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Mestrado em Biologia Marinha

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Declaração de autoria de trabalho:

Declaro ser autor deste trabalho, e que o mesmo é original. Todos os autores e artigos consultados estão devidamente citados no texto e estão incluídos na lista de referências.

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Carolina Dias

Resumo

O tubarão azul, *Prionace glauca*, é uma espécie particularmente afetada pela atividade humana, não só devido à pesca de palangre, como também às alterações climáticas. Por um lado, os aumentos de temperatura provocam um afastamento de espécies marinhas dos trópicos, enquanto que a pesca de palangre contribui para o declínio populacional das espécies mais vulneráveis. O tubarão azul é uma das espécies mais abundantes e com distribuição mais abrangente dos elasmobrânquios pelágicos, e é também a espécie do grupo mais afetada pelo género de pesca referido anteriormente. Um dos fatores que contribui para este facto é a o facto da atividade pesqueira não ser regulada eficientemente no comércio do tubarão azul. Embora sejam realizados esforços para controlar a pesca não regulamentada, é praticamente impossível ter dados totalmente fidedignos quanto ao exato número de indivíduos pescados. Pelas razões supramencionadas, o impacto da pesca no tubarão azul permanece um assunto polémico. O presente estudo teve como objetivos aferir o efeito das alterações climáticas na distribuição do tubarão azul, bem como identificar as áreas nas quais os tubarões estão mais vulneráveis à pesca de palangre. No decorrer do projeto, recorrendo a dados de biotelemetria e a projeções futuras de condições climáticas, foram implementados modelos para avaliar o nível de adequação dos habitats em condições presentes e futuras, na região nordeste do Oceano Atlântico. Adicionalmente, os modelos de distribuição dos tubarões foram agrupados com os dados de monitorização da pesca, de modo a obter uma sobreposição geográfica. Num contexto de alterações climáticas, os modelos de distribuição futura do tubarão azul demonstraram cenários de redução de *habitat* e desvios de distribuição em algumas regiões, concordantes com os efeitos observados em outras espécies marinhas. Relativamente à vulnerabilidade à pesca, foram obtidas áreas extensas de sobreposição, tanto em cenários para o presente como para o futuro. É importante salientar que algumas zonas de elevada vulnerabilidade coincidiram com zonas de berçário, tais como a região dos Açores e a costa portuguesa. Para além das pressões atuais, é esperado que estas sobreposições se mantenham e, em certas regiões, expandam até ao fim do século, arriscando a sobre-exploração da espécie devido a uma exposição prolongada às pescas. Atendendo a este facto, foram sugeridas medidas protetoras adicionais, e.g., restrição de capturas por tamanho, de modo a evitar uma pesca insustentável da espécie. Em adição, uma melhor regulação e monitorização da pesca é crucial para obter melhores medidas de conservação do tubarão azul.

Palavras-chave: Tubarão azul; Pesca de palangre; Telemetria de satélite; Alterações climáticas

Abstract

The blue shark is highly impacted by human activity, particularly by climate change and longline fishing. While rising temperatures are driving marine species away from the tropics and turning multiple regions into unsuitable habitats, longline fishing further contributes to population declines of the most vulnerable species. The blue shark, *Prionace glauca,* is one of the most abundant and widespread pelagic shark species. It is also the most targeted species by longline fishing. Although efforts are made to control blue shark exploitation, unregulated fishing practices remain common, hindering the ability to obtain reliable catch data. Hence, there is still a lack of consensus regarding fishing impact on blue sharks. The present study aimed to assess the effect of climate change on the blue shark's distribution, and to identify suitable areas of higher vulnerability to longline fishing. Using satellite biotelemetry data and climate change predictions, blue shark tracks were used to model habitat suitability for present and future conditions, focusing on the eastern North Atlantic Ocean. In addition, shark distribution prediction maps were overlapped with fishing vessel monitoring data. Future blue shark distribution models showed scenarios of habitat reduction and range shifts in some regions, as observed for numerous other marine species. In terms of fishing vulnerability, extensive overlaps were observed for present and future conditions. Most importantly, high vulnerability was shown to coincide with nursery areas, such as the Azores and the coast of mainland Portugal. Adding to the current pressures, overlaps with fisheries are expected to be maintained and even expand in some regions by the end of the century, risking an overexploitation of the species by an extended exposure to fishing activity. Attending to this high pressure experienced by sharks, it was suggested that additional protective measures ought to be adopted, e.g., catch restrictions by size, in order to avoid unsustainable fishing. In addition, an increased regulation and monitoring of fishing activity is crucial for attaining better conservation measures for the blue shark.

Keywords: Blue shark; Longline fishing; Satellite telemetry; Climate change

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List of abbreviations and acronyms

AIC - Akaike Information Criterion

AIS – Automatic Identification System

AUC – Area Under the Curve

CHL – Chlorophyll a

CMEMS - Copernicus Marine Environment Monitoring Service

DO – Dissolved Oxygen

EDF – Estimated Degrees of Freedom

GAM – Generalized Additive Model

GBIF - Global Biodiversity Information Facility

GEBCO - General Bathymetric Chart of the Oceans

GFW -Global Fishing Watch

IUU – Illegal, Unregulated and Unreported

LL – Log Likelihood

MLD - Mixed Layer Thickness

NPP – Net Primary Productivity

OBIS – Ocean Biodiversity Information System

RCP – Representative Concentration Pathway

SPOT – Smart Position-Only Tag

SSH – Sea Surface Height

SST – Sea Surface Temperature

T_slope – Sea Surface Temperature slope

TAC – Total Allowable Catch

wAIC – weighted Akaike Information Criterion

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1. Introduction

1.1. Longline fishing

When assessing the distribution of a given species, looking into its surrounding environment is an essential step. In marine environments, particularly, commercial fishing is the most significant source of influence and the greatest driver of mortality among fish populations (Jackson et al., 2001; Baum et al., 2003; Hutchings & Reynolds, 2004; Kroodsma et al., 2018; Queiroz et al., 2019). Among all fishing methods, longlining is the most prevalent technique (Baum et al., 2003; Kroodsma et al., 2018). The gear is composed by a set of up to 4000 baited hooks appended to a line that may be as long as 100 km. After the line is deployed, it remains for a few hours (i.e., soak time) at sea surface, suspended from floating buoys (Ward et al., 2008). Usually, longlining fleets focus on a few target species, such as swordfish and tuna (Amorim et al., 2002; Buencuerpo, 1998; Coelho et al., 2012). Nonetheless, when the abundance of the target species is low, a shift to other species of higher availability occurs (Amorim et al., 2002; Camhi et al., 2008; Camhi et al., 2009). Overfishing has been reported in numerous species, and longlining is one of the largest contributors (Simpfendorfer, 2002; Baum et al., 2003; Hutchings & Reynolds, 2004; Bearzi et al., 2006). Aside from intentional captures, incidental ones (i.e. bycatch) are highly frequent in longlining. This practice, often leading to discards at sea, is largely unreported and it is one of the most serious threats to sustainable fishing (Camhi et al., 2009; Dapp et al., 2013; Oliver et al., 2015). Elasmobranchs, in particular, are more prone to these practices, due to their slow life-history traits, i.e. low reproductive output and slow population growth rates (Musick, 1999).

1.2. Distribution and habitat use of the blue shark

The blue shark can be found in tropical and temperate waters, from latitudes of approximately 60ºN to 50ºS. In the Atlantic Ocean, its distribution ranges from Newfoundland to Argentina in the west and from Norway to South Africa in the east (Figure 1.1; Compagno, 1984; Rigby et al., 2019). This species spends most of its lifetime in oceanic regions, although at times it also moves to coastal areas, particularly in narrow shelf areas (Compagno, 1984). The blue shark is usually found within the top 350 m of depth, although it occasionally descends to higher depths of up to 1700 m (Carey & Scharold, 1990; Campana et al., 2011; Vedor et al., 2021a). The distribution of the blue shark's highly influenced by environmental features, such as prey availability and water temperature, and by their reproductive cycle (Pratt, 1979; Camhi et al., 2008; Queiroz et al., 2010; Queiroz et al., 2012; Vedor et al., 2021a). In the Atlantic Ocean, blue sharks display size segregation, as larger individuals are more frequently found at tropical regions, particularly in the north-west and south-east Atlantic, while smaller, immature individuals tend to remain in temperate areas, particularly in the north-east and south-west Atlantic (Camhi et al., 2008; Vandeperre et al., 2014; Coelho et al., 2018). The sex ratio also varies according to the season and the region of the Atlantic, variations that are highly associated with the blue shark's reproductive cycle (Mejuto & García-Cortés, 2005; Coelho et al., 2018).

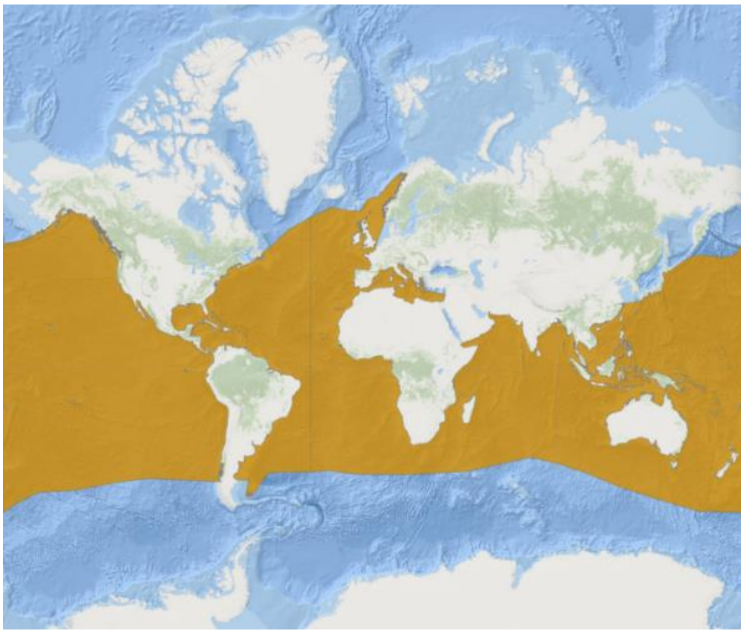

Fig. 1.1. Distribution of the blue shark *Prionace glauca.* Adapted from IUCN SSC Shark Specialist Group 2018. *Prionace glauca*. The IUCN Red List of Threatened Species. Version 2024-1.

1.3. Movement, migration and environmental preferences

The blue shark can withstand a wide thermal range from 7ºC to 28ºC, although it prefers waters at 12ºC to 20ºC (Compagno, 1984; Carey & Scharold, 1990; Camhi et al., 2008; Campana et al., 2011). In addition, water temperature influences the shark's vertical habitat. In temperate areas, where temperatures are lower, sharks are more often found at surface or near-surface areas. When moving towards tropical regions, they submerge and remain at depths below the surface (Compagno, 1984; Vedor et al., 2021a). Throughout the day, the blue shark is a highly mobile species, as it performs recurrent movements between the sea surface and higher depths. During daytime, this species is often found at higher depths, while at night, it remains more confined to areas near the thermocline or the lower mixed layer (Carey & Scharold, 1990; Queiroz et al., 2010; Campana et al., 2011). This diving behaviour has been associated with sharks searching for prey in distinct vertical regions of the water column (Carey & Scharold, 1990; Queiroz et al., 2010; Campana et al., 2011; Queiroz et al., 2012; Vedor et al., 2021a), but it may also function as a mechanism to regain heat loss after deep dives. As heterotherms, blue sharks have a limited ability to conserve heat and raise their body temperature, hence, they rely on the water temperature to regulate their internal temperature (Carey & Scharold, 1990). This vertical movement behaviour occurs throughout the year, except from May to July, coinciding with their mating season (Pratt, 1979).

Blue sharks also take part in numerous migrations throughout the year, often in association with their reproductive cycle and prey distribution (Camhi et al., 2008; Camhi et al., 2009). These migrations might occur on a longitudinal or a latitudinal scale. Several tagging studies have marked individuals in the eastern North Atlantic, off Portugal coast, or in the central North Atlantic, and recaptured them in the western North Atlantic and vice versa, indicating the occurrence of trans-Atlantic migrations (Camhi et al., 2008; Vandeperre et al., 2014). Extensive latitudinal movements have also been observed (Camhi et al., 2008; Vandeperre et al., 2014; Queiroz et al., 2012), although trans-equatorial migrations were shown to be rare (Queiroz et al., 2005; Queiroz et al., 2010; Vandeperre et al., 2014; Queiroz et al., 2017; Vedor et al., 2021b; Mas et al., 2024). Apart from these migratory movements, the blue shark also displays site fidelity to certain locations, including the Azores, the Southwest Atlantic and frontal areas, promoted by higher productivity or improved environmental conditions in these areas (Queiroz et al., 2012; Vandeperre et al., 2014; Vedor et al., 2021a; Mas, 2024).

1.4. Life-history traits: growth, age and reproduction

Blue sharks have a long and slender body (Figure 1.2), ranging in size from 36 cm to 394 cm of fork length (Coelho et al., 2015; da Silva et al., 2021). In terms of age, the oldest individuals encountered in the Atlantic Ocean were between 15 to 16 years of age (Skomal & Natanson, 2003; Jolly et al., 2013; Hsu et al., 2015), while longevity estimates for the blue shark varied between 20 years and 27 years of age (Skomal & Natanson, 2003) Therefore, further research is needed to ascertain the blue shark's longevity in the Atlantic Ocean. In contrast, the oldest individual found in the Indian Ocean had 25 years of age, indicating that longevity may differ between populations of different oceans (Andrade et al., 2019; da Silva et al., 2021). Reproduction has been documented in numerous studies (Pratt, 1979; Compagno, 1984; Nakano & Seki, 2003; da Silva, 2021). According to previous reports, sexual maturity is achieved at four to five and five to six years of age for males and females, respectively. Reproduction occurs mainly between May and June for adult females, while subadult females and males are sexually active all year long (Pratt, 1979). The gestation period lasts about nine to twelve months, after which females give birth to up to 135 pups per litter, depending on the female is size and the region (Compagno, 1984; Nakano & Seki, 2003). After females give birth to their young, the latter will remain in nursery areas, along with other juveniles, until they are grown and sexually mature (Vandeperre et al., 2014). In the North Atlantic, nursery areas exist in the central Atlantic, off the Azores islands, and the eastern side, off the Iberian Peninsula (Vandeperre et al., 2014; Coelho et al., 2018). In the southern hemisphere, nursery areas are located at the eastern side, off South Africa and Namibia, and at the western side, off southern Brazil and Uruguay (Kohler, 2002; Montealegre-Quijano & Vooren, 2010; Coelho et al., 2018).

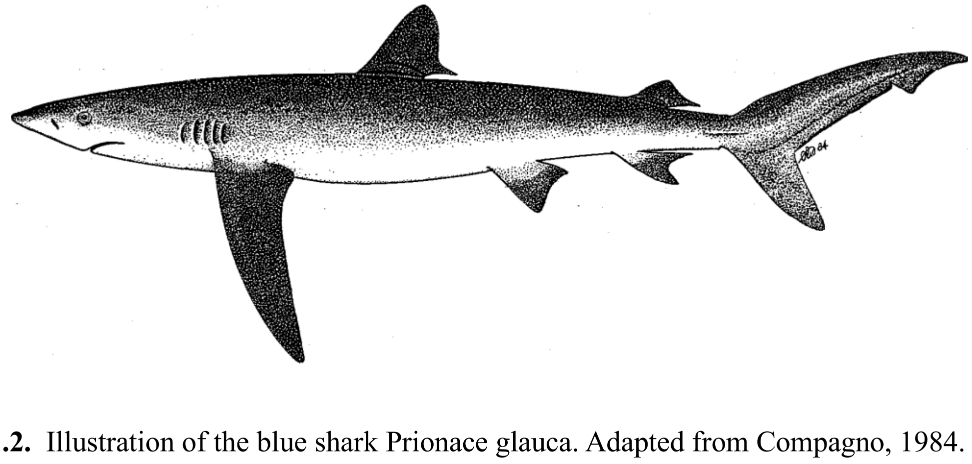

Figure 1.2. Illustration of the blue shark Prionace glauca. Adapted from Compagno, 1984.

1.5. Fisheries and conservation status

1.5.1. Blue shark exploitation and catch statistics

In the fishing market, the blue shark is the most prevalent species among all elasmobranchs, mostly captured as by-catch in longlining fleets targeting swordfish (*Xiphias gladius*) and different tuna species (*Thunnus* sp.) (Buencuerpo, 1998; Stevens et al., 2000; Mejuto et al., 2006; Camhi et al., 2008; Coelho et al., 2012). On occasion, swordfish-targeted fisheries also target blue sharks, when swordfish abundance levels are low (Hareide et al., 2007; Aires-da-Silva et al., 2008). In some cases, blue shark captures surpass 50% of the total fish catch and amount to up to 85% to 90% of the total elasmobranch catch (ICCAT, 2008; Coelho et al., 2012; Burns et al., 2023).

Once a species deemed of low commercial value, its commercial interest has grown in more recent years, especially in the shark fin market, where this species is prevalent (Compagno, 1984; Camhi et al., 2009; Clarke et al., 2006; da Silva et al., 2021). Usually in this trade, the sharks' fins are removed, and the remaining body is discarded at sea, often with no record of their capture being made (Clarke et al., 2004; Campana et al., 2005; Aires-da-Silva & Gallucci, 2007). This practice, known as "finning", constitutes an example of illegal, unregulated and unreported (IUU) fishing. These activities violate fishing regulations and pose a serious threat to fisheries management and hinder the achievement of reliable catch data (Lack & Sant, 2008). Apart from their fins, the blue shark is also exploited for their meat and skin (Camhi et al., 2008), being particularly predominant in Spanish and Portuguese longlining catches (García-Cortés & de la Serna, 2002; Aires-da-Silva et al., 2008; Aires-da-Silva & Gallucci, 2007; ICCAT, 2023).

Depending on the season and the region being exploited by fisheries, captured sharks may vary in sex and level of sexual maturity. In temperate areas of the North Atlantic, preferred by sexually immature sharks, captured specimens are smaller in size. In tropical areas, where adult sharks are more abundant, catches display higher sizes (Kohler, 2002). In the western North Atlantic, male catches have shown to be much more significant than adult female catches. Past decreases in male abundance were possibly a result of fishing exploitation (Simpfendorfer, 2002; Camhi et al., 2008).

1.5.2. Blue sharks' vulnerability to fishing

Like any exploited marine species, the blue shark is not immune to fishing activity, even though it is one of the most productive sharks (Aires-da-Silva & Gallucci, 2007; Dulvy et al., 2008). Elasmobranchs are described as k-selected species, since they display slow growth rates, late maturity stages and low number of offspring (Musick, 1999). Hence, the capacity of the blue shark to recover from overfishing is lower than other commercially relevant species (e.g., sardines), making this species more prone to suffer population declines (Gallucci et al., 2006; Simpfendorfer, 2015). Another source of vulnerability arises from the exploitation of nursery areas, such as the northeastern Atlantic and the Azores, where early life stages are more prevalent. Juvenile survival is crucial for maintaining the stability and prosperity of populations, thus, catches dominated by juveniles constitute a higher ecological risk, as they may lead to population declines (Gallucci et al., 2006; Aires-da-Silva & Gallucci, 2007; Hsieh et al., 2009; Kinney & Simpfendorfer, 2009). These areas should, therefore, be prioritized for conservation efforts.

1.5.3. Stock structure and conservation status

Because blue sharks are highly mobile, understanding their population structure is particularly challenging. Previous studies on the matter recurred to mitochondrial deoxyribonucleic acid (DNA) or microsatellites as phylogenetic markers, and no significant genetic differentiation was detected along the Atlantic Ocean (Veríssimo et al., 2017). On the other hand, the northern and southern Atlantic blue shark populations were considered as two separate stocks in previous studies and by the International Commission for the Conservation of Atlantic Tunas (ICCAT; Kohler, 2002; Camhi et al., 2008; ICCAT, 2015). More recently, Nikolic et al. (2022) performed a genome scan and found distinct patterns of genetic differentiation between both hemispheres of the Atlantic Ocean, and between the North (central-eastern) Atlantic Ocean and the Mediterranean Sea, indicating that multiple genetically distinct populations of blue sharks exist in the Atlantic Ocean. These findings have implications for this species' conservation and exploitation management, as it may require the reformulation of management units to achieve sustainable fishing practices.

The impact of fisheries on blue sharks in the Atlantic Ocean remains unclear. Previous assessments have reported significant declines in abundance of blue shark populations, especially in the western North Atlantic (Simpfendorfer, 2002; Baum, 2003; Cortés, 2007;

Aires-da-Silva et al., 2008). In opposition, other studies and stock assessment reports have challenged the previous findings and reported that blue shark populations were not overfished or under high ecological risk (Burgess, 2005; ICCAT, 2008; Cortés, 2010; ICCAT, 2015; ICCAT, 2023). However, these results should be considered with caution. Many blue shark catches are unreported, not properly identified by the species or discarded at sea, promoting the underestimation of blue shark catch statistics (Pham et al., 2013; ICCAT, 2015).

The blue shark is globally listed as Near Threatened by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, considering the estimated global population declines of 20-29% over three generations time (Rigby et al., 2019). Yet, given the high underestimation of stock assessment reports, it is likely that the blue shark may be listed as Vulnerable in the future (Rigby et al., 2019). In the latest IUCN assessment, the global panmictic population scenario was followed, originating a single global conservation status (Veríssimo et al. 2017; Rigby et al., 2019). However, given recent findings of high genetic differentiation (Nikolic et al., 2022) and the distinct population trends among ocean basins (Rigby et al., 2019), the blue shark's conservation status in the Atlantic may be more severe than its current global status. For instance, in the Mediterranean Sea, the blue shark population was considered as a differentiated subpopulation and listed as Critically Endangered, owning to its significant declines in abundance of 96.5%–99.8% from the 19th century (Ferretti et al., 2008; Rigby et al., 2019).

1.6. Climate change

Temperature is a highly relevant abiotic factor, influencing numerous biological processes from physiological mechanisms to growth and movement (O'Connor et al., 2007; Angilletta Jr. & Angilletta, 2009), ultimately impacting individual fitness levels (Angilletta Jr. & Angilletta, 2009) and mortality rates (Hochachka & Somer, 2002). Due to climate change, concern regarding temperature effects on marine life has increased. Climate change has numerous effects on marine environments, including distribution shifts to higher latitudes and depths (Perry et al., 2005; O'Connor et al., 2007; Brierley & Kingsford, 2009; Hoegh-Guldberg & Bruno, 2010; Poloczanska et al., 2016). This impact may be particularly detrimental to ectothermic sharks, such as the blue shark, given their dependence on water temperature to regulate their own internal temperature (Carey & Gibson, 1987).

1.7. Objectives

The blue shark is one of the most exploited species of all elasmobranchs, even though its population status remains unclear. Proper conservation management of this species requires more studies addressing the impact of fisheries. Furthermore, climate change is another driver of changes in marine species distribution and abundance (Perry et al., 2005; Poloczanska et al., 2016), raising the need for an assessment of its effect on blue shark populations. In this study, the tracking data of 49 blue sharks was used to assess the shark's habitat suitability (HS) in the Atlantic Ocean for present and future (2090-2100) conditions. The resulting models were, then, compared to fishing activity data to identify areas of overlap between blue sharks and fishing vessels. The present study aimed to 1) assess changes in blue shark habitat suitability in the North Atlantic in light of climate change, and 2) identify regions of major vulnerability to fisheries.

2. Materials and Methods

2.1. Study area and tagging

2.1.1. Study area

From February 2009 to July 2017, 49 sharks were tagged in multiple sites in the North Atlantic Ocean (Figure 2.1). Of the 49 sharks, 22 were tagged near the Azores, three in the south coast of Portugal, ten around Cape Verde and 14 others in the central North Atlantic, between 10ºN and 42ºN of latitude. The study area with the extent (70º W, 10º E, 10º S, 60º N) was considered for further analysis (Figure 2.1).

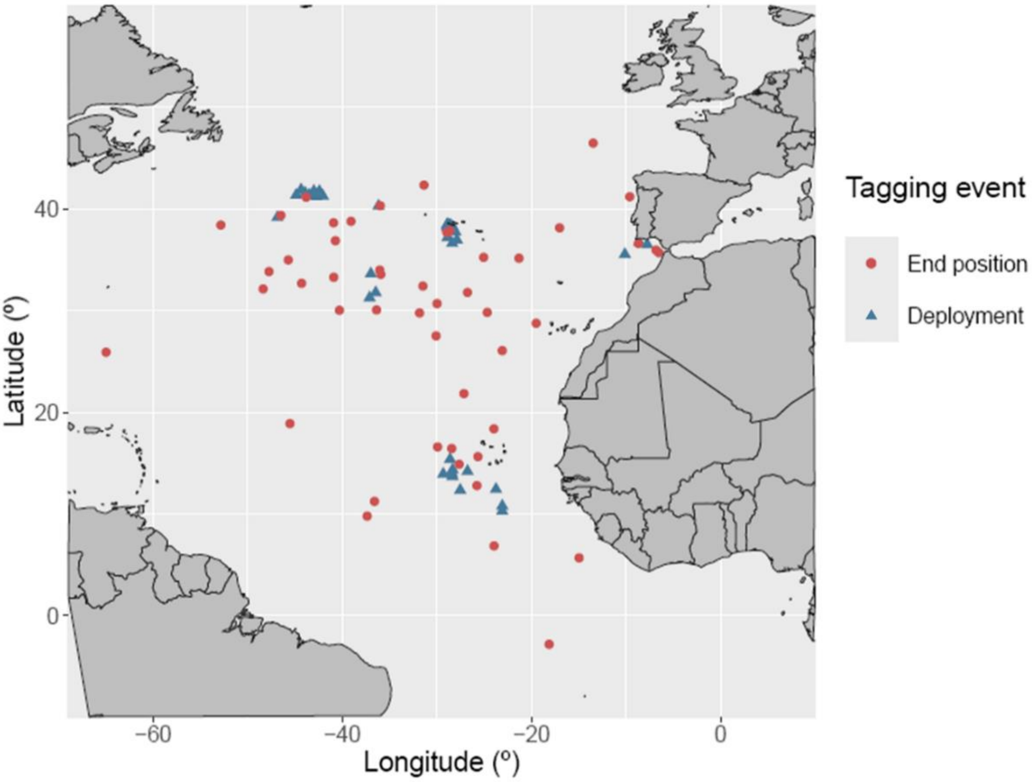

Figure 2.1. Deployment (blue) and end-position (red) locations of the 49 tagged sharks.

2.1.2. Tagging methods

The blue sharks were caught in commercial fishing vessels using longlines in oceanic areas. Once captured, sharks were lifted alongside the vessel and tagged, by attaching a Smart Position Only satellite transmitter Tag (SPOT5, Wildlife Computers, Redmond, WA, USA) to the first dorsal fin. The tag was attached with stainless steel bolts, nuts and neoprene washers.

In coastal regions, sharks were captured using drumlines. Once captured, sharks were brought alongside the boat, or to a partly submerged platform, and tagged in a similar way to oceanic locations.

2.2. Data sources

2.2.1. Occurrence data

Raw data was processed using the software WC-GPE, provided by the SPOT tag manufacturer (Wildlife Computers). Failed position estimates (i.e. location class Z data) were removed from the dataset. Each position was also filtered using a continuous-time state-space model and parameterized with model parameters in the crawl R package (Johnson & London, 2018), obtaining a single, most probable track, using daily positions.

2.2.2. Fishing data

Fishing data was retrieved from Global Fishing Watch (GFW), an open-access project that aims to monitor fishing activity using an automated identification system (AIS) network (Merten et al., 2016; Kroodsma et al., 2018). All data included in the study area between 2012 (starting date of the GFW project) and July 2017 was retrieved from the website (https://globalfishingwatch.org/data-download/). GFW data includes mostly large fishing vessels, higher than 24 meters long, given that smaller vessels are not so frequently registered in local or global public vessel registries. In addition, small vessels are less likely to use AIS, thus, less information on these vessels is available (Merten et al., 2016). In the dataset, each vessel geolocation is provided, along with its flag state, gear type and the amount of time (in hours) spent fishing in a given location and day.

2.2.3. Environmental data

Environmental data was collected from multiple platforms. From the Copernicus Marine Environment Monitoring Service (CMEMS) website (http://marine.copernicus.eu/), oceanic physical variables – sea surface temperature (SST), salinity and mixed layer depth (MLD) were retrieved from the Global Ocean Ensemble Physics Reanalysis. Oceanic biogeochemical variables - surface O_2, chlorophyll a concentration (CHL) and net primary productivity (NPP) - were retrieved from the Global Ocean Biogeochemistry Hindcast. All data was collected at a monthly periodicity from February 2009 to July 2017, which corresponded to the total tagging period, and grouped by seasons. The selected grid corresponded to tropical and temperate regions of the Atlantic Ocean, with longitude ranging from 70º W to 10º E and latitude ranging from 10º S to 60º N. The bathymetric data was obtained from the General Bathymetric Chart of the Oceans (GEBCO) website (https://www.gebco.net/data_and_products/gridded_bathymetry_data/). These variables were shown to be relevant determinants of the blue shark distribution in previous studies (Compagno, 1984; Queiroz et al., 2005; de Sousa, 2009; Queiroz et al., 2010; Queiroz et al., 2016; Vedor et al., 2021a; Vedor et al., 2021b).

Future oceanic conditions were assessed for the following variables – SST, surface O_2, salinity, NPP, MLD and CHL – and were retrieved from BioORACLE (Assis et al., 2017). Retrieved data corresponded to mean projected values for the decade 2090-2100, following the RCP 5-8.5 scenario. This scenario represents the pathway of the highest future greenhouse gas emissions, as a result of a no imposed climate change mitigation policies (Bindoff et al., 2019).

2.3. Data processing and analysis

2.3.1. Data import and manipulation

Initially, occurrence data from the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/) and Ocean Biodiversity Information System (OBIS; https://obis.org/) databases was retrieved and combined with the biotelemetry data for model implementation. Since the resulting models displayed low performance, only biotelemetry data was included in the final models.

Shark track records were imported into R (R Core Team, 2024) where duplicated and NA records were removed. The data was then filtered by removing records more than two days apart and less than five km apart from the previous records, thereby removing possible outliers and duplicate records, respectively. Following the filtering process, all records were grouped by each season (i.e. winter, spring, summer and autumn).

Environmental data was imported into R and converted from a netCDF format to a raster, composed by $27.75 \, . \, 27.75 \text{ km}^2$ grid cells. From the temperature raster, a temperature slope raster was created by calculating the standard deviation between a given cell and its eight neighbouring cells, using the package raster (Hijmans, 2024). Subsequently, all monthly variables were stacked by seasons and scaled for further model implementation, using the package raster (Hijmans, 2024).

Daily fishing data was imported into R, where all NA and duplicate records were removed and records outside of the study area were excluded. In terms of fishing métiers, only longlining fleet data was kept, given its significance in the blue shark's exploitation (Buencuerpo et al., 1998; ICCAT, 2023). Additionally, only data with fishing hours equal to or higher than one hour were included, as shorter soak times may not be sufficient to capture blue sharks (Ward et al., 2004; Morgan & Carlson, 2010). Finally, all data was grouped by seasons and aggregated in 27.75 . 27.75 km^2 grid cells (i.e. same resolution as the variables raster) to obtain fishing vessel abundance.

2.3.2. Preliminary analysis

Before applying the blue shark species distribution model (SDM), a brief analysis of the shark records' summary statistics was performed. Initially, the number of tagging days per ID and the time interval between tracks was obtained. In terms of location, both tag deployment and end-position locations were collected and plotted using the package ggplot2 in R (Wickham, 2016). Finally, distances travelled between positions was calculated.

2.4. Shark distribution modelling

2.4.1. Model data preparation

The blue shark's habitat suitability was assessed by computing generalized additive models (GAMs) for present and future conditions. The present models were created to identify suitable habitats for the blue shark and for comparing with the future models. The datasets corresponding to each season were used separately for model implementation, since this species' distribution varies seasonally (Coelho et al., 2018). Initially, pseudo-absence points were created, by generating random points at a 10:1 pseudo-absences:presences ratio (Barbet-Massin et al., 2012) and a minimal distance of 100 km from each track. Subsequently, the data was split by a 50:50 ratio into a training subset, which was used for model implementation, and a testing subset, used for model validation. To assess variable correlation, a correlation matrix was performed using the Pearson correlation method. Variable pairs with strong correlations - ρ higher than 0.5 - were not included in the same model.

2.4.2. Model implementation

The GAM was created by using the package mgcv in R (Wood, 2011). Initially, all non-correlated variables were combined in the initial models. The model was implemented using the binomial family and each covariate was fitted by spline-smoothers, with an adjusted number of knots to assure optimal model performance (Table A.1).

2.4.3. Model evaluation

Model selection was performed to identify which covariates to keep in the final model. by comparing each model's weighted Akaike Information Criterion (wAIC) and Area Under the Curve (AUC; Phillips et al., 2006) values. Then, the AUC for the model predictions on the test subset were calculated. The model with the lowest wAIC and highest AUC was selected as the final model. Variable importance was considered as the difference between the deviance explained of the full model and the deviance explained of the model without a given variable. Finally, the response curves of the variables were plotted and taken in consideration during model evaluation.

2.5. Fishing and blue shark distribution overlap

The geographical overlap between fishing vessels' locations and the blue shark's suitable habitats was calculated for the present and future (2090-2100). For this assessment, only suitable areas for the blue shark (defined here as probability values above median) were considered. The present overlap was computed by merging the blue shark's present suitable areas raster predicted by the model with the fishing vessel abundance raster. The future overlap was inferred by following the assumption that fishing activity does not suffer significant location changes in the future. Thereby, the future blue shark's model prediction raster was merged with the present fishing vessel abundance data. Finally, the resulting overlaps were plotted with ggplot2 (Wickham, 2016), where the shark's habitat suitability was represented by colour.

3. Results

3.1. Shark movement patterns

Shark movements were recorded throughout eight years, from 19 February 2009 to 16 July 2017. Sharks were monitored for an average of 68.56 days (range of nine to 214 days; Figure A.1). Distance between deployment and pop-off locations varied from 10.59 km to 4381.75 km. Sharks travelled, on average, 36.72 km, and up to 119.45 km per day. Transatlantic movement is evident in the North Atlantic, between the Iberian Peninsula and Nova Scotia. No sharks tagged here travelled to polar regions or the South Atlantic. In terms of seasonality, there was no distinctive movement variation between seasons (Figure 3.1).

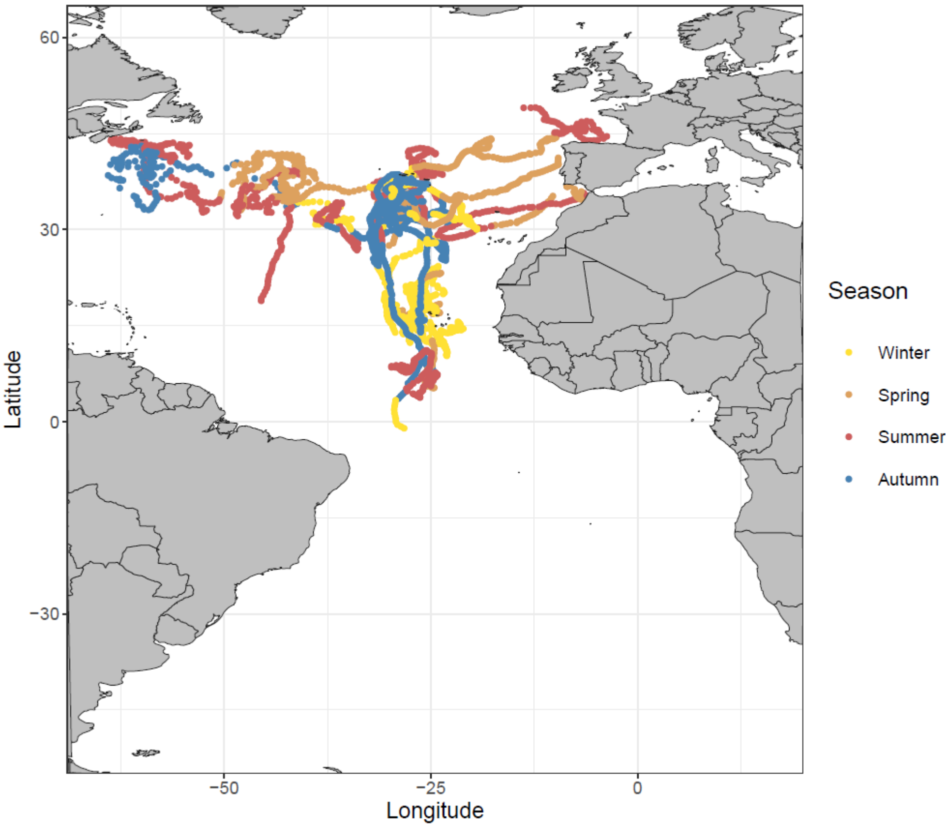

Figure 3.1. Track locations of the 49 tagged sharks, coloured by season. Yellow dots represent winter tracks, orange dots represent spring tracks, red dots represent tracks recorded in the summer and blue dots represent winter tracks.

3.2. Shark distribution model

All chosen models displayed a relatively good performance, with AUC values higher than 0.9 in each season (Table 3.2). Of the covariates incorporated in the models, SST was the most relevant variable in most models (Table A.2). Variable response curves are represented in the Figures A.2 to A.7. Overall, seasonal shifts in habitat suitability were seen throughout the present and future model predictions.

3.2.1. Shark present distribution model

In winter, more suitable areas occurred in the central Atlantic, off the Azores, and the eastern Atlantic, off the northwestern coast of Africa and the south of Portugal (Figure 3.2). At equatorial regions and at higher latitudes (above 40º N), habitat suitability was significantly lower. Suitable areas (probability > 0.5) corresponded to 10.1 % of the total marine area, which was the lowest of all seasons (Table 3.1). All covariates, apart from salinity (i.e., surface O_2, CHL, SST and SST slope), displayed a negative response curve (Figure A.2). In particular, CHL was the most relevant covariate in the final model, with 12.4 % of the data deviance explained (Table A.2).

In springtime, an expansion towards higher latitudes was visible (Figure 3.2). In the central Atlantic, numerous areas became suitable and the region around the Azores displayed higher levels of suitability. Around Portugal and northwestern Africa, fitted areas were seen closer to the shore. In contrast, equatorial and southern regions became less suitable. Suitable areas occupied 23.3% of the total area (Table 3.1). In this season, some of the model's covariates showed different responses. SST and MLD displayed a negative parabolic response curve, while SST slope displayed a positive parabolic curve (Figure A.3). The highest contributing covariate was SST, as it explained 15.1% of the data deviance (Table A.2).

In summer, adequate areas were observed at their highest latitudes, having reached British and Irish waters (Figure 3.2). In the Mediterranean Sea, an increase in suitability was displayed. On the other hand, the equatorial region remained highly unsuitable, apart from the region off northwestern Africa and Cape Verde. This season displayed the highest level of suitability, as suitable areas occupied 25.1% of the total area (Table 3.1). In this model, MLD and NPP displayed a negative response, while salinity displayed a positive response curve (Figure A.5). The highest contributing covariate was SST, with 27.9% of deviance explained, and its response curve was similar to the previous model (Table A.2).

During autumn, a notable shift to lower latitudes was observed, particularly in regions above 40ºN (Figure 3.2). The regions off Portugal and northwestern Africa displayed extremely high levels, in similarity to the pattern observed in spring. Surrounding regions, such as the Mediterranean Sea and the Bay of Biscay, became more fitting as well. Around the equator, suitability levels remained similar. In this season, suitable areas corresponded to 18.1% (Table 3.1). In this model, MLD and NPP displayed a negative response, while SST slope displayed a positive response curve (Figure A.6). The highest contributing covariate was SST, with 26.2% of deviance explained, and its response curve was similar to the previous model (Table A.2).

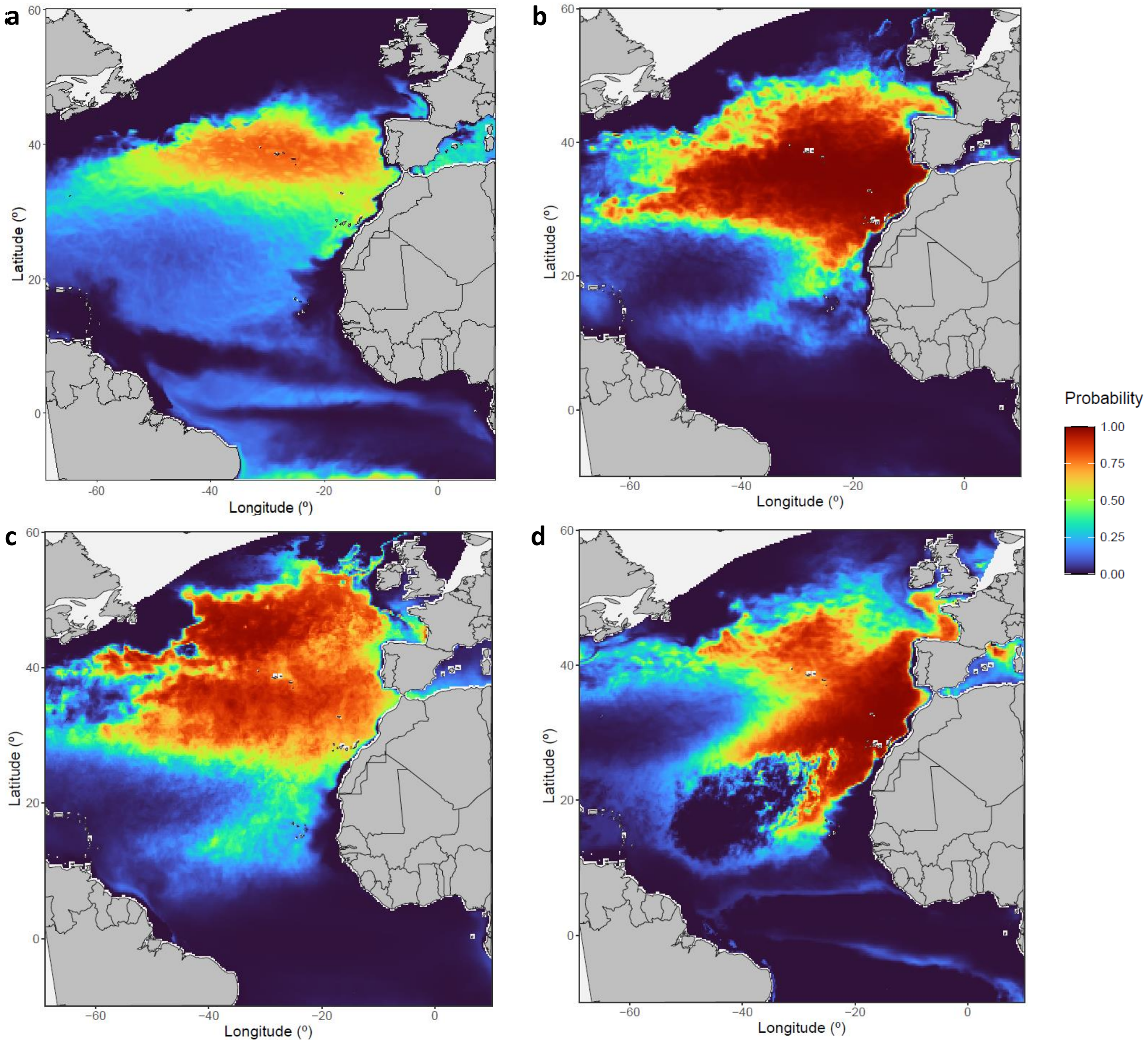

Figure 3.2. Predictive map of the shark's present distribution model for the winter (a), spring (b), summer (c) and autumn (d). Probability of occurrence is represented by the colour gradient.

3.2.2. Shark future distribution model

The future (2090-2100) winter model displayed similar hotspots as the present model. In detail, the Azores and the temperate eastern regions of the Atlantic are expected to remain highly suitable in the future (Figures 3.3 and 3.4). In this season, scenarios of habitat suitability expansion were more common, particularly in the central north Atlantic and in coastal areas around the Iberian Peninsula and northwestern Africa. In regions at 40ºN, a few regions in the western Atlantic were also predicted to become more suitable. On the other hand, a considerable region located northwest of the Azores was predicted to become less suitable. Suitable areas occupied 13.7% of the whole study area, corresponding to an increase of 6% of the total region by the end of the century (Table 3.1). Covariates displayed contrasting response curves, in relation to the present model. CHL and SST slope displayed negative responses, while salinity, SST and surface O_2 displayed positive response curves (Figure A.2). The highest contributing covariate was CHL, with 7.9% of deviance explained (Table A.2).

In the spring, higher suitability shifted towards higher latitudes, as observed in the present models (Figure 3.3). Overall, habitat suitability remained similar to the present model in most regions. Habitat suitability reduction occurred mostly in a broad area between 30ºN and 40ºN of latitude in the central Atlantic, although it was also observed in coastal areas of the eastern Atlantic. In this season, suitable areas occupied 19.7% of the study area, hence, a reduction of 3.6% of the study area was predicted (Table 3.1). In this model, some of the model's covariates displayed a different response. SST and MLD displayed a negative parabolic response curve, CHL and SST slope displayed a negative curve and salinity showed a positive curve (Figure A.4). The highest contributing covariate was SST, with 26.6% of deviance explained (Table A.2).

In the summer, habitat suitability shifted towards higher latitudes, as in the present model (Figure 3.3). However, northern regions around 50ºN of latitude were predicted to become less suitable over time. Other regions were also predicted to become less fitting, such as coastal areas around western Europe and northwestern Africa and, more broadly, in the central Atlantic at 30ºN latitude. In opposition, habitat suitability expansion was predicted to occur in the region surrounding Mauritania and, less significantly, in dispersed regions of the western Atlantic. Suitable areas are expected to decrease by 2.7% of the whole area, resulting in 22.4% of suitable areas in the future (Table 3.1). In this model, SST, MLD and salinity displayed a negative parabolic response curve, while NPP showed a slight positive parabolic curve (Figure A.5). The most relevant covariate was SST, with 40.0% of deviance explained (Table A.2).

The autumn model displayed a scenario of habitat expansion, particularly between 30ºN and 50ºN and in the region off Mauritania (Figure 3.3). In contrast, the northeastern Atlantic displayed less suitable areas, particularly in the Bay of Biscay and the off the Spanish coast. Other dispersed regions in the central Atlantic also displayed a reduction of habitat suitability. Suitable areas occupied 23.8% of the study area, reflecting an increase of 5.7% of the study area (Table 3.1). In this model, SST, MLD and SST slope displayed a negative parabolic response curve, while NPP showed a slight positive parabolic curve (Figure A.6). The highest contributing covariate was NPP, with 19.6% of deviance explained (Table A.2).

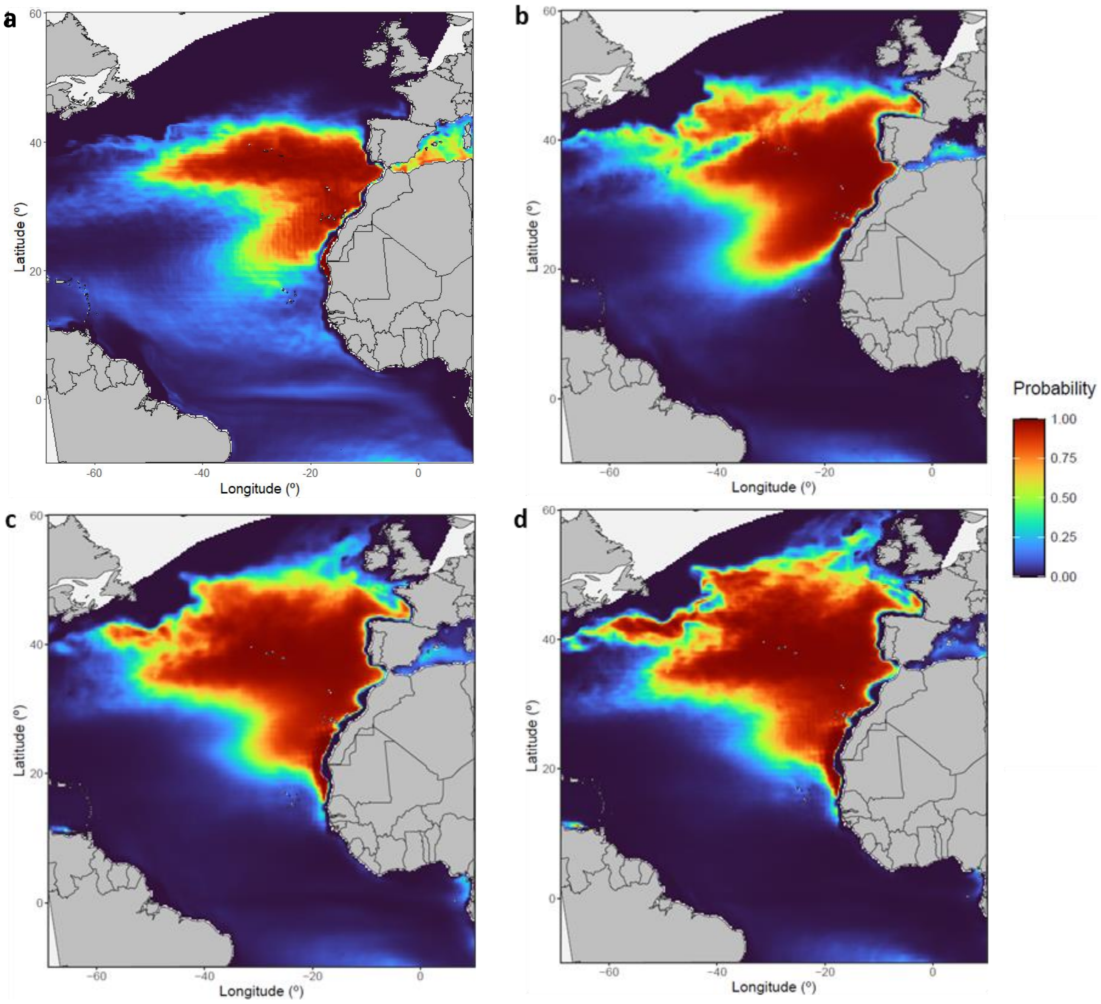

Figure 3.3. Predictive map of the shark's future distribution model for all seasons - winter (a), spring (b), summer (c) and autumn (d). The probability of occurrence is represented by the colour gradient.

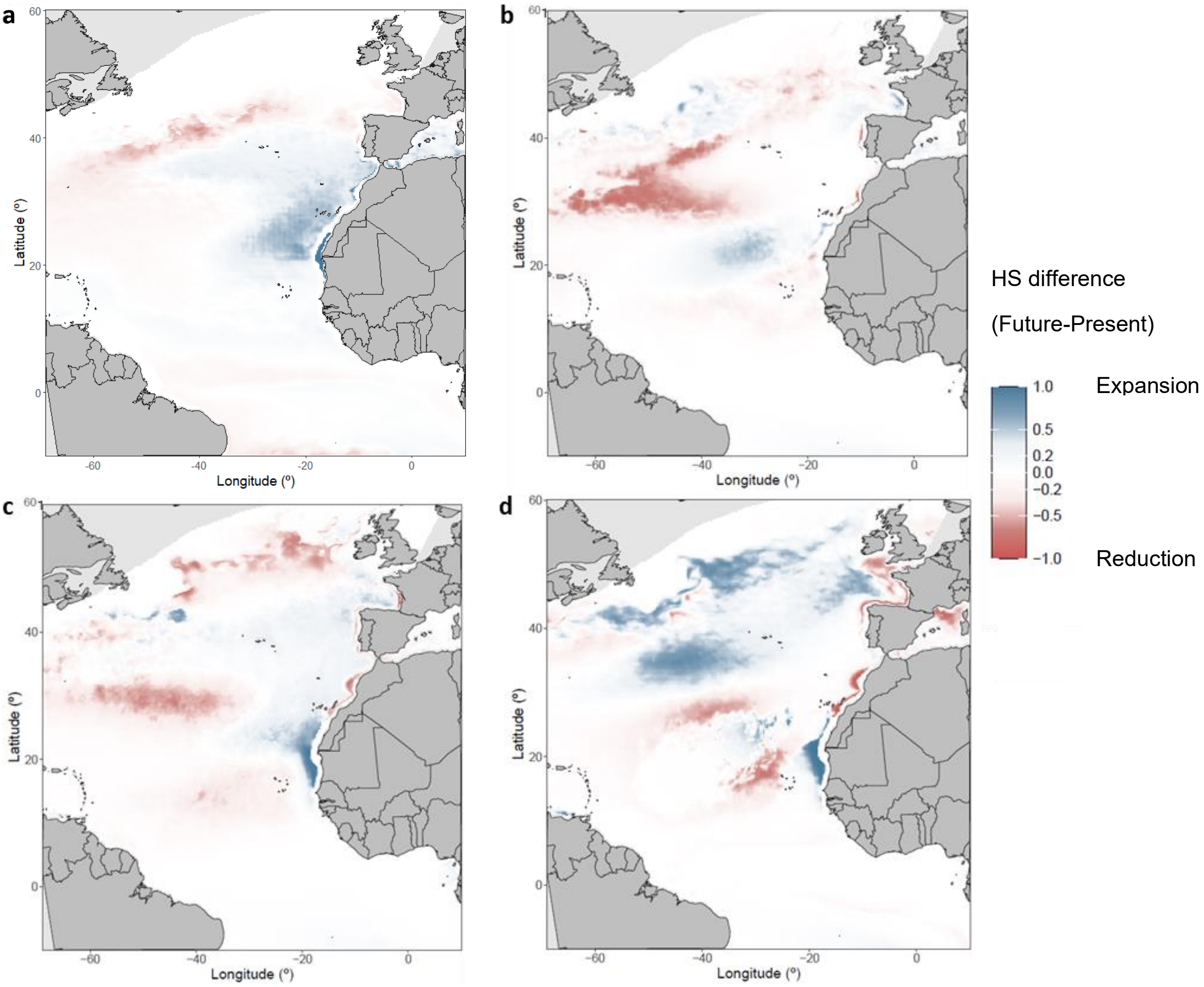

Figure 3.4. Present and future distribution model differences (Future - Present) of the shark's habitat suitability for the winter (a), spring (b), summer (c) and autumn (d).

Table 3.1. *Suitable areas for the blue shark displayed by the habitat suitability models.*

		Total suitable area (P above 0.5; km^2)	**Study area coverage of suitable areas (%)**
Winter	Present	3969034	10.1
	Future	5387772	13.7
Spring	Present	9198814	23.3
	Future	7765770	19.7
Summer	Present	9909044	25.1
	Future	8816224	22.4
Autumn	Present	7114034	18.1
	Future	9371170	23.8

Table 3.2. *Summary statistics of the blue shark's distribution models.*

		AUC	Δ LL	Deviance explained (%)	EDF	HS mean value	HS maximum value
Winter	Present	0.902	-1233.451	38.5	10	0.200	0.992
	Future	0.969	-699.740	48.2	16	0.236	1.000
Spring	Present	0.957	-591.945	69.6	9	0.266	0.998
	Future	0.956	-647.414	66.4	9	0.223	0.996
Summer	Present	0.925	-1161.87	54.6	8	0.287	0.977
	Future	0.910	-1011.013	59.4	7	0.252	0.999
Autumn	Present	0.937	-1225.59	52.4	8	0.221	0.991
	Future	0.964	-824.163	67.7	8	0.264	1.000

3.3. Fishing activity

Overall, fishing vessels were widely distributed across the Atlantic Ocean. Fishing activity is represented by the distribution and abundance of fishing vessels in the Atlantic Ocean (Figure 3.5). In each season, higher fishing activity was evident in numerous regions, including the area between 30ºN and 45ºN latitude and open ocean regions adjacent to the western coastline of Africa. A seasonal variation of fishing vessel abundance and area coverage was observed, since higher levels were displayed in the summer and autumn (Table 3.3). This variation was particularly visible in the region above 40ºN, the Mediterranean Sea and the region below 15ºS of latitude, adjacent to the coastline.

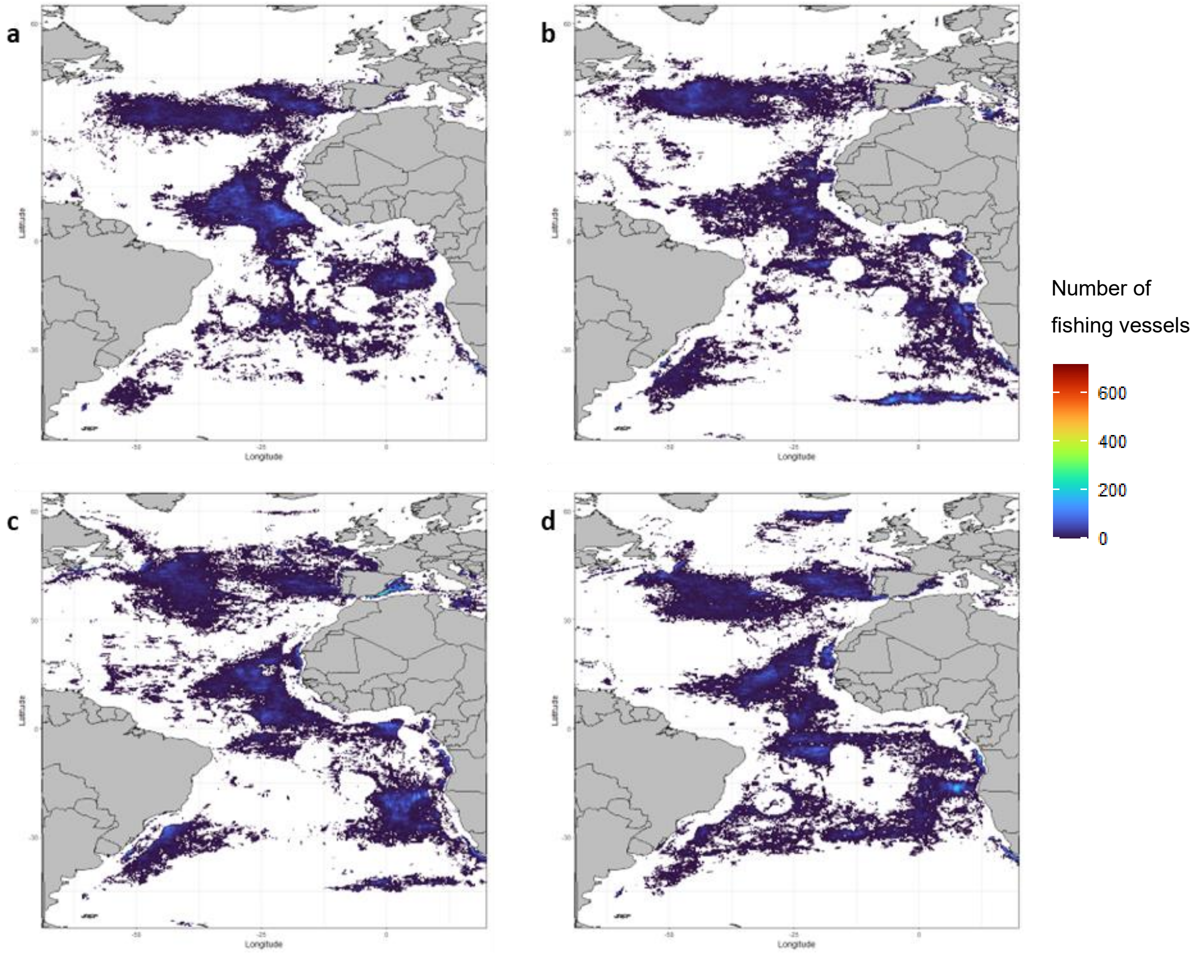

Figure 3.5. Large vessel longliners' abundance in all seasons - winter **(a)**, spring **(b)**, summer **(c)** and autumn **(d)**.

Table 3.3. *Fishing vessel abundance statistics.*

Season	Winter	Spring	Summer	Autumn
Number of vessel locations	268641	296908	327471	320371
Portion of study area occupied by vessels (%)	0.1751	0.2068	0.2118	0.2077
Mean abundance per cell	9.71	9.10	9.80	9.76
Maximum abundance per cell	227	402	717	629

3.4. Overlap between sharks and fishing vessels

3.4.1. Present overlap between blue shark suitable habitat and fishing effort

Overall, the overlapping area ranged in its majority from 10ºN to 50ºN, with a higher prevalence towards the eastern side (Figure 3.5). In winter, overlaps ranged from 10ºS to 45ºN of latitude (Figure 3.5). The largest overlapping zone occurred at 30ºN to 40ºN, from the central to eastern Atlantic. In the central Atlantic, the highest overlap was observed offshore in the Azores region. In the eastern Atlantic, the largest overlapping area extended towards the regions off the Iberian Peninsula and northwestern Africa, including the Canary Islands. Near the equator, smaller overlapping zones were displayed in the central Atlantic. Overall, he largest overlapping area occurred in this season, amounting to 7.46% of the study area (Table 3.4).

In spring, the overlap area displayed was similar to the previous season (Figure 3.5). In the northern temperate (30ºN-40ºN) region, the largest overlap coincided with the blue shark's most suitable areas. In the northeastern Atlantic, a smaller overlap was observed in the region off the Iberian Peninsula. Overall, total overlapping area corresponded to 6.79% of the whole region (Table 3.4).

During the summer, the major overlapping area in the 30ºN-40ºN region was more dispersed (Figure 3.5). At higher latitudes, small areas of overlap were observed at around 50ºN. In the northeastern Atlantic, overlaps were displayed closer to shore, particularly in the Iberian Peninsula coast. In this season, the overlapping area amounted to 6.08% of the study area (Table 3.4).

In the fall, overlapping regions extended further north, having reached the British and Irish waters (Figure 3.5). In the central Atlantic, the region of overlap was also broader than in the previous seasons. In the northeastern side, the portuguese coastal areas and the adjacent region displayed a more prominent overlap. The Bay of Biscay and the Mediterranean Sea followed the same pattern. In northwestern Africa, the overlap adjacent to the coastline displayed a reduction. In total, the overlap corresponded to 6.77% of the study area (Table 3.4).

Table 3.4. *Overlap of the blue shark-fishing vessel spatial overlap.*

		Overlap area (km^2)	**Study area coverage (%)**
Winter	Present	$4.91 . 10^6$	7.46
	Future	$5.94 . 10^6$	9.02
Spring	Present	$4.47 . 10^6$	6.79
	Future	$4.04 . 10^6$	6.14
Summer	Present	$4.00 . 10^6$	6.08
	Future	$4.19 . 10^6$	6.37
Autumn	Present	$4.45 . 10^6$	6.77
	Future	$4.43 . 10^6$	6.73

3.4.2.Future overlap between blue shark suitable habitat and fishing effort

The future (2090-2100) overlapping area in winter is represented in Figure 3.6. The broadest overlap in the 30ºN-40ºN region is expected to expand towards the Iberian Peninsula coast. In the centre of the North Atlantic, small changes were also predicted. The most significant overlap expansion was predicted for the region off northwestern Africa, with new overlapping zones further south extending to the equator (Figure 3.7). This season displayed the largest overlap expansion, extending from 7.46% in the present to 9.02% by the end of the century (Table 3.4).

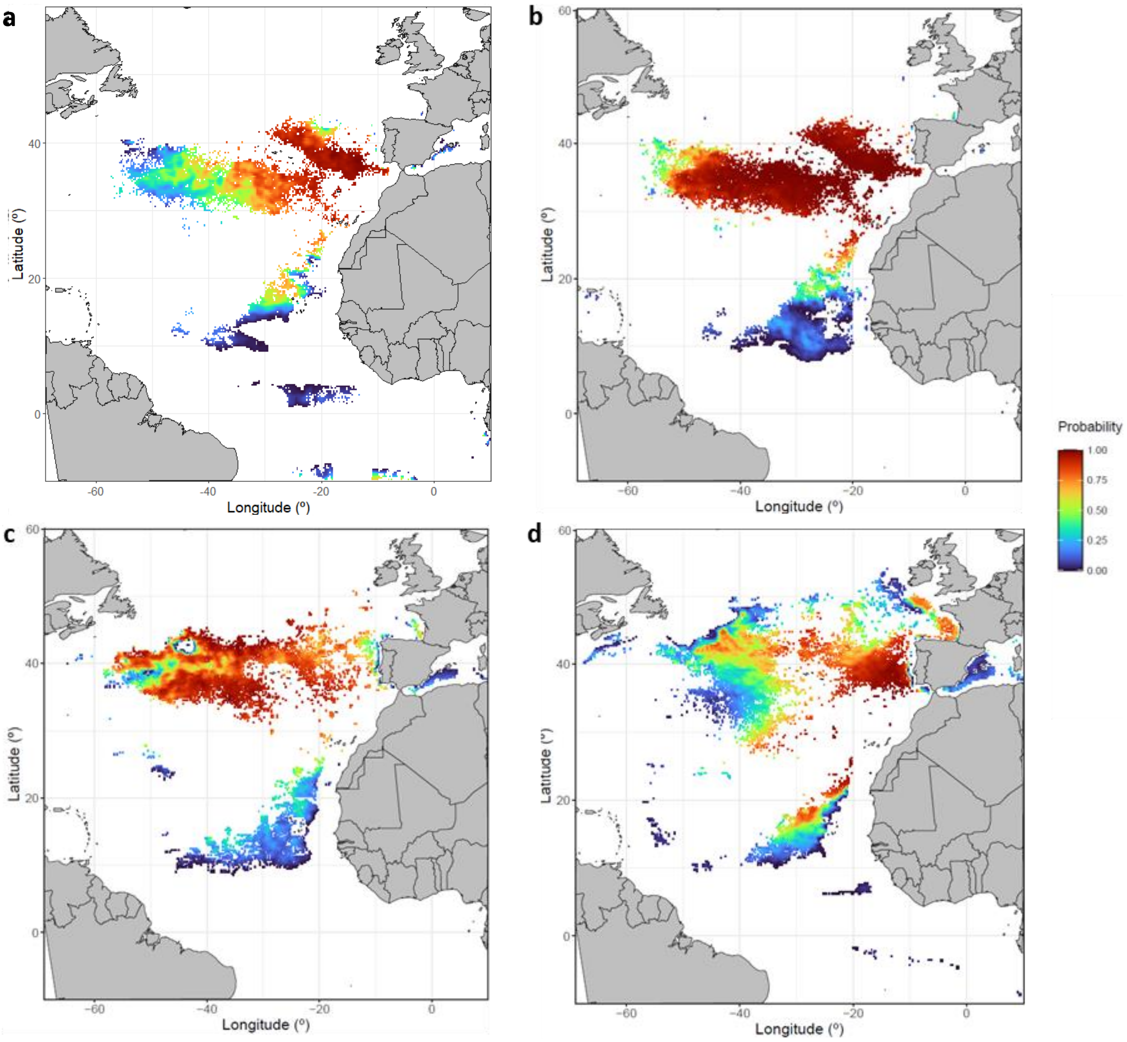

Figure 3.6. Spatial overlap between the blue shark's habitat suitability present model and fishing activity for winter (a), spring (b), summer (c) and autumn (d). Shark habitat suitability is represented by the colour gradient.

In spring, the overlapping area in temperate regions was mostly maintained, apart from the expansion in the Mediterranean Sea (Figure 3.6 and 3.7). At lower latitudes, a significant reduction was observed in regions nearest to the equator. The largest expansion was displayed in the southern hemisphere, between 5ºS and 10ºS. By the end of the century, the overlapping region is expected to decrease from 6.79% to 6.14% (Table 3.4).

In summer, the overlapping area in the North Atlantic was kept throughout time, expanding in the Mediterranean Sea and around Cape Verde (Figure 3.7). In contrast, the most significant reduction was observed in the region located south of Cape Verde. In tropical regions, small expansions of overlap were predicted, as it was observed in the previous season. In the summer, the total overlapping area displayed a slight increase throughout time, from 6.08% to 6.37% of the study area (Table 3.4).

During autumn, the largest overlap in the northern hemisphere was also observed in future conditions (Figure 3.7). At lower latitudes, the overlap around northwestern Africa displayed an expansion closer to shore and a reduction in the most southern regions. Consistent with other seasons, small overlap expansions were observed near the equator. In this season, the total overlap is expected to decrease slightly, from 6.77% to 6.73% by the end of the century (Table 3.4).

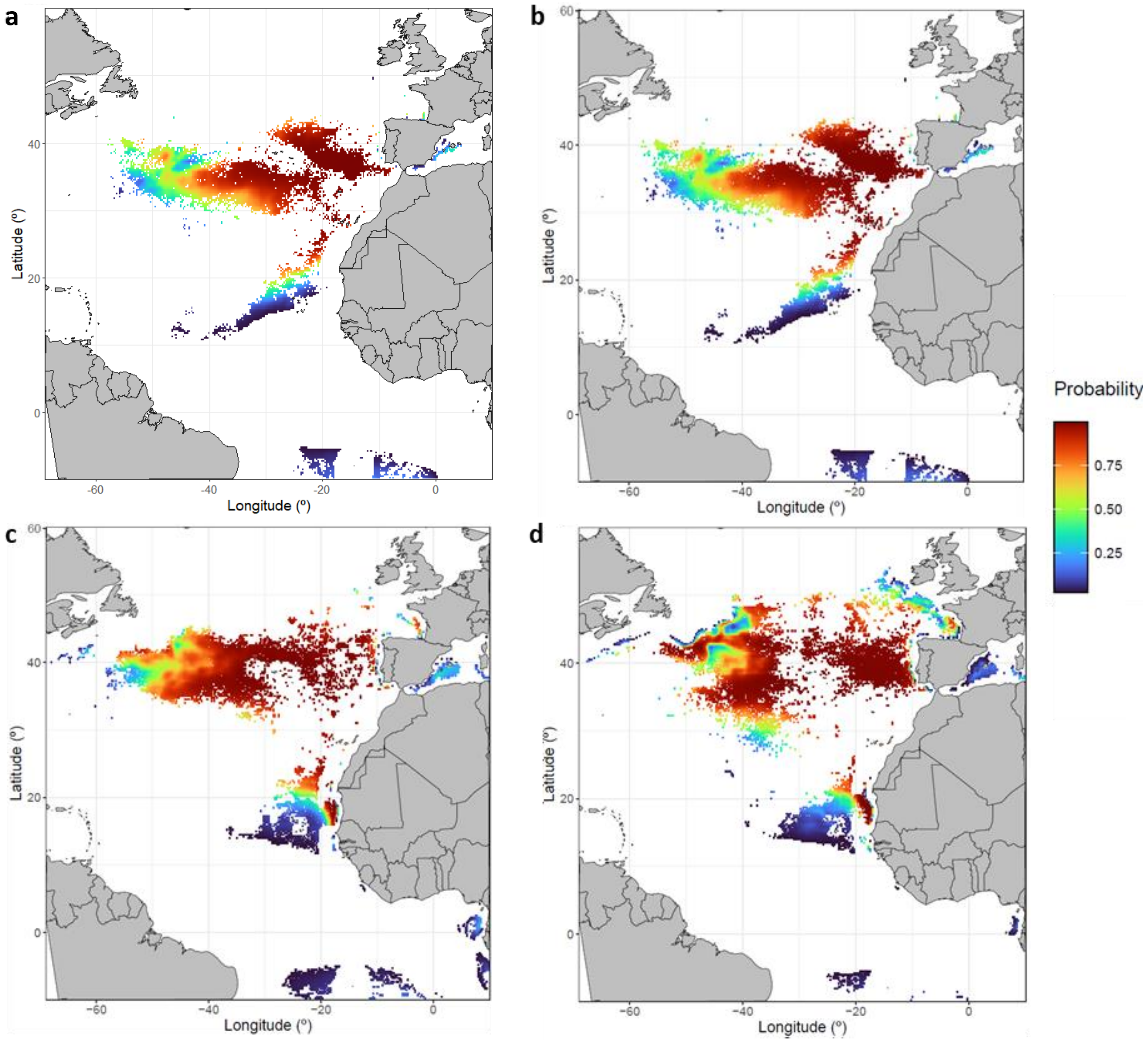

Figure 3.7. Spatial overlap between the blue shark's habitat suitability in the future (2090-2100) and current fishing activity in the winter (a), spring (b), summer (c) and autumn (d). Shark habitat suitability is represented by the colour gradient.

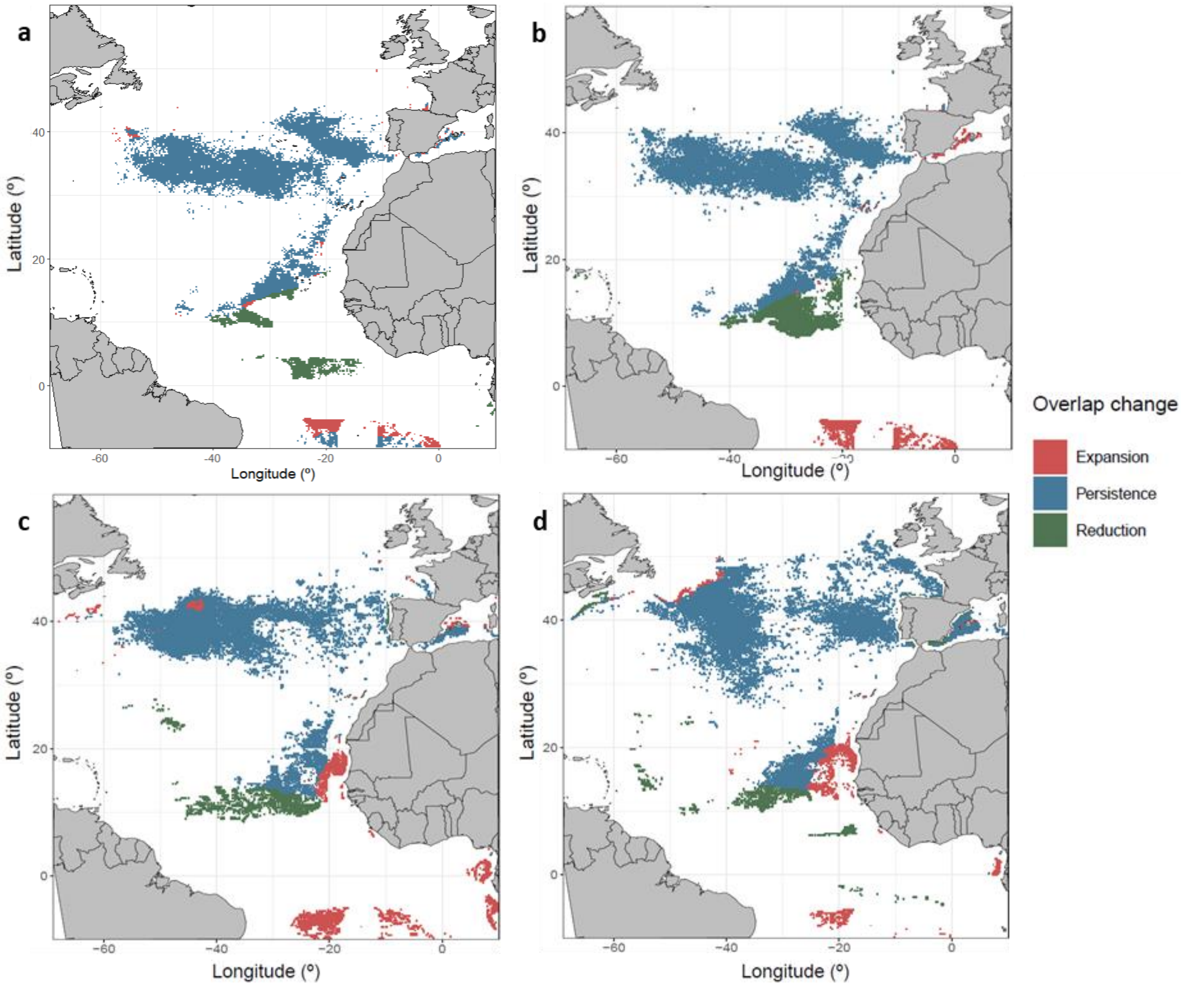

Figure 3.8. Present vs. future spatial overlap between the blue shark's suitable areas and fishing activity in the winter (a), spring (b), summer (c) and autumn (d). Overlap changes may follow a scenario of expansion (red), persistence (blue) and reduction (green). Results were presented separately for the winter (a), spring (b), summer (c) and autumn (d) seasons.

4. Discussion

Marine species are exposed to changing environments, such as increasing temperatures and ocean deoxygenation, caused by climate change (Bindoff et al., 2019; Vedor et al. 2021b), triggering changes in populations (Perry et al., 2005; Rosa et al., 2014; Birkmanis et al., 2020; Crear et al., 2020; Gervais et al., 2020; Osgood et al., 2021). The complexity and diversity of sharks' responses to climate change (Rosa et al., 2014; Birkmanis et al., 2020; Gervais et al., 2020; Osgood et al., 2021) raise the need for further studies. Since this species is also affected by fishing activity (Simpfendorfer, 2002; Baum et al., 2003; Cortés et al., 2007; Aires-da-Silva et al., 2008; Coelho et al., 2012), the combined action of these two stressors may lead to drastic changes in this species' populations (Vedor et al., 2021b). Hence, exploring the impact that these factors have on blue sharks is of particular interest.

This study provides the first future projection in the North Atlantic of suitable surface habitats for blue sharks and overlapping areas with fisheries within a climate change scenario. It was demonstrated that habitat suitability may suffer declines due to climate change, although this pattern was not consistent throughout the year. In colder months (i.e. autumn and winter), where suitable areas are narrower, a scenario of habitat expansion was observed. Warmer seasons, however, displayed a reduction of suitable habitats in the future (2090-2100) scenario. Changes in overlap were also inconsistent between seasons, although the eastern region displayed an overlap throughout the year in both scenarios.

4.1. Shark distribution modelling (present)

The present habitat suitability model displayed marked differences between seasons, thus, demonstrating that the blue shark's distribution varies according to the seasons (Coelho et al., 2018).

In winter, suitable areas were more prominent in the eastern side of the North Atlantic, from 15ºN to 50ºN. These results were consistent with the movements performed by sharks within this region, heading towards the equator in search for warmer regions (Queiroz et al., 2016). In contrast, the spring model displayed higher suitability towards the central and western Atlantic, and further north within the 50ºN limit. The results obtained are concordant with previous studies showing extensive movement that takes place in this season for mating purposes (Pratt, 1979; Simpfendorfer et al., 2002; Queiroz et al., 2016).

In the summer season, the model showed a significant increase in habitat suitability in more northern regions up to 55ºN. These results, along with the covariate's response curve, suggest that SST may have been a limiting factor for the suitability of lower latitudinal regions. Thus, sharks may move further north to avoid high SSTs (Queiroz et al., 2005; Queiroz et al., 2012; Queiroz et al., 2016). In addition, the prevalence of highly suitable areas extending from the western to the eastern side was consistent with the migrations performed by females after mating, towards the eastern North Atlantic (Simpfendorfer et al., 2002).

In the fall, suitable areas were more confined to regions of the eastern side and below 40ºN, which was supported by the movement of blue sharks towards warmer regions in this season (Queiroz et al., 2005; Queiroz et al., 2012), However, other patterns observed were inconsistent with the previous SDM (Sousa, 2009). For instance, significantly higher suitability levels in the British and Irish waters and the Bay of Biscay were observed in the present study.

Throughout the year, the models displayed low levels of suitability at the Mediterranean Sea, in comparison with neighbouring regions. This pattern was also inconsistent with the previous study (Sousa, 2009), which demonstrated higher levels of suitability in this region. Yet, the suitable areas in the present study extended closer to the coastline of the Iberian Peninsula and northwestern Africa (Sousa, 2009).

A limitation of this study was the geographical constraint of the shark tagging data. As most sharks were tagged in the eastern North Atlantic, the results may have been biased towards this region. Since blue sharks display an extensive movement within the Atlantic Ocean (Camhi et al., 2008), the collection of data in other regions, e.g., the western North Atlantic and the South Atlantic, would be pertinent to assess future impacts of fisheries and climate change in these areas, particularly in regions that are relevant for the reproductive cycle of the species, such as Brazil and South Africa (Tavares et al., 2012; Coelho et al., 2018). Furthermore, a few relevant variables were not included in the models, including the distribution of common prey species, (e.g. deep-water squids and mackerel; Stevens, 1973; Queiroz et al., 2010; Queiroz et al., 2012), and bathymetry data. These factors have shown to be important determinants of the blue shark's movement and distribution (Sousa, 2009; Queiroz et al., 2010; Queiroz et al., 2012). A future projection of these variables was not available and, therefore, could not be incorporated. Hence, the findings in the present study should be considered with caution.

4.2. Shark distribution modelling (future)

In comparison with the present model, the future model displayed changes, that were inconsistent among seasons. In warmer seasons, a reduction of suitable habitats was predicted, while the opposite pattern was observed in the colder months. This outcome demonstrates the complexity of the blue shark's distribution, influenced by multiple factors that promote different results at different levels. The winter model showed habitat expansion towards the Portugal coast and northwestern Africa, as well as in some regions of the central Atlantic. These results suggest future environmental conditions (e.g. surface O_2 and SST) may promote the expansion of the species towards these regions, at least at the surface.

During spring and summer, similar patterns were observed. The lower habitat suitability observed in some regions in the central North Atlantic, particularly in the spring model, may reflect some implications for the extensive movement of blue sharks between both sides of the North Atlantic (Queiroz et al., 2005; Queiroz et al., 2012; Queiroz et al., 2016). Additionally, the lower suitability around Cape Verde and adjacent regions below 20ºN in the summer model may be a result of limiting high SSTs, as indicated by the covariate's response curve.

The autumn model displayed a slight shift in habitat suitability towards higher latitudes, particularly at 40ºN and above. This pattern may consist of a shift towards more productive waters, as suggested by the NPP's response curve and relative importance in the model (Queiroz et al., 2012).

4.3. Overlap between sharks and fishing vessels

This study was limited by the unpredictability of the distribution of fishing vessels. The former process is complex and influenced by multiple factors, particularly the movement of target species, which drive its variation on small time scales (Ward & Myers, 2005; Bertrand et al., 2007; Queiroz et al., 2016; Crespo et al., 2018). Thus, the predictions for the future may not constitute the most geographically resolute representation of overlapping areas, but rather demonstrates how the spatial overlap may evolve in regions of interest.

Overall, the present overlap presented in this study was consistent with other studies reporting blue shark intentional and by-catch captures by longline fisheries in the eastern (Buencuerpo et al., 1998; Coelho et al., 2016) and western (Aires-da-Silva et al., 2008; Mandelman, 2008;

Fowler & Campana, 2009; Cortés et al., 2010) North Atlantic. Additionally, the overlap seasonality observed in the present study seemed to reflect the blue shark's migratory patterns and was consistent with previous studies regarding blue shark overlap with longline fisheries (Queiroz et al., 2016). In detail, a higher overlap was observed towards the western side of the North Atlantic during warmer seasons (i.e., spring and summer), while in colder months a broader overlap was seen near the Mid-Atlantic Ridge and the Azores islands (Queiroz et al., 2016).

In the winter, the central North Atlantic contained the broadest overlap. In this region, the area between the Azores and mainland Portugal was of particular interest, as it displayed high suitability for the blue sharks. Therefore, it is highly likely that sharks encounter fishing activity as they move within this region (Simpfendorfer et al., 2002; Queiroz et al., 2016). Throughout time, this overlapping area persisted and increased slightly, suggesting a prolonged fishing pressure and, ultimately, significant decreases in blue shark abundance levels.

The overlapping areas observed during spring were consistent with the model presented by Queiroz et al. (2016), mainly located in the temperate North Atlantic and throughout the northwestern coast of Africa. The overlap of the temperate (30ºN-40ºN) North Atlantic may pose as a region of higher vulnerability, as it coincides with the migratory path some sharks follow, migrating from east to west in this season (Pratt, 1979; Simpfendorfer et al., 2002; Queiroz et al., 2016). Future projections suggest that this overlap will persist over time, hence, blue sharks may suffer from a prolonged exposure to fisheries in this season as well.

In the summer, the spatial overlap is broadly present along the 35ºN-45ºN latitudinal region, where predicted habitat suitability is higher and extensive movement occurs (Simpfendorfer et al., 2002; Queiroz et al., 2005; Queiroz et al., 2012; Queiroz et al., 2016). The region off south Portugal is included in the overlapping area. This region functions as a nursery area for the species (Camhi et al., 2008; Vandeperre et al., 2014a; Vandeperre et al., 2014b). Thus, the predicted overlap may result in the capture of juveniles or sub-adults, thus, ultimately affecting juvenile survivability and population stability (Kinney & Simpfendorfer, 2009). Overall, a high exposure to fishing was suggested in the summer, which is expected to persist in the future in most regions.

The autumn overlap displayed was broadly present around the Iberian Peninsula, where suitable areas are prominent and latitudinal movement occurs at this time (Queiroz et al., 2016).

Therefore, the region surrounding the Iberian Peninsula reflected a higher vulnerability to fishing activity in this season.

In future projections, the spatial overlap persisted in most regions. These findings suggest that blue sharks will suffer from a prolonged exposure to fisheries into the future. Throughout the year, different regions were identified as areas of higher vulnerability. Some of the most vulnerable areas were located in the northeastern Atlantic, off the Portugal coast, and the central Atlantic, off the Azores islands. In these regions, a broad overlap was demonstrated during most of the seasons (Queiroz et al., 2016), in both present and future predictions, indicating a long-term exposure to fisheries. Given the vital role these areas play in the blue shark's reproductive cycle (Pratt, 1979; Coelho et al., 2018), longline fishing may ultimately lead to changes in abundance and the population structure of the blue shark populations in the North Atlantic, especially if coupled with a reduced habitat range driven by climate change.

Apart from a spatial horizontal overlap, the assessment of a vertical overlap would be equally important in determining the vulnerability of blue sharks to fisheries (Mas et al., 2024). Blue sharks display high vertical movement while searching for prey. Additionally, in some regions, their vertical habitat is constrained by the hypoxic conditions of oxygen minimum zones (Vedor et al., 2021b). Hence, assessing both types of overlap, while incorporating the factors mentioned above, would produce interesting results regarding the blue shark's horizontal and vertical habitat suitability.

4.4. Blue shark fisheries and management

Blue shark fishing and its impact is a matter of concern, considering the role this species plays in its ecosystems. As apex predators, blue sharks play a crucial role in marine ecosystems by preying on meso-consumers and controlling their abundance. Significant reductions in blue shark abundance may cause an imbalance in the ecosystem's trophic web and structure (Stevens et al., 2000; Frid et al., 2008; Ferretti et al., 2010). Hence, the exploitation of blue sharks and other elasmobranchs has been carefully considered throughout the years. Every few years, assessments of the blue shark's landing statistics and population status are conducted by the ICCAT, which posed an international TAC of 30,000 tonnes (ICCAT, 2023). Adding to this, in 2013, the EU took an important step towards the end of shark finning, by demanding the landing of the sharks' full body. The purpose of this was to avoid unreported catches and discards after detaching the fins (Regulation (EU) No 605/2013). Nevertheless, these protective measures are based on reported catches of the blue shark, which represent only a fraction of the actual blue shark catches (ICCAT, 2009; ICCAT, 2023). Thus, additional protective measures are necessary to ensure the sustainability of blue shark exploitation. For instance, the implementation of size limits would provide more selectivity in the captures towards sexually mature sharks. By avoiding the capture of juveniles, the population's resilience and productivity would be maintained (Aires-da-Silva & Gallucci, 2007).

As a final remark, the climate change scenarios of distributional shifts observed in the blue shark, as well as in other marine species (Perry et al., 2005; Poloczanska et al., 2016), will also have an economic impact on fisheries. On one hand, lower population abundance levels will likely lead to reduced TACs of some commercial species to avoid overfishing, leading to lower profits. On the other hand, commercial species that adapt through poleward shifts will lead to the redistribution of fishing fleets towards these regions with higher fish stock availability, resulting in higher fishing costs (Ramos Martins et al., 2021).

5. Conclusion

Present habitat suitability models for the blue shark were proven helpful in identifying habitat suitability hotspots for the blue shark, as well as corroborate previous studies regarding its distribution and movement patterns in the North Atlantic. Of all variables considered, the importance of SST as a distribution determinant was demonstrated, as it was suggested by previous studies (Queiroz et al., 2005; Queiroz et al., 2012; Queiroz et al., 2016).

In the present study, future suitable areas for the blue shark were modelled in a climate change scenario, serving as the first future habitat suitability projection for this species. Models displayed different outcomes depending on the season, reflecting the complexity of these processes. While suitable areas for the blue sharks suffered a reduction in warmer seasons, other regions appeared to be suitable in future climate conditions in colder seasons. In some cases, scenarios suggestive of habitat reduction and poleward distribution shifts were shown as an outcome of climate change under the RCP5-8.5 scenario. Such patterns have been observed in numerous other marine species (Perry et al., 2005; Poloczanska et al., 2016).

The overlap of the blue shark's suitable areas with fishing activity demonstrated the extensiveness of the shark's vulnerability to fishing, particularly the persistent overlap in the northeastern Atlantic. The overlap in this region included areas that are relevant for the species' movement and reproduction. Long-term exposure to fisheries was suggested in this study, with potentially detrimental effects on the species' population stability and migratory patterns. Thus, further studies regarding this issue are needed, in order to ascertain which effects an extended exposure to fishing activity may have on the species.

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7. Annexes

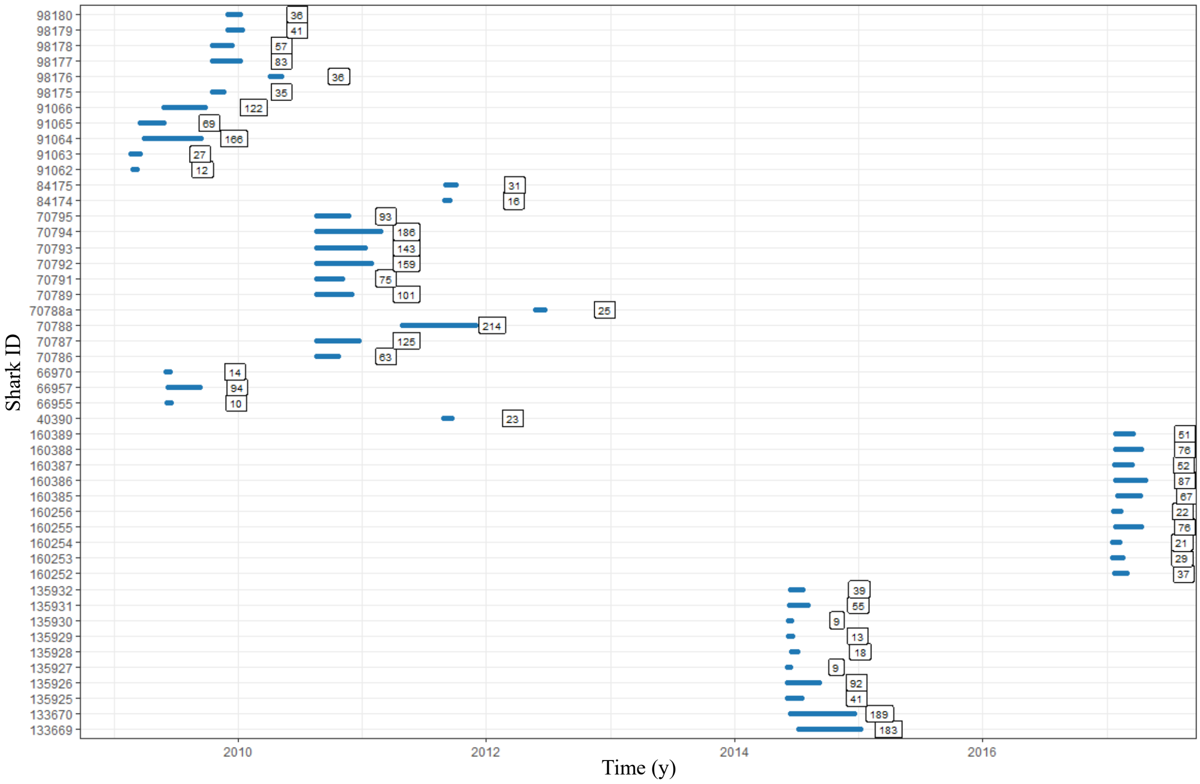

Figure A.1. Timeline of tagging events by ID. Numbers adjacent to line segments represent the number of days each ID was tagged.

Table A.1. *Formulas of the best performing models.o2 – DO; temp – SST; chl – CHL; npp – NPP; mld – MLD; t_slope – SST slope.*

	Model formula
Winter	s(o2, k=3) + s(chl, k=3) + s(salinity, k=3) + s(t_slope, k=3)
Spring	s(chl, k=4) + s(salinity, k=3) + s(temp, k=3)+ s(mld, k=3)+ s(t_slope, k=3)
Summer	s(npp, k=3) + s(salinity, k=3) + s(temp, k=3) + s(mld, k=3)
Autumn	s(npp, k=3) + s(temp, k=3)+ s(mld, k=3)+ s(t_slope, k=3)

Table A.2. *Variable importance of the best performing models.o2 – DO; temp – SST; chl – CHL; npp – NPP; mld – MLD; t_slope – SST slope.*

		Deviance explained (%)						
		s(o2)	s(SST)	s(CHL)	s(NPP)	s(salinity)	s(MLD)	s(t_slope)
Winter	Present	0.9		**15.7**		4		0.5
	Future	**17.5**		7.7		4.9		1.6
Spring	Present		**15.1**	14.4		6.7	2.4	0.5
	Future		**26.6**	2.5		3.9	4.6	0.4
Summer	Present		**27.9**		10.6	5.5	10.6	
	Future		**40.0**		15.2	4.9	1.4	
Autumn	Present		**26.2**		24.5		10.0	2.0
	Future		16.6		**19.6**		2.8	3.4

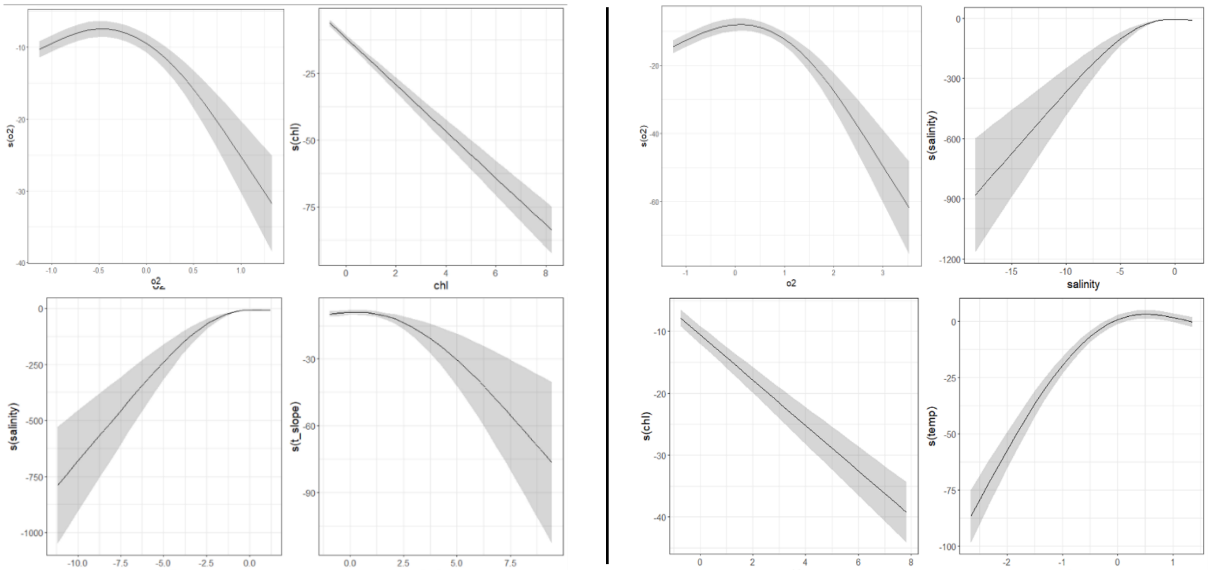

Figure A.2. Response curves of the winter present model. o2 – DO; chl – CHL; npp – NPP; mld – MLD; t_slope – SST slope.

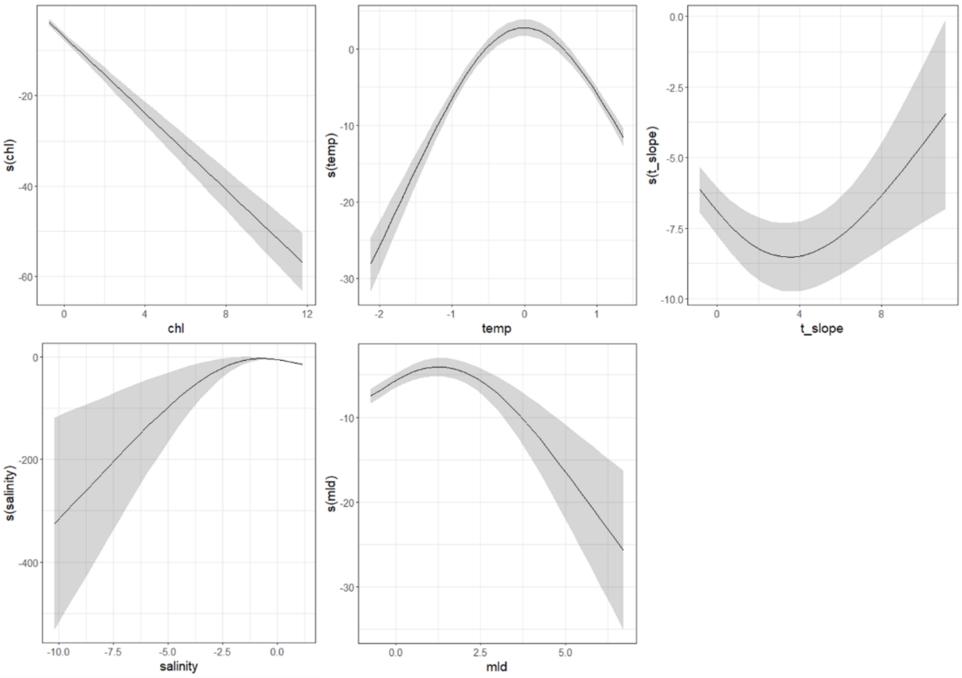

Figure A.3. Response curves of the spring present model. o2 – DO; temp – SST; chl – CHL; npp – NPP; mld – MLD; t_slope – SST slope.

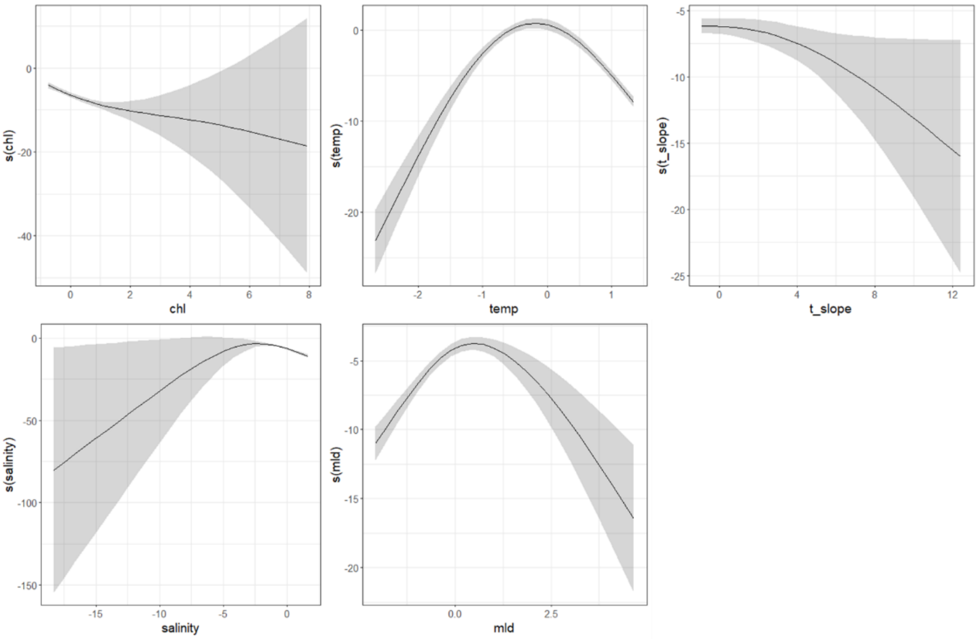

Figure A.4. Response curves of the spring future model. o2 – DO; temp – SST; chl – CHL; npp – NPP; mld – MLD; t_slope – SST slope.

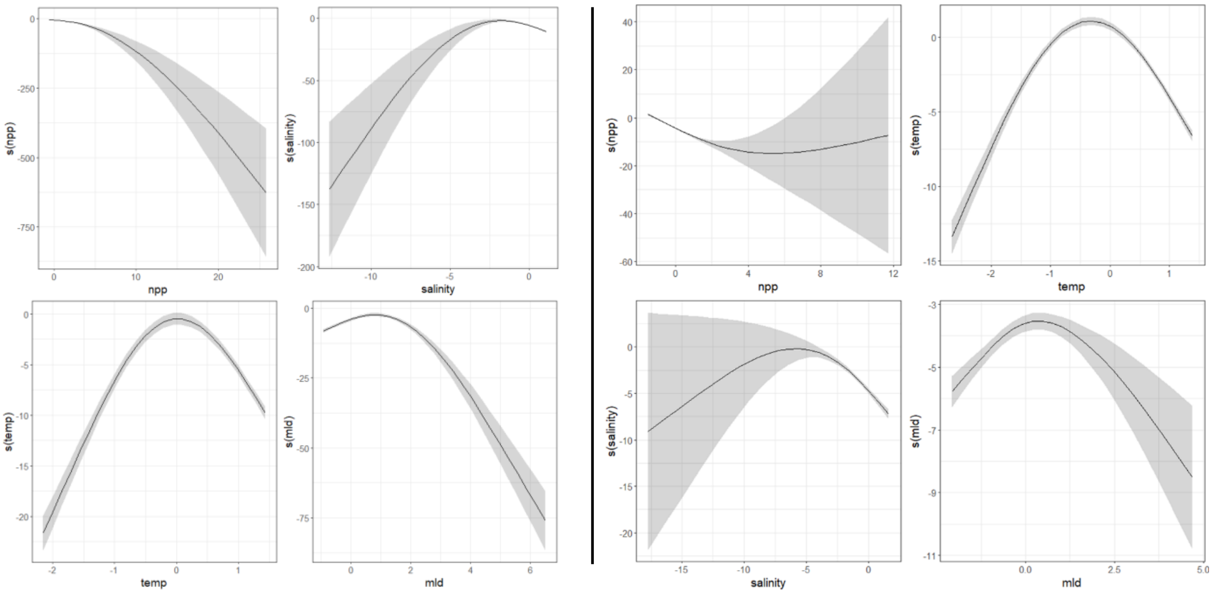

Figure A.5. Response curves of the summer present (left) and future (right) models. o2 – DO; temp – SST; chl – CHL; npp – NPP; mld – MLD; t_slope – SST slope.

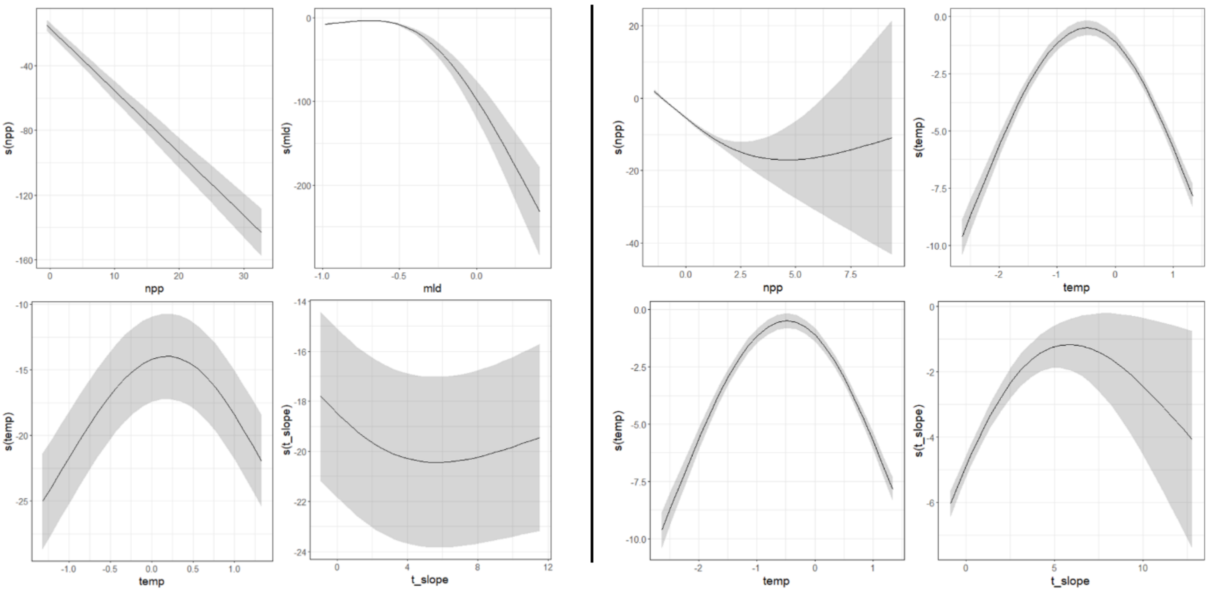

Figure A.6. Response curves of the autumn present (left) and future (right) models. o2 – DO; temp – SST; chl – CHL; npp – NPP; mld – MLD; t_slope – SST slope.