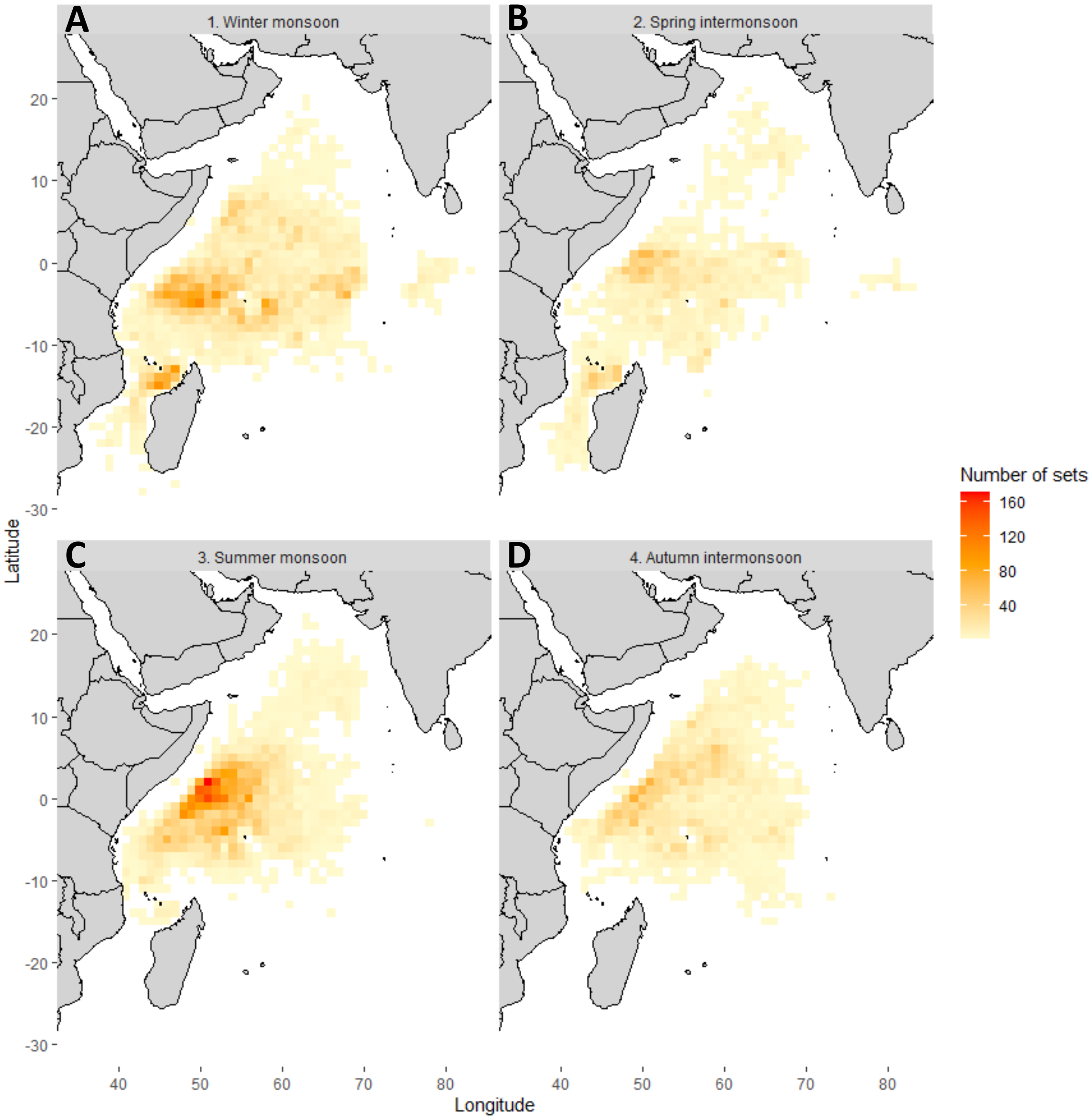

Figure S1. Spatial distribution of the cumulative effort (observed sets) in the EU purse seine fishery from 2010-2020 by monsoon regimes (A: Winter monsoon, B: Spring intermonsoon, C: Summer monsoon and D: Autumn intermonsoon). Darker red colors indicate higher observed sets, white colors indicate no observed sets.

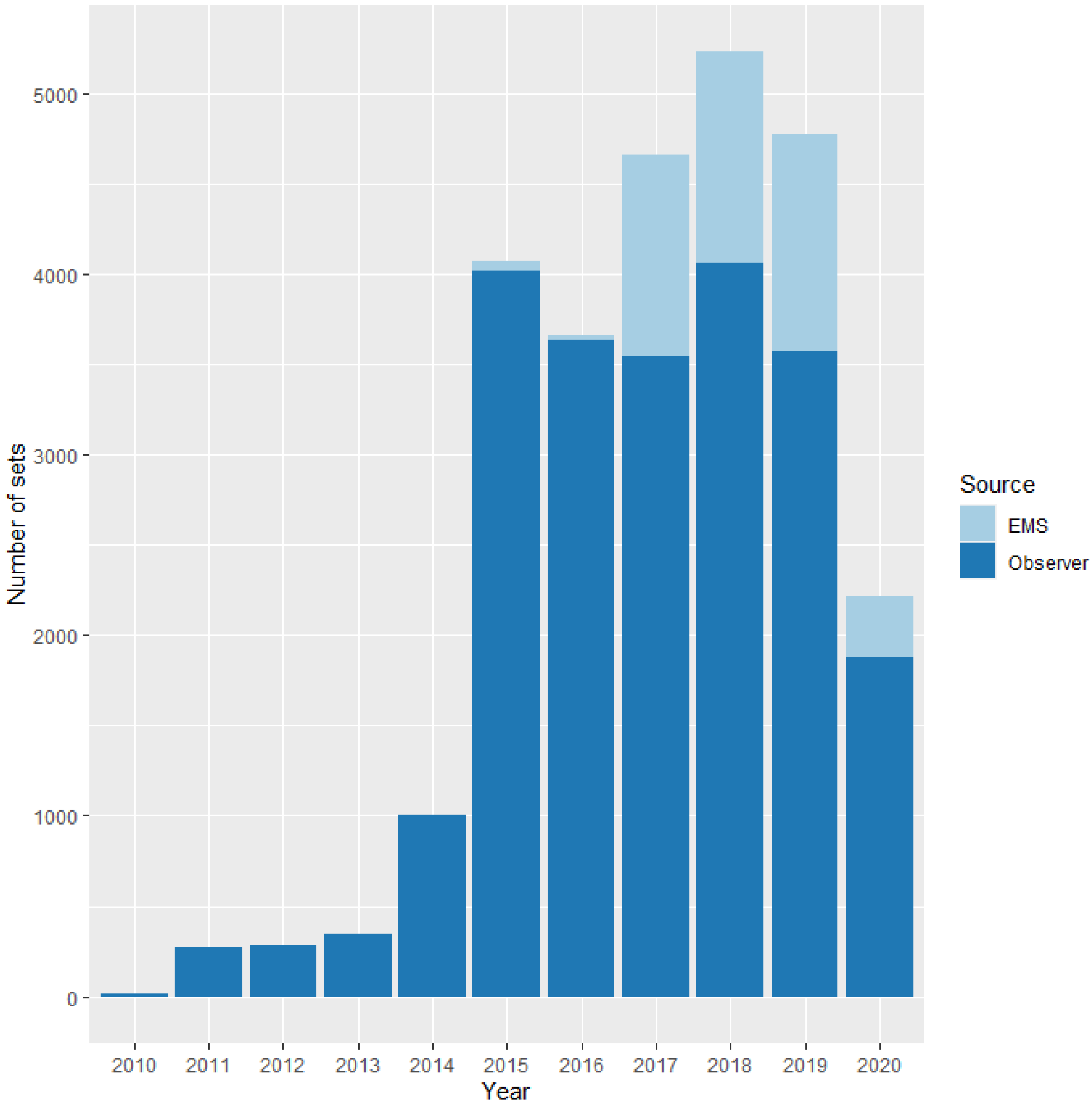

Figure S2. Temporal distribution of the observed sets in the EU purse seine fishery from 2010-2020 collected by Electronic Monitoring System (EMS) or human observers.

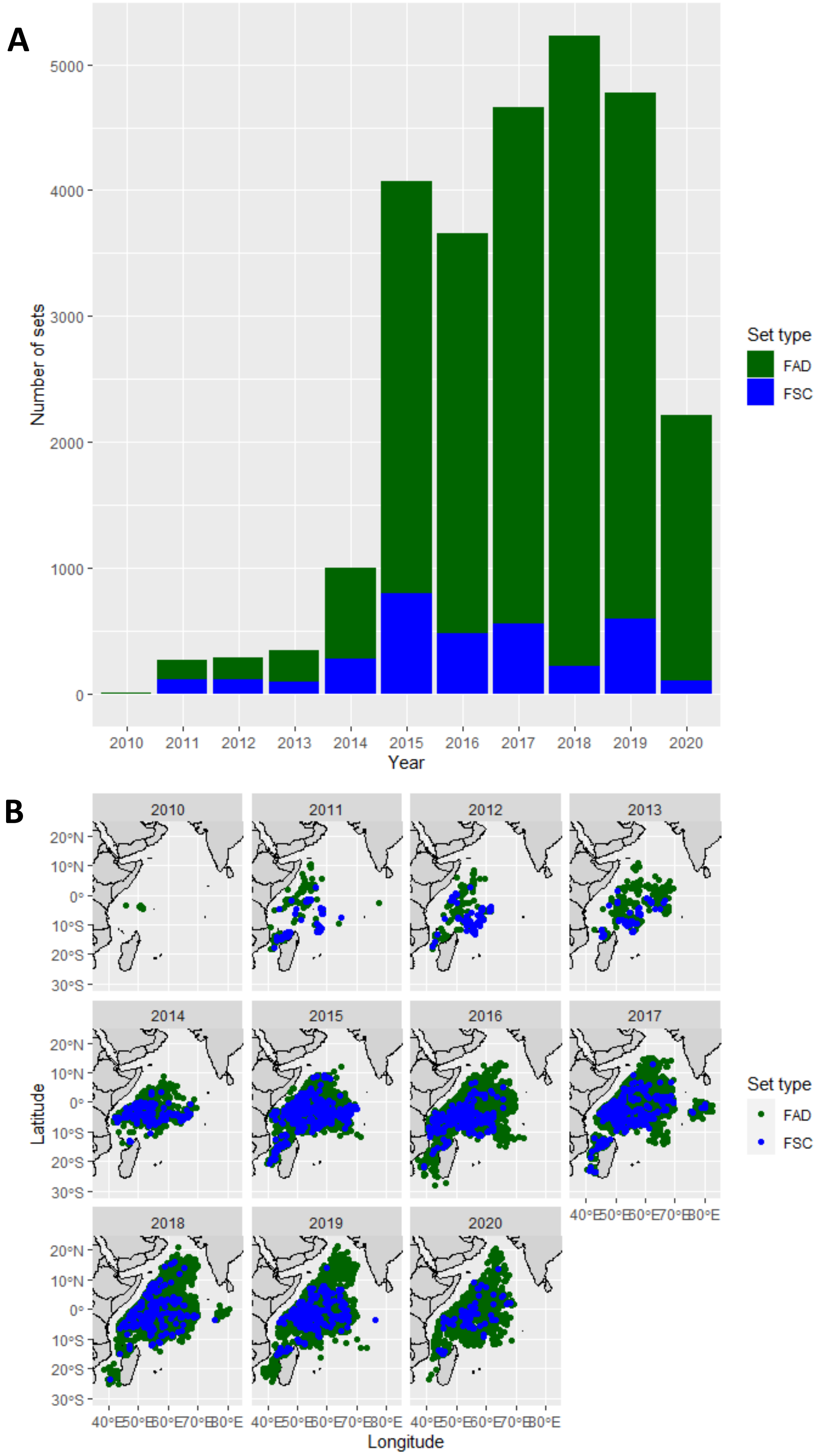

Figure S3. Temporal and spatial distribution of the observed sets (FAD and FSC). (A) Total number of observed sets per year. (B) Spatial distribution of the observed sets per year.

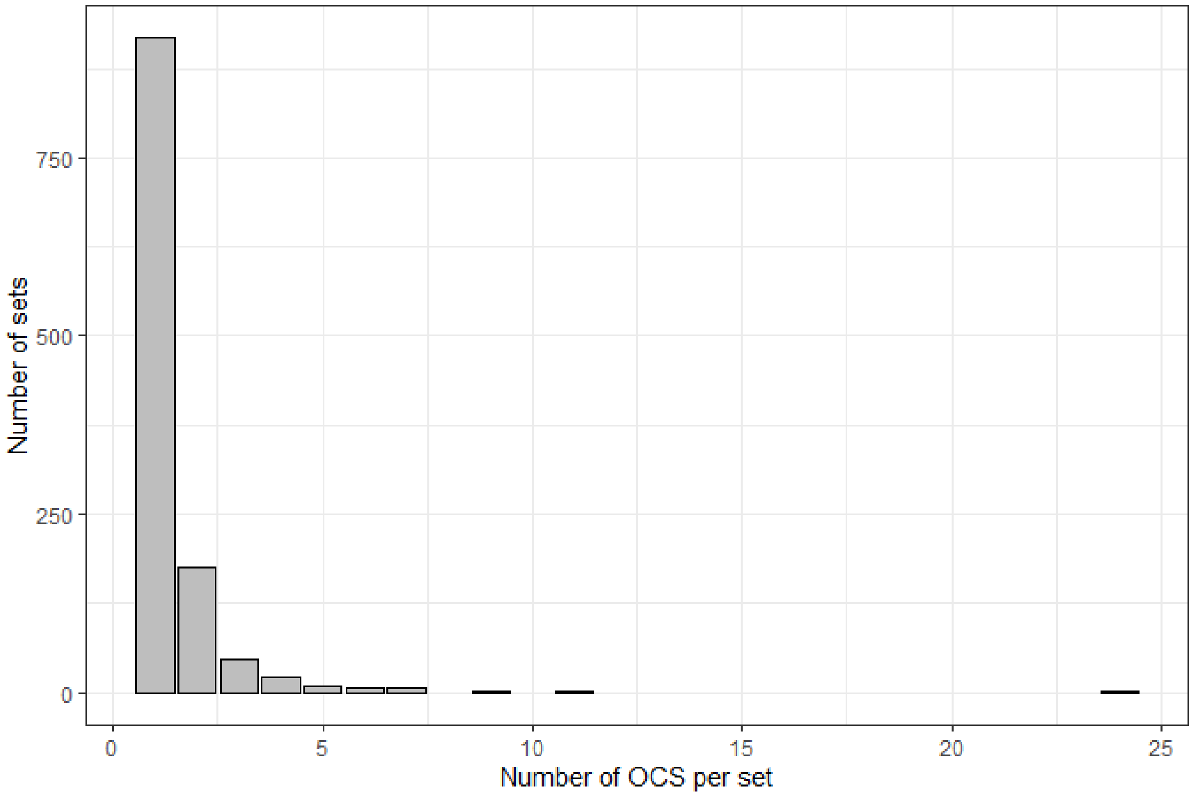

Figure S4. Distribution of the number of oceanic whitetip shark (OCS) per set. Only sets with presence of OCS are included.

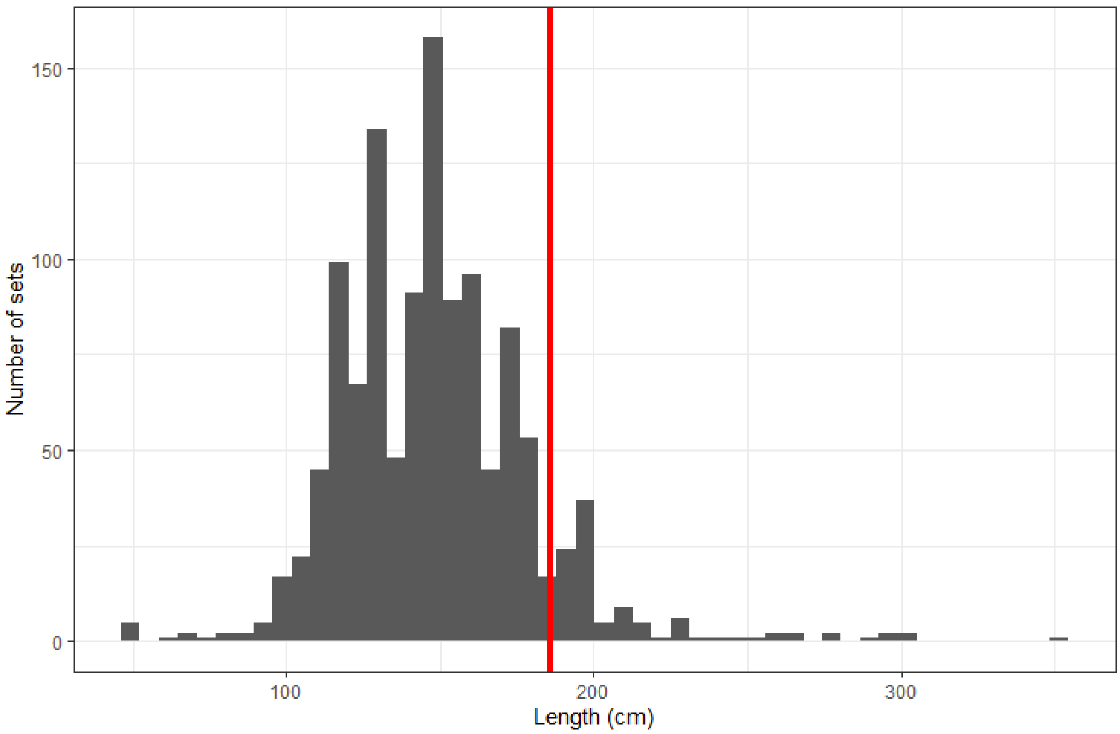

Figure S5. Mean length frequency distribution of oceanic whitetip shark (OCS) per set. Red line indicates length at maturity (186 cm) for OCS.

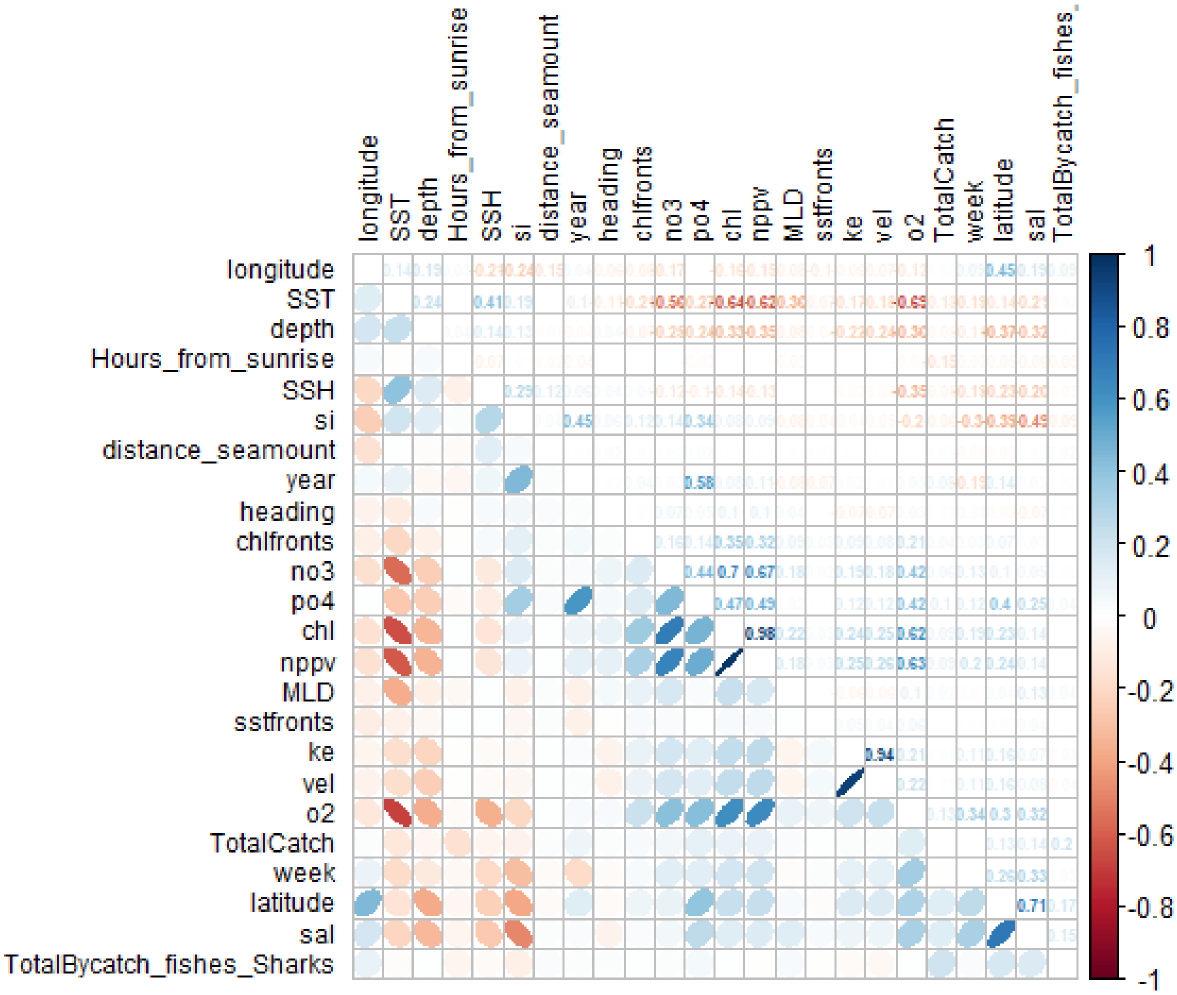

Figure S6. Pearson's correlation test for all the explanatory variables.

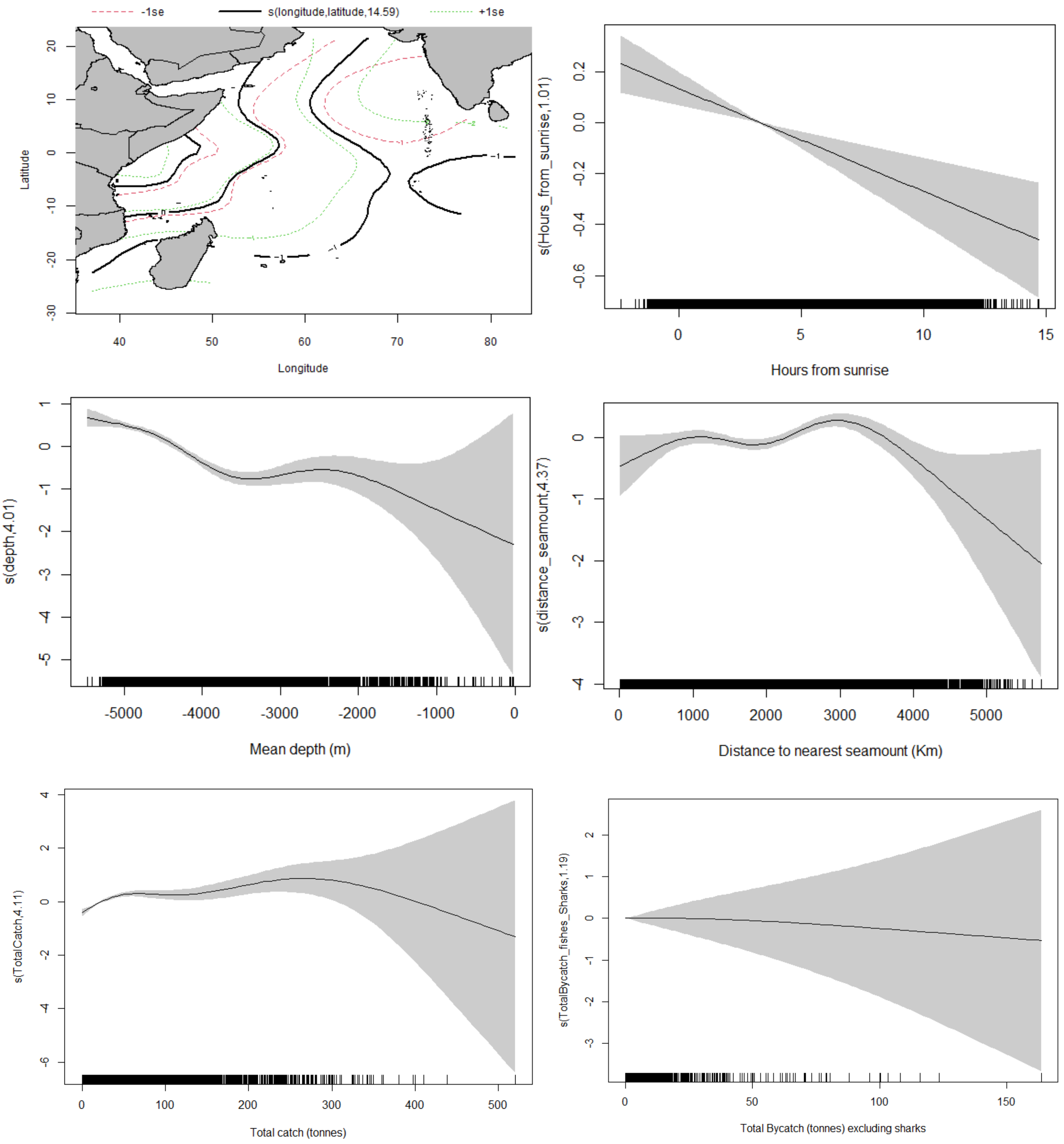

Figure S7. Univariate GAMs for each predictor variable.

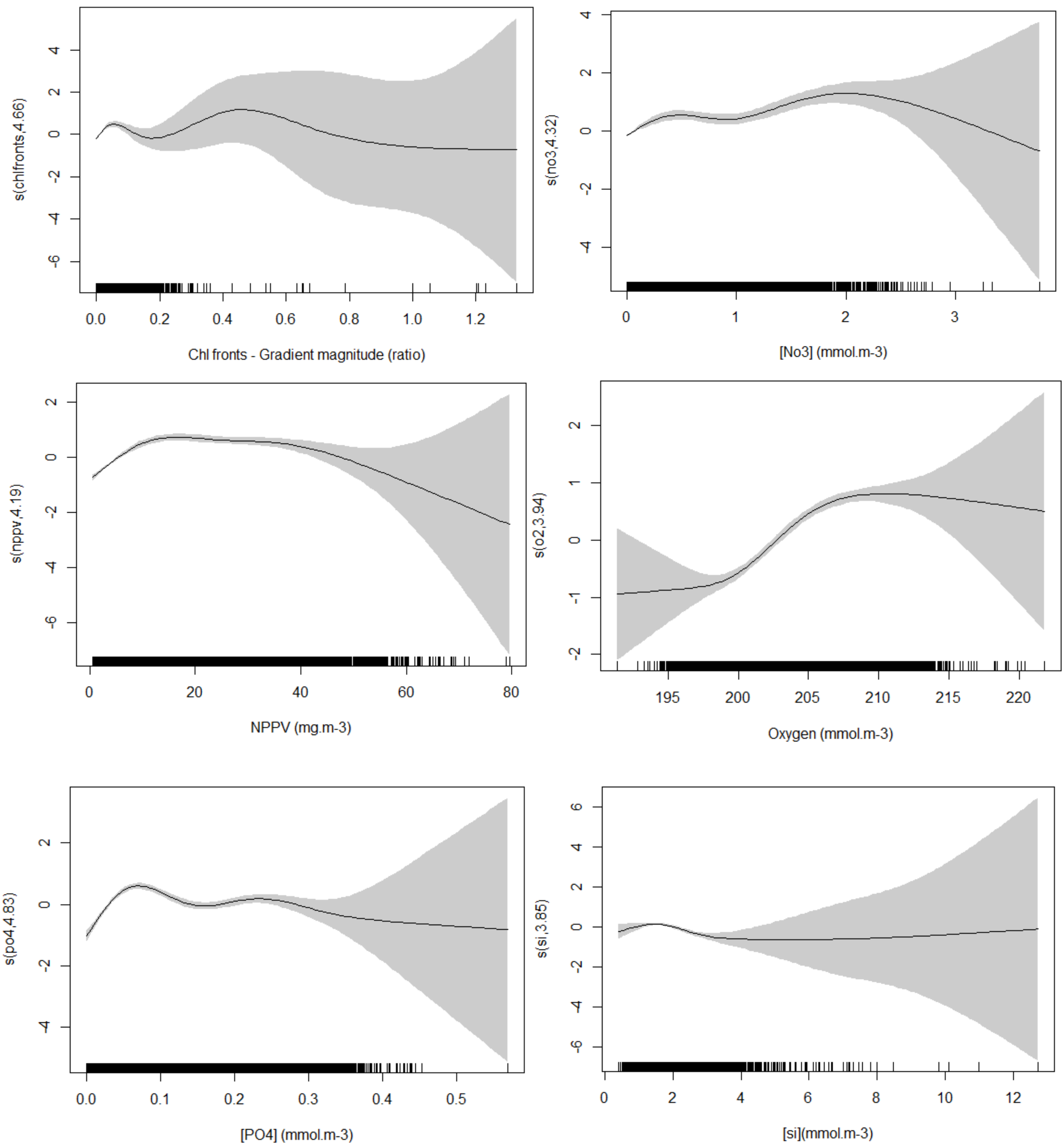

Figure S7. Continued.

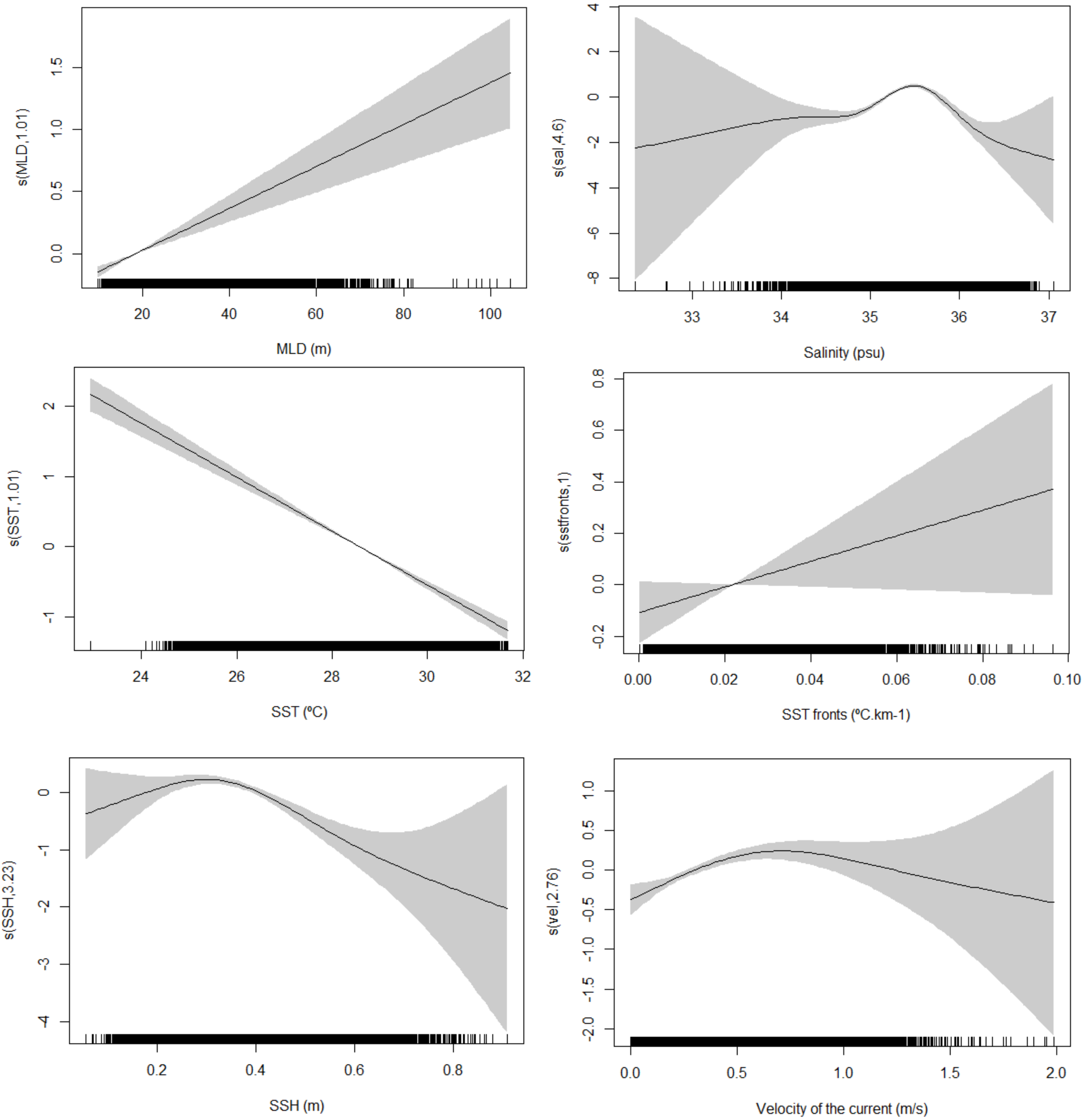

Figure S7. Continued.

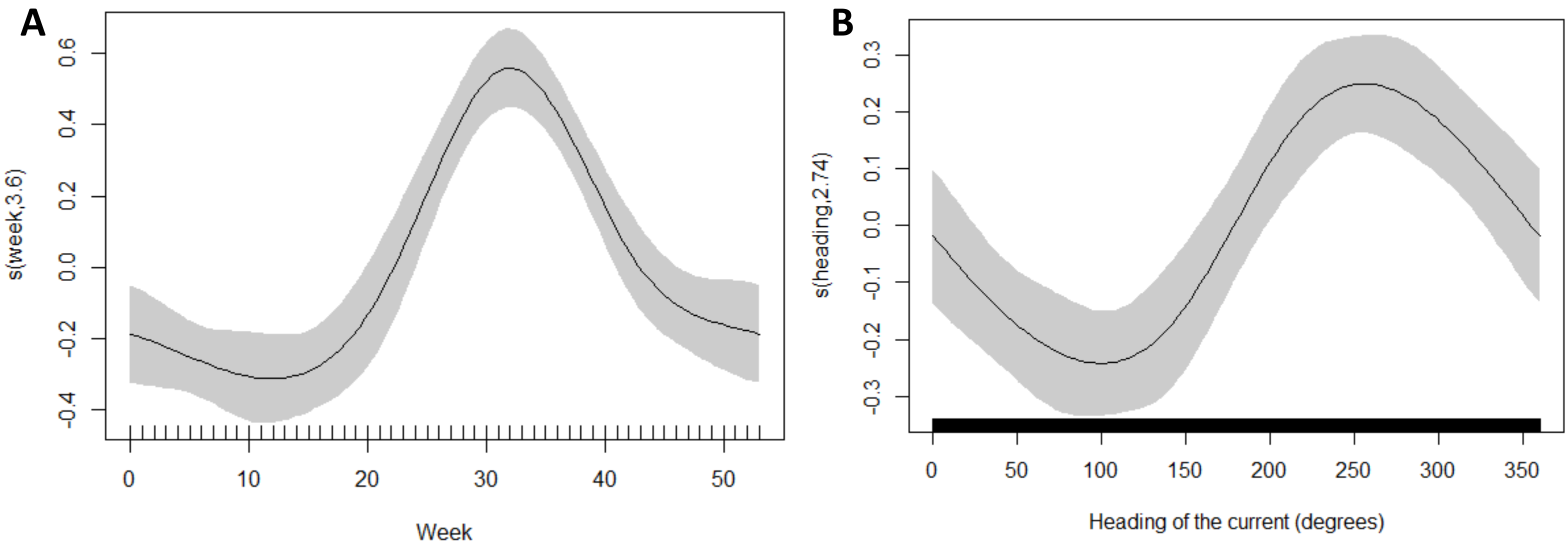

Figure S8. Univariate GAMs for the variables (A) week and (B) heading of the current showing a similar cyclical pattern.

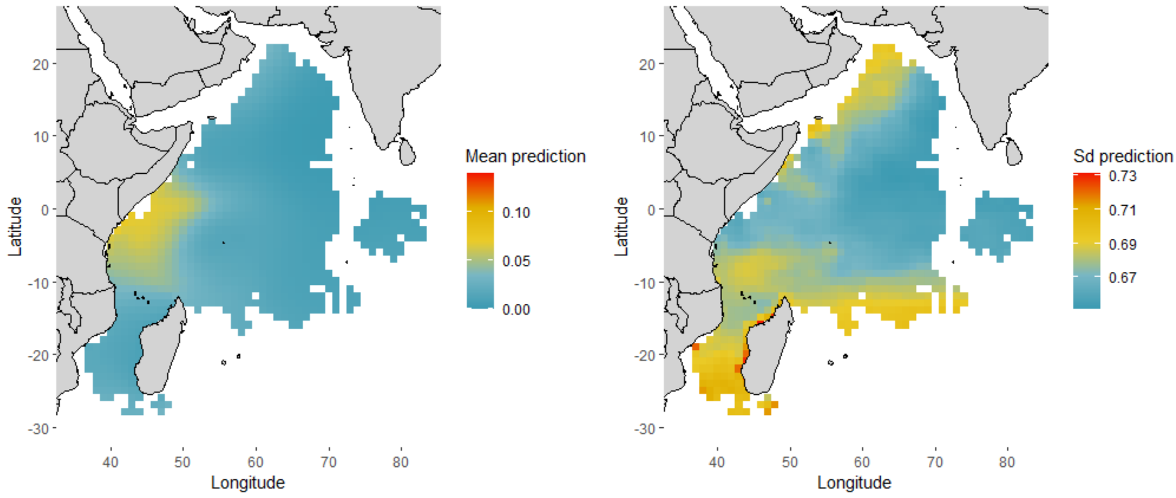

Figure S9. Mean prediction and standard deviation (Sd) of the presence of oceanic whitetip shark bycatch from tropical tuna purse seine fishery (2010-2020) in the western Indian Ocean based on the FSC fishing technique.

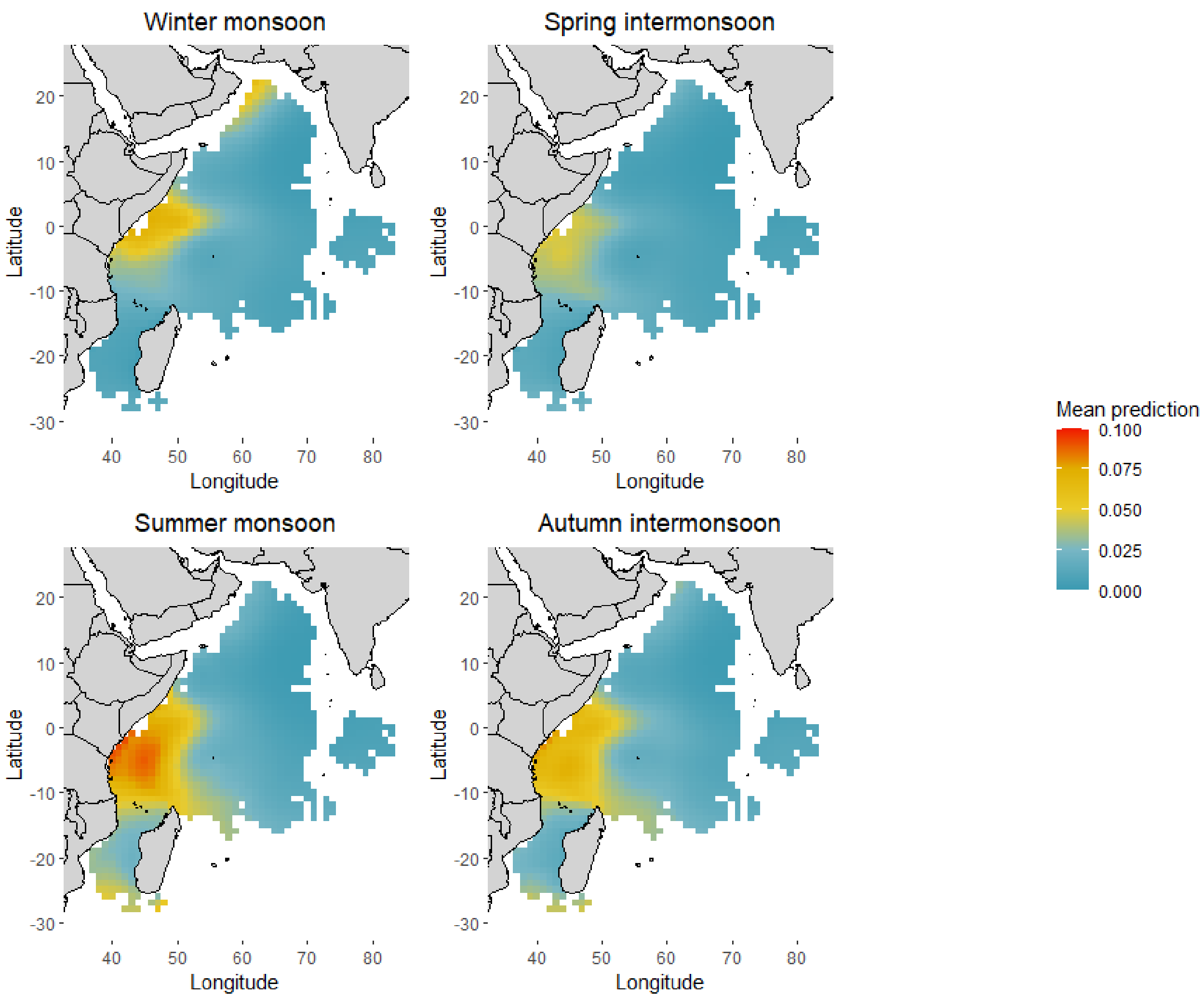

Figure S10. Mean prediction by monsoon regime (Winter: December-March; Spring: April-May; Summer: June-September; Autumn: October-November) of the presence of oceanic whitetip shark in the western Indian Ocean based on the FSC fishing technique.

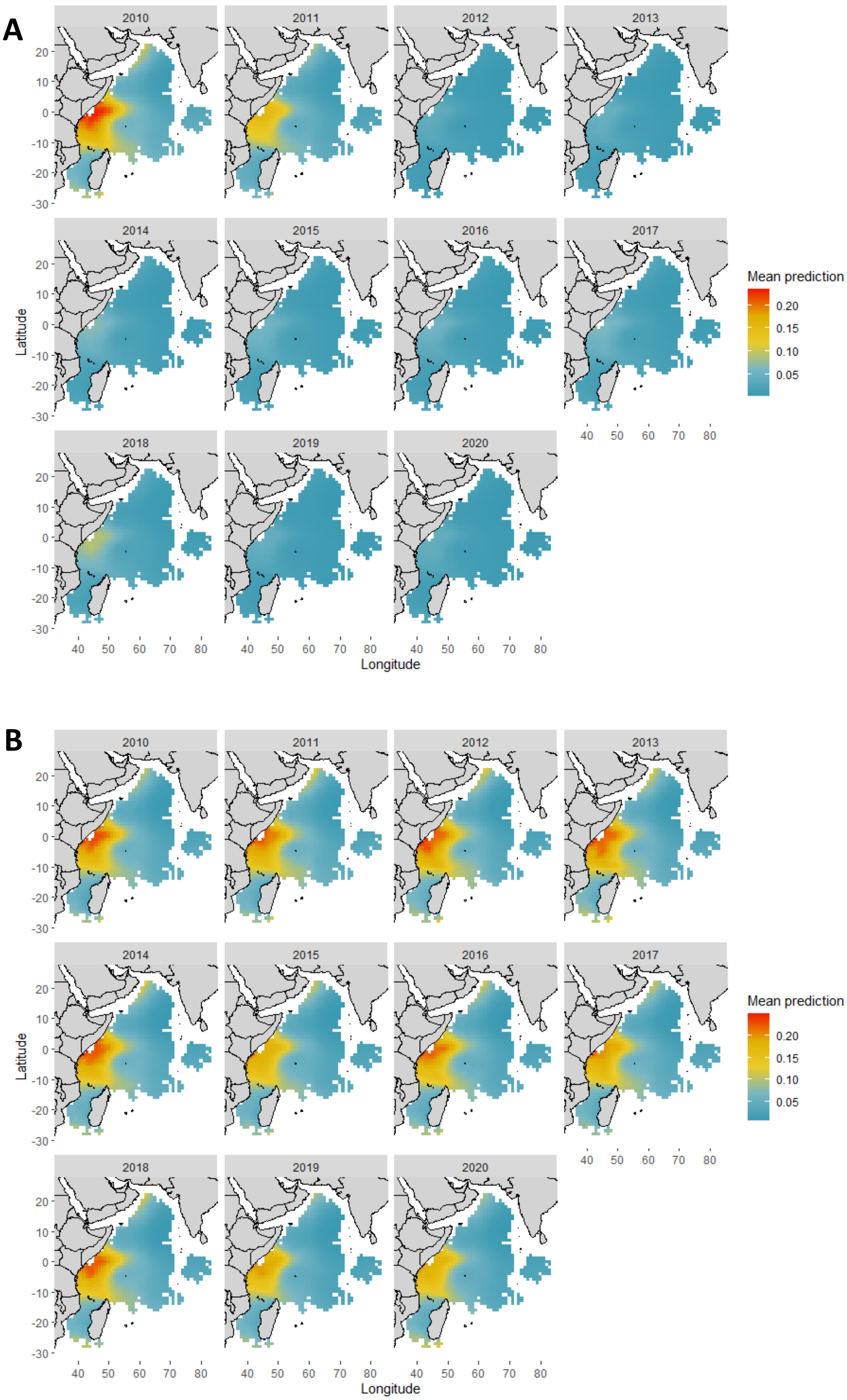

Figure S11. Mean prediction by years of the presence of oceanic whitetip shark in the western Indian Ocean based on the FSC fishing technique, (A) year effect included, (B) taking 2010 year as baseline.