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Mestrado em Biologia Marinha

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The influence of oxygen fronts and mesoscale eddies on the foraging patterns and space-use of blue and mako sharks.

Declaro ser o autor deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída.

I hereby declare to be the author of this work, which is original and unpublished. Authors and works consulted are properly cited in the text and included in the reference list.

(Diogo Costa)

(Diogo Costa)

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Resumo

As populações de predadores pelágicos de topo têm vindo a decrescer drasticamente nas últimas décadas, sendo a sobrepesca considerada a principal responsável por estes declínios. As repercussões destes decréscimos são especialmente graves para as populações de tubarões, uma vez que, dado o seu lento ciclo de vida, estas espécies apresentam uma maior dificuldade em restabelecer os seus números após períodos de pesca intensiva. Além disso, dada a sua posição de topo na cadeia trófica, a remoção de tubarões dos ecossistemas gera efeitos em cascata nos níveis tróficos inferiores, tendo consequências graves e imprevisíveis para todo o ecossistema. Os tubarões azul (*Prionace glauca*) e anequim (*Isurus oxyrinchus*) são as duas espécies de tubarões pelágicos mais pescadas no Oceano Atlântico, constituindo, em conjunto, mais de 95% de todos os tubarões pelágicos capturados anualmente neste oceano e estando, respetivamente, classificadas como "quase ameaçada" e "em perigo" pelo IUCN. No entanto, continuam a existir graves problemas ao nível da regulamentação, monitorização e reporte da pesca destas duas espécies, tendo apenas no ano passado (2020) sido estabelecida uma quota máxima para a captura de tubarão azul no Oceano Atlântico, enquanto o tubarão anequim continua sem qualquer quota a restringir a sua captura.

A determinação de áreas prioritárias para a conservação de predadores pelágicos de topo é complicada pela extrema mobilidade destes animais e a consequente dificuldade em identificar zonas de agregação devido à falta de dados fiáveis, uma vez que os estudos destas espécies estão historicamente restringidos a dados inerentes às pescas, sendo, por isso, extremamente enviesados. Porém, o advento da tecnologia de telemetria de satélite tem permitido descrever novos comportamentos, bem como uma melhor compreensão da real distribuição espacial e utilização de habitat, horizontal e vertical, destes predadores. Neste sentido, estudos anteriores utilizando dados de esforço de pesca e/ou telemetria de satélite têm sugerido a atração de uma grande variedade de predadores de topo por fenómenos dinâmicos de média dimensão, tais como frentes térmicas e vórtices oceânicos, que estará relacionada com movimentos de procura de alimento.

Neste estudo, os movimentos de procura de alimento de 34 tubarões azuis e 24 tubarões anequins foram analisados relativamente à presença de frentes de oxigénio dissolvido (OD), que até agora não tinham sido consideradas na literatura. Para tal, estes tubarões foram capturados em 5 localizações diferentes do Oceano Atlântico Norte (Açores, Cabo Verde, ao largo de Nova Iorque e a sudoeste de Portugal e Inglaterra) e marcados com transmissores de satélite SPOT, que são fixados à barabatana dorsal e permitem seguir os seus movimentos

horizontais com elevada precisão. Todas as variáveis ambientais foram extraídas da plataforma CMEMS's (Copernicus Marine Environment Monitoring Service) Ocean Products, que disponibiliza dados oceanográficos diários e mensais recolhidos através de uma combinação de medições de satélites e de boias à superfície e a meia água. Para identificar a presença de frentes, foram calculados os gradientes máximos de OD (e temperatura) entre células adjacentes.

Os resultados aqui apresentados sugerem que frentes de OD podem representar extensas zonas de alimentação para estas duas espécies, sendo esta relação particularmente evidente para os tubarões azuis. Dois tipos de frentes de OD foram identificadas como atrativas para estas espécies: frentes conjuntas de temperatura e OD, forte, persistente e verticalmente estruturadas, onde a grande produtividade existente cria importantes áreas de alimentação que, por sua vez, atraem predadores de níveis tróficos subsequentemente mais elevados; e frentes exclusivas de OD, associadas a zonas hipóxicas, onde a compressão de presas nas águas superficiais, mais oxigenadas, da coluna de água aumenta a probabilidade de encontro entre predador e presa. No entanto, apesar de ambas as espécies terem revelado afinidade para com estes fenómenos, diferenças importantes foram constatadas. Os tubarões azuis demonstraram uma maior relação com as frentes de OD que os tubarões anequins, enquanto o contrário se verificou em relação às frentes de temperatura, resultados que se coadunam com as diferentes estratégias metabólicas apresentadas pelas duas espécies. Presumivelmente, dada a menor taxa metabólica associada a uma estratégia ectotérmica, os tubarões azuis terão uma maior tolerância a diminuições momentâneas de oxigénio, explorando, por isso, zonas de frentes exclusivas de OD quando possível, tal como acontece nas zonas de oxigénio mínimo (ZOMs). Por outro lado, os tubarões anequins, dada a sua capacidade em manter uma temperatura corporal mais ou menos constante – endotermia - combinada com uma maior necessidade de oxigénio, tenderão a favorecer zonas de fortes gradientes térmicos.

Este estudo reforça ainda a importância dos vórtices oceânicos para a alimentação de predadores pelágicos em águas oligotróficas, tendo os tubarões anequins revelado uma clara preferência por vórtices ciclónicos (VCs). Por outro lado, os tubarões azuis demonstraram uma utilização mais equilibrada de VCs e vórtices anticiclónicos (VACs), corroborando parcialmente estudos anteriores que sugerem uma relação entre procura de alimento por parte de predadores de topo e VACs, apesar de estes, há muito, serem considerados apenas como "desertos biológicos".

Os resultados aqui apresentados sugerem que a integração de frentes de OD em modelos utilizados para identificação e gestão de áreas prioritárias de conservação destas duas espécies poderá melhorar significativamente os seus resultados. Além disso, a adoção de medidas de gestão de stocks em tempo real, de acordo com a informação inferida destes modelos, tal como é feito, na Austrália, com o Atum Rabilho do Sul (*Thunnus maccoyii*), uma espécie ameaçada e com uma quota limite estabelecida, poderá melhorar significativamente a gestão e conservação destas espécies, sendo o mesmo, possivelmente, aplicável ao caso de outros predadores pelágicos de topo.

Finalmente, este estudo realça a importância da telemetria de satélite para a aquisição de informação relativa aos padrões ecológicos de movimentação a larga escala de grandes predadores marinhos. Acresce que a análise destes movimentos em conjunto com dados oceanográficos permite inferir com maior confiança quanto à importância de determinadas áreas e fenómenos para estas e outras espécies, possibilitando assim, decisões mais informadas no que respeita à gestão de stocks e proteção de habitats de extrema importância ecológica e económica. Pois apenas melhorando o conhecimento que temos sobre os hábitos destas espécies podemos almejar impedir uma total perda da biodiversidade e uma completa disrupção dos ecossistemas marinhos.

Abstract

Pelagic top predator populations worldwide have suffered sharp decreases in abundance over the last decades, with overfishing being the main cause of such declines. Blue (*Prionace glauca*) and mako sharks (*Isurus oxyrinchus*) are the two most caught pelagic shark species in the Atlantic Ocean, being classified, respectively, as “near-threatened” and “endangered” by the IUCN red list. However, their catches remain highly unregulated, unmonitored, and unreported. Identification of priority areas for pelagic top predators’ conservation is hampered by the high mobility of these animals and the consequent difficulty in determining aggregation areas, yet mesoscale dynamic features such as thermal fronts and eddies have been suggested to attract a variety of large apex predators while foraging.

In this study, the foraging movements of 34 blue and 24 mako sharks, satellite-tagged across 5 different locations in the North Atlantic Ocean, were analysed in relation to dissolved oxygen (DO) fronts, which until now had not been considered. The results presented here suggest that DO fronts might represent extensive foraging areas for these two species, but particularly for blue sharks. Two different DO front types were noticed to attract these species: strong, persistent, and vertically structured thermal-oxygen fronts, where high productivity creates important foraging opportunities; and oxygen-only fronts associated with hypoxic areas where the compression of prey in the more oxygenated surface waters results in higher predator-prey encounters. This study also reinforces the importance of eddies for pelagic predators foraging in oligotrophic waters. In addition, mako sharks revealed a clear preference for cyclonic eddies (CEs) while blue sharks showed a more balanced usage of CEs and anticyclonic eddies. These results strongly suggest the integration of DO fronts in conservation and management modelling, as they can substantially improve the identification of priority conservation areas for these two sharks and, possibly, many other pelagic top predators.

Keywords: Animal telemetry, marine predators, foraging, DO fronts, eddies, conservation

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List of Abbreviations, Acronyms and Symbols

ACE - Anticyclonic Eddy

ARGOS - Advanced Research and Global Observation Satellite

ARS - Area-Restricted Search

AVISO - Archiving, Validation and Interpretation of Satellite Oceanographic data

BIC - Bayesian Information Criteria

CE - Cyclonic Eddy

CHL - Chlorophyll-a concentration

CITES - Convention on International Trade in Endangered Species

CMEMS - Copernicus Marine Environment Monitoring Service

CTCRW - Continuous-Time Correlated Random Walk

DO - Dissolved Oxygen

DO FDist - Dissolved Oxygen closest Front Distance

DOM - Dynamic Ocean Management

DSL - Deep Scattering Layer

FPT - First-Passage Time

GIS - Geographical Information Systems

GPS - Geographic Position System

HSP - Heat Shock Proteins

ICCAT - International Commission for the Conservation of Atlantic Tunas

IUCN - International Union for Conservation of Nature

MPA - Marine Protected Area

NOAA - National Oceanic and Atmospheric Administration

OMZ - Oxygen Minimum Zone

PHIC - Phytoplankton concentration

PP - Primary Production

PTT - Platform Transmitter Terminal

PSAT - Pop-up Satellite Archival Tags

RM - Red Myotomal muscle fibres

RSPF - Resource Selection Probability Function

SCRS - Standing Committee on Research and Statistics

SFPT - Spherical First-Passage Time

SLA - Sea Level Anomaly

SPOT - Smart Position-Only Tags

SSH - Sea Surface Height

SST - Sea Surface Temperature

SST FDist - Sea Surface Temperature closest Front Distance

VRS - Volume-Restricted Search

WM - White Myotomal muscle fibres

General Introduction

Shark Declines and Study Relevance

Declines in marine populations and the collapse of global fisheries as a result of overfishing have been widely described in the last decades (Pauly *et al.*, 1998; Jackson *et al.*, 2001; Sethi *et al.*, 2010; Pinsky *et al.*, 2011; McCauley *et al.*, 2015). One of the greatest threats contributing to this collapse is the removal of apex predators from the top of food webs, with the consequent lack of top-down control leading to cascading effects that can be far-reaching and unpredictable (Estes *et al.*, 2011). This has been particularly evident as a result of large sharks declines in the oceans (Stevens *et al.*, 2000; Baum *et al.*, 2003; Baum and Myers, 2004; Dulvy *et al.*, 2008; Worm *et al.*, 2013), with increasing evidence showing the widespread effects on mesopredator prey from the removal of these top predators (Heithaus and Dill, 2002; Myers *et al.*, 2007; Heithaus *et al.*, 2008; Ferretti *et al.*, 2010).

As all apex predators, sharks are K-selected, i.e., they have slow life-histories (Hutchings *et al.*, 2012). These low productivity rates result in low rebound potentials from fishing pressure, thus making sharks highly sensitive to increasing fishery exploitation (Smith *et al.*, 2008), with the least reproductive sharks estimated to require as long as four decades to recover from depletion (Au *et al.*, 2008). Nonetheless, direct and indirect shark fishing mortality (including reported and unreported landings, discards and shark finning) have been estimated to round the 100 million sharks annually, and exploiting rates of many sharks are thought to be exceeding their rebound rates (Worm *et al.*, 2013). Oceanic sharks are estimated to have suffered declines of up to 99% (for oceanic whitetips, *Carcharhinus longimanus*) since the 1950s (Camhi *et al.*, 2008). Yet, catches remain highly unregulated, unmonitored and unreported. In this regard, only last year (2020) an annual catch limit was established for blue sharks (*Prionace glauca*, Linnaeus, 1758 and, although live retention has been banned for shortfin-mako sharks (*Isurus oxyrinchus*, Rafinesque, 1810; hereafter mako shark), current catches still remain with no quotas established (ICCAT, 2020) and widely surpassing those suggested by ICCAT's (International Commission for the Conservation of Atlantic Tunas) scientific committee (ICCAT SCRS, 2020).

Blue and mako sharks, the model species of this study, are the two pelagic sharks at higher risk in the North Atlantic (Queiroz *et al.*, 2019), together comprising more than 95% of all pelagic shark landings in the Atlantic Ocean (Camhi *et al.*, 2008). Blue sharks, although classified as "near-threatened" by the IUCN red list (Rigby *et al.*, 2019a), are the pelagic sharks most-commonly caught as by-catch in tuna fisheries (Babcock and Nakano, 2008), but especially by longline fishing fleets (comprising ~80% of the total pelagic shark catches of these fisheries) (Camhi *et al.*, 2008). Similarly, mako sharks, classified as "endangered" (Rigby *et al.*, 2019b) and recently included in CITES Appendix II (CITES, 2019), make up about 16% of all pelagic shark catches (Camhi *et al.*, 2008). Furthermore, both species, but blue sharks in particular, are highly targeted for the high price of their fins in the Asian market (Musick *et al.*, 2000; Camhi *et al.*, 2008; Fields *et al.*, 2018) and not even regional regulation prohibiting shark finning seems to be reducing their mortality (Clarke *et al.*, 2013).

In addition, similar to the majority of sharks, mako sharks have relatively slow life-history traits, with females maturing at late age (6-18 years according to different authors), average litter sizes of 12 pups, gestations of 15-18 months and reproductive cycles of 3 years (Pratt & Casey, 1983; Mollet *et al.*, 2000; Campana *et al.*, 2005). Hence, rendering these sharks even more susceptible to high fishing pressure and highly restraining their rebound capacity. Contrarily, the blue shark, due to its high abundance and considerably higher average litter sizes (up to 135), has long been considered to be resilient to fisheries (Nakano and Stevens, 2008). Yet, evidence suggests that exploiting rates might be exceeding the maximum sustainable yield, with estimated declines rounding the 60% in the Northwest Atlantic since the 1980s (Baum *et al.*, 2003; Hueter and Simpfendorfer, 2008).

Finally, lagrangian coherent structures, such as mesoscale fronts and eddies, have been demonstrated to be hotspots of longline fisheries overlap with marine megafauna in general, and blue and mako sharks in particularly (Queiroz *et al.*, 2016, 2019; Scales *et al.*, 2018). However, no studies have yet addressed the relationship of pelagic top predators with dissolved oxygen (DO) fronts. Accordingly, the distinct metabolic strategies of these two sharks make them remarkably good models to assess how temperature and oxygen conditions may impact species with different energetic requirements and thermoregulatory strategies, providing information that may also be relevant to assess other pelagic fishes, especially those with high commercial interests, namely, other sharks, tunas and billfishes.

Historical Framing and Importance of Biotelemetry as a Conservation Tool

Technology Evolution

For many decades, population assessments of the most exploited large fishes were dependent on fisheries, and information regarding many aspects of their life-history and spatial dynamics was largely scarce (Sims, 2010). Historically constrained to the vastness, three-dimensionality and harsh conditions of aquatic environments, as well as the cryptic nature of aquatic fauna, which spends most of the time submerged, research on the behaviour and movement of aquatic organisms was utterly revolutionized with the advent of what we now refer to as “biotelemetry” (Hussey *et al.*, 2015). These new technologies, together with biologgers/archival tags (animal-borne sensors that record and store information of both internal and external environments), have enabled the remote monitoring of undisturbed, free-ranging animals in their natural environments while, at the same time, collecting information on the environmental processes they are experiencing (Cooke *et al.*, 2004; Hussey *et al.*, 2015). Thus, contributing with crucial insights on the behaviour, physiology, and ecology of many marine organisms.

Pushed by the increasing need for better quality and more informative data on the distribution patterns and spatial dynamics of large marine predators at/or near risk of overexploitation, biotelemetry and biologging technologies have greatly improved over the last decades (Cooke, 2008; Hussey *et al.*, 2015; Wilmers *et al.*, 2015). For instance, in the 1960s, scientists had to resort to methods such as towing balloons to marine mammals to track their movements (Rutz and Hays, 2009). Since then, these technologies have spread amongst the scientific community, with an exponential increase in studies using aquatic telemetry observed since the beginning of the millennium (Hussey *et al.*, 2015).

The first approach to track animal movements consisted of capture-recapture studies, in which large numbers of fish were marked and released in the hope of later being captured during fishing operations and, this way, provide some information on their movements (Arnold and Dewar, 2001; Sims, 2010). Acoustic tracking devices, on the other hand, were the first electronic tags used to study fish movements and have been used since the late 1950s. These tags consist of electronic transmitters either implanted under the skin or externally attached to the animals. These transmitters emit high-frequency sounds, which when within the appropriate range, allow a fixed (or mobile) receiver to locate the emitting transmitter and record it, with information being later retrieved from these receivers (Arnold and Dewar, 2001). Yet, due to the small detection range of acoustic receivers, most acoustic research has focused on coastal species (Hussey *et al.*, 2015). Later, in 1978, satellite telemetry emerged with the incorporation of ARGOS (Advanced Research and Global Observation Satellite) system on NOAA (National Oceanic and Atmospheric Administration) satellites, which allowed to determine the location of an animal-attached platform transmitter terminal (PTT) anywhere on the planet, as long as it stayed out of the water for enough time (Sims, 2010). Radio telemetry is also feasible in freshwater environments, yet, due to the incapacity of electromagnetic waves to propagate in saltwater, this approach is often less used (Hussey *et al.*, 2015).

By the early 1990s, there was still one great issue with satellite telemetry: due to the inability of electromagnetic waves to be transmitted on saltwater, organisms being studied had to spend enough time on the surface to transmit their position to satellite receivers. This was only feasible for marine mammals and turtles due to their need to surface regularly to breathe and, to a minor extent, for large sharks that commonly swim at the surface. Likewise, archival transmitters had one great disadvantage: to access the data, these tags had to be retrieved, with recovery rates extremely low and dependent on fisheries returns (Arnold and Dewar, 2001). Two technological revolutions were crucial for solving these problems. The ability to transmit data from the tag to an orbiting satellite and from this to a land-based station, and the development of microprocessors that made it possible to reduce the size of these devices (Kooyman, 2004). Size reduction not only made it possible to study the movements of much smaller organisms (including earlier life stages of species already studied) but also permitted to incorporate a greater variety of sensors into one single device. Today tags are available with sensors measuring ambient and internal temperature, speed, heart rate, among many others.

Thus, by the late 1990s, the substantial decrease in size and improvement in both battery and memory capacities had made these loggers able to store considerable amounts of high-quality data (archival data) (Sims, 2010), which led to the development of the first electronic tags combining sensor data logging with satellite transmission, the pop-up satellite archival tags (PSATs). These externally attached devices are capable of autonomously release themselves from the animal, at a predetermined time, and float to the surface, where they can communicate with the ARGOS satellite system and transmit a summary of the data collected along the time (Arnold & Dewar, 2001; Musyl *et al.*, 2011). PSATs collect in-situ depth and temperature measurements, providing a good characterization of diving behaviour and used thermal habitat. However, information regarding horizontal movements has a significant error associated (Musyl *et al.*, 2011), as geolocation is estimated based on light-level information, by comparing times of sunrise and sunset to determine the position (Musyl *et al.*, 2001). Therefore, these tags are adequate to track large-scale movements but insufficient when studying small-scale movements. To inspect how the animal’s movements might relate to seasonal or sporadic changes in environmental conditions, good spatial data is required (that is, high geolocation accuracy and few temporal gaps). Small errors in location estimate may lead to erroneous interpretations of movements and behaviours in relation to encountered conditions. For this reason, to investigate smaller-scale movements, researchers rely mostly on ARGOS PTTs directly attached to the animals, which spatial error is substantially smaller (usually less than 1.5 km) when compared with PSATs (Sims, 2010).

More recently, developments in tagging technology have enabled improvements in both geolocating accuracy and decreasing temporal gaps. Fastloc GPS receivers, which allow fixing a location in less than 80 ms, have provided better track estimations by reducing temporal gaps. Furthermore, their accuracy is also substantially higher than that of ARGOS PTTs, increasing as a function of the number of GPS satellites used to calculate the location. However, these devices need to be recaptured to access the data or used together with ARGOS PTTs for it to be transmitted via ARGOS, which explains why single ARGOS PTTs still remain as the preferred devices to assess small-scale movements (Costa *et al.*, 2010; Sims, 2010).

Finally, tri-axial accelerometer sensors and cameras have been used in attempt to capture rare interactions that may help to better perceive how these animals use their environment and how they interact with each other (Wilmers *et al.*, 2015). For instance, Watanabe & Takahashi (2013), deployed a video camera and two accelerometers on Adélie penguins (*Pygoscelis adeliae*), which revealed a remarkable efficiency in capturing krill with rapid head movements. Furthermore, these authors were able to link prey captures with the intensity of head movements in relation to body acceleration, meaning that every time the accelerometer provided this specific signature, the penguin had captured a prey. This technology can also be used to reconstruct an animal's trajectory with high precision, by measuring its speed, compass heading, and time between changes in compass heading, a technique called dead reckoning. Yet, its greater disadvantage is that it is only feasible for animals that return to the same location on a regular basis (for data retrieving) which is highly unusual amongst most large marine fauna (Sims, 2010).

Biotelemetry Crucial Role in Conservation

These technologies have allowed scientists to observe and describe previously unknown behaviours, such as spatial distribution and habitat-use (both horizontal and vertically), transoceanic migrations, spawning, site fidelity, among others, as well as the environmental processes and physiological constraints underlying them. For example, Bonfil *et al.* (2005) placed electronic tags on white sharks (*Carcharodon carcharias*), which revealed unanticipated transoceanic migrations linking the extremely distant populations of South Africa and Australia. Likewise, Thums *et al.* (2013), using satellite transmitters capable of recording depth-temperature profiles were able to relate the diving behaviour of whale sharks, and its affinity to the surface layers in slightly colder waters, with physiological thermoregulation.

This information is also providing scientists with better indicators of how species will respond to climate change (Hussey *et al.*, 2015). For instance, Hazen *et al.* (2013), examined the distribution of 23 Pacific top predators to which electronic tags had been attached. Based on global climate model to 2100 and by analysing species' preferences for sea surface temperature (SST), chlorophyll-a and bathymetry, these researchers predicted a change in core habitat of up to 35% for some species, as well as an overall northward displacement across the North Pacific. Moreover, it has been essential to aiding conservation management of many species. For example, Daly *et al.* (2018), by tracking 26 tiger sharks (*Galeocerdo cuvier*) off the east coast of South Africa and Mozambique, concluded that only roughly 6% of tiger shark hotspots coincided with marine protected areas (MPAs). Yet, that area could be significantly increased to as high as 41% if some strategic expansions of, already existing, MPAs took place. Also, more recently, Queiroz *et al.* (2019), by analysing the movements of 23 shark species and those of fishing vessels, at a global scale, found that longline fisheries overlap with commercially valuable and internationally protected species by 76% and 64%, respectively. In addition, by revealing the extreme vulnerability of mako sharks to longline fisheries, this paper was crucial for listing this species under the CITES Appendix II.

Nevertheless, as mentioned above, many exploited species still lack effective conservation measures, as are the cases of blue and mako sharks, for which inadequate (or nearly absent) fishing regulations are alarmingly threatening. In this regard, the collection of fisheries independent data on highly mobile pelagic predators over large spatiotemporal scales has revealed crucial in providing increasing knowledge on their spatial dynamics and habitat preferences (Sims, 2010). Thus, further informing management actions such as the establishment of international catch limits or the implementation and effective assessment of MPAs, as well as to better predict animal responses in face of changing environmental conditions, especially for threatened and near-threatened species.

Study Species

General Biology and Ecology

Blue and mako sharks are two large, mesopelagic and highly migratory sharks that inhabit the tropical and temperate waters of most oceans from about 60ºN to 50ºS latitude, though being more abundant in higher latitudes (Compagno, 2001), and from the surface to more than 1000 m depth (Queiroz *et al.*, 2012; Queiroz, unpublished data). Both these sharks, but especially mako sharks, have been shown to actively select areas with steep thermal gradients and/or productivity, where they remain for extended periods (Queiroz *et al.*, 2016, 2019; Scales *et al.*, 2018), presumably due to the presented increased foraging opportunities.

The blue shark belongs to the Carcharhinidae family and is both the most abundant and best-studied species of all pelagic sharks (Nakano and Stevens, 2008). Large-scale movements, including ocean-basin scale migrations, have been often described and its movement patterns are thought to be mainly driven by sex and size segregation and prey distribution (Nakano, 1994; Queiroz *et al.*, 2010, 2012, 2016; Stevens *et al.*, 2010; Vandeperre *et al.*, 2014). Yet, juvenile sharks do not engage in these large migrations before they reach about 130 cm in length, remaining in nursery areas until then (Nakano and Stevens, 2008). Blue sharks are ectothermic, i.e., they cannot actively control their body temperature, which consequently fluctuates according to the surrounding temperatures, and have a thermal preference between 12 and 20ºC (Nakano and Stevens, 2008). Accordingly, and due to the physiological constraints of spending extended periods in cold waters, they are usually found deeper in tropical waters than in temperate waters. Finally, blue sharks are somewhat opportunistic feeders, eating anything of appropriate size, though cephalopods make up the bulk of their diet, followed by small-sized teleosts (Cortés, 1999; Henderson *et al.*, 2001; McCord and Campana, 2003; Nakano and Stevens, 2008).

Mako sharks belong to the Lamnidae family and are considerably less studied than blue sharks (Stevens, 2008). They, too, are known to perform extensive movements, though to a lesser extent than blue sharks, with trans-oceanic migrations being less common (Casey and Kohler, 1992). Similarly, some sex segregation is known to occur, though not as pronounced (Stevens *et al.*, 2010), and especially during the cold season, when juvenile sharks move to, warmer offshore waters, such as the Gulf Stream (Casey and Kohler, 1992; Vaudo *et al.*, 2017). Also, mako sharks are endothermic, i.e., they are capable of generating heat and, this way, maintain their body temperature above that of the surrounding environment and, for this reason, are able to endure a broader range of temperatures, having been found in waters from 5 to 24ºC (Casey and Kohler, 1992; Vaudo *et al.*, 2016). These metabolic traits, associated with its thunniform, bulky body, allow this shark to predate on larger and highly energetic prey, such as billfishes, cetaceans and other elasmobranchs, although smaller pelagic teleosts constitute the majority of their diet (Stillwell and Kohler, 1982; Cortés, 1999; Stevens *et al.*, 2010).

Energetics and Metabolism

The most significant differences between these two sharks have essentially to do with their metabolic strategies. Although both are obligate ram ventilators and continuous swimmers, striking differences still exist between the two species (Bernal *et al.*, 2012).

As endothermics, mako sharks can maintain their body core and some other regions at a higher temperature than the surrounding waters, particularly their aerobic swimming muscles, which continuous activity generates heat that is retained in the shark's body (Wolf *et al.*, 1988). These swimming muscles are spread along the body and are composed of white (WM) and red (RM) myotomal muscle fibres. Anaerobic WM fibres are used in short duration burst swimming, while aerobic RM fibres are used in continuous swimming, thus, continuously generating heat, which is then retained by a highly complex vascular system (Bone, 1988). Increased thermal capacity provided by RM endothermy is thought to allow these sharks to exploit resources in cooler waters than ectotherms, both at higher latitudes and greater depths. For instance, mako sharks have been recorded at temperatures as low as 5ºC (Vaudo *et al.*, 2016), although these authors also concluded that waters below 15ºC created a depth limit to most dives. Also, they noticed tagged sharks to spend substantially more time at greater depths when comparing warm to cold waters.

In addition, mako sharks are the fastest sharks in the oceans, reaching speeds of up to 70 km/h (Díez *et al.*, 2015), which together with the higher metabolic costs associated with endothermy, ranks them with the highest routine and maximum metabolic rates among all shark species (344 ± 22 mg O2 kg^{-1} h^{-1} and 541 mg O2 kg^{-1} h^{-1}, respectively; Sepulveda *et al.*, 2007). Moreover, Sepulveda *et al.* (2007) found the slope of power-performance curves (i.e., swimming speed vs. oxygen consumption) of this shark to be 0.92, which is considerably higher than the average among ectothermic species (0.27 to 0.36; Bernal *et al.*, 2012). In order to cope with their elevated swimming costs, mako sharks evolved the capacity for a larger aerobic scope (Bernal *et al.*, 2012), made possible due to their physiological and anatomical adaptations, such as a large gill surface area, high muscle capillarity density and high haemoglobin and myoglobin concentration (which enable a high rate of oxygen uptake and delivery) (Bernal *et al.*, 2003; Wegner *et al.*, 2010). However, the high metabolic rates needed to maintain body temperature and striking speeds, require minimal concentrations of DO to cope with the high oxygen demand. In this sense, Abascal *et al.* (2011) found a tendency in mako sharks to remain at depths with DO concentrations over 3 ml l^{-1}.

On the other hand, ectotherms, as the blue shark, regulate their internal temperature through behavioural thermoregulation (Carey *et al.*, 1990; Campana *et al.*, 2011). By actively selecting different temperature conditions, these sharks are able to increase their energetic uptake and minimize energetic expenditures (Bernal *et al.*, 2012). For instance, Carey *et al.* (1990) recorded frequent short periods at the surface between blue shark dives during the winter, suggesting that this behaviour would allow them to re-warm their bodies and, this way, extend their foraging time below the thermocline.

Notwithstanding, blue sharks inhabit a similar latitudinal and vertical range to mako sharks and have been recorded in temperatures down to 9ºC (Carey *et al.*, 1990). However, differences are noticed when comparing both the frequency and duration of deep diving behaviour. As endotherms, mako sharks are capable of maintaining their body cores within operating temperatures for a longer period, whereas blue sharks' body temperature decreases more rapidly to unattainable temperatures, restraining them to shorter periods in deep, cold waters (Bernal *et al.*, 2012). Furthermore, when performing multiple dives, this pattern becomes even more evident, with blue shark's attainable time at depth progressively decreasing with repeated vertical movements while mako sharks are able to maintain more stable and warmer temperatures and, therefore, endure low temperatures for a longer period (Bernal *et al.*, 2012). A similar scenario takes place regarding latitude, as endotherms are capable of spending longer periods at higher latitudes, especially porbeagle (*Lamna nasus*) and salmon sharks (*Lamna ditropis*) (Campana & Joyce, 2004; Goldman *et al.*, 2004). Thus, endothermy essentially provides a larger temperature tolerance along the time, which can be an advantage over their ectothermic competitors in further exploiting resources both at higher latitudes and deeper, colder waters.

Fronts and Eddies

Physics and Biology

The open ocean is highly dynamic and continuously shaped by physical processes such as fronts and eddies. These processes are represented by areas of intense lateral flow, which induce vertical circulation, often resulting in the upwelling of nutrient-rich waters. For this reason, fronts and eddies have long been known to sustain high levels of biomass and, consequently, to be hotspots of marine fauna (Owen, 1981; Lutjeharms *et al.*, 1985; Le Fèvre, 1987; Franks, 1992; Olson *et al.*, 1994; Oschlies and Garçon, 1998; Mann and Lazier, 2013). Yet, in recent years, the interest by the scientific community in these processes has regrown and many studies have come up, especially using satellite-tagged animals and remote sense of environmental variables, methods not available a few decades ago (Belkin *et al.*, 2014).

Fronts are areas of laterally convergent flows characterized by high horizontal contrasts in different properties such as temperature, salinity, or density (Olson, 2002), which separate different water masses or different stratification levels of the same water mass (Belkin *et al.*, 2009). They can have their origin in different physical processes, such as abrupt topographic changes, tidal mixing areas, convergence of ocean currents or wind-driven upwelling (Owen, 1981; Belkin *et al.*, 2009). Differently, eddies are areas denoted by circular currents of water that induce vertical motion to compensate for the lateral flow, which results from the deflection caused by the Coriolis effect on ocean currents' shears (Owen, 1981). If the flow exhibits a counter-clockwise rotation, in the northern hemisphere, it pushes the water away from the centre, resulting in the, compensating, upward movement of cold waters below. These are called cyclonic eddies (CEs) and are considered divergent systems as the sea level in these areas is slightly lower than the surrounding waters. In contrast, eddies with clockwise rotation, or anticyclonic eddies (ACEs), are characterized by convergent flows, resulting in downward motion in their centres, transporting warm waters to greater depths and generating a positive sea level anomaly (Owen, 1981).

Fronts and eddies can greatly vary in both space and time. These processes can be either virtually permanent or prevail for just a few hours and range from a few meters to thousands of kilometres in extent and up to 1000 m in depth. Both time and space scales are invariably related as the most extensive fronts and eddies are virtually perpetual, such as the seasonally persistent Polar Front, which runs around the whole globe (Owen, 1981; Belkin *et al.*, 2009). Vertical water flow in fronts is highly localised and intense, in contrast to eddies, where they are weaker and less localised. As a result, horizontal gradients of water properties such as temperature and salinity are sharper in fronts than in eddies (Owen, 1981).

As mentioned, both these processes are usually characterized by high primary and secondary production (Le Fèvre, 1987; Gaube *et al.*, 2014). In fronts, the strong horizontal pressure gradient forces and the high increase in vertical advection induced by Coriolis acceleration lead to enhanced productivity on the high-density side of the front, mostly as a result of the upwelling of nutrient-rich waters and to the passive accumulation derived from the surface convergence of two water masses (Lutjeharms *et al.*, 1985; Le Fèvre, 1987; Olson *et al.*, 1994). In eddies, CEs are regions of intense upwelling and, therefore, characterized by high concentrations of near-surface chlorophyll-a, whereas ACEs are generally associated with low concentrations (Gaube *et al.*, 2014). Consequently, the steep productivity accumulated in fronts and CEs is passed on to higher trophic levels, creating regions of increased foraging opportunities, thus, attracting large marine predators such as tunas and billfishes (Block *et al.*, 2005; Braun *et al.*, 2015; Hsu *et al.*, 2015), turtles (Gaube *et al.*, 2017; López-Mendilaharsu *et al.*, 2009), marine mammals (Fieldr *et al.*, 2001; Bailleul *et al.*, 2010) and sharks (Sims & Quayle, 1998; Pade *et al.*, 2009; Queiroz *et al.*, 2016), which remain in these areas for extended periods of time.

For instance, the filter-feeding basking shark (*Cetorhinus maximus*) has been shown to aggregate and actively forage on frontal systems. Sims & Quayle (1998) recorded several of these sharks distributing (and apparently orientating) themselves along the Plymouth Front (southwest of England) from May to July of 1996 and 1997, while actively feeding on zooplankton rich patches, usually in the well-mixed, cooler water. Furthermore, although front locations slightly changed between the two years, shark's locations closely followed those of the changing fronts. Analogous trends are found in eddies, for example, Bailleul *et al.* (2010), observed elephant seals (*Mirounga leonina*) foraging in eddies, and found them to preferentially select the edge of CEs, where high productivity resultant from central upwelling of nutrients generates high concentrations of prey. Also, elephant seals were recorded diving deeper in CEs than in ACEs.

DO Fronts

Fronts are defined as areas of steep horizontal gradients in water properties. Yet, sharp differences in one water property across frontal systems are necessarily associated with differences in other water properties, especially temperature, density and salinity, as saltwater density is the result of the interdependence between these properties (Belkin *et al.*, 2009). Likewise, oxygen solubility is conditioned by fluctuations in these properties (Xing *et al.*, 2014). Thus, strong temperature differences across persistent thermal frontal systems are likely to be reflected in substantial variations in DO concentrations too.

In addition, there is a different type of DO fronts, those associated with hypoxic areas such as oxygen minimum zones (OMZs). OMZs occur in areas where intense productivity couples with strong stratification of the water column and poor oxygenation from greater depths. In short, the high phytoplankton production observed in these areas leads to high rates of both respiration and remineralization, resulting in high oxygen consumption. This, combined with the upwelling of already poorly oxygenated waters and the weakening of wind-driven ventilation in the upper water layers (100 to 300 m) due to the intense stratification of tropical oceans, results in the formation of these hypoxic areas (Helly and Levin, 2004; Breitburg *et al.*, 2018; Levin, 2018).

Yet, even though most species are expected to avoid hypoxic areas (Stramma *et al.*, 2008), previous studies have described top predators such as sharks, billfishes and tunas to regularly use surface waters within OMZs (Prince and Goodyear, 2006; Jorgensen *et al.*, 2009; Nasby-Lucas *et al.*, 2009; Stramma *et al.*, 2011). Explanation for these observations seems to rely on the high densities of hypoxic non-tolerant, mesopelagic, prey that are compressed to the upper layers of the water column, as well as some vertical displacement of hypoxia-tolerant species. The aggregation of high numbers of, more lethargic, mesopelagic prey at near-surface waters leads to higher predator-prey encounters and consequently, enhanced foraging opportunities which attract top pelagic predators (Koslow *et al.*, 2011; Stewart *et al.*, 2013).

In addition, ocean deoxygenation is severely impacted by global warming, since warmer waters result in lower oxygen solubility, higher stratification of the water column and higher rates of oxygen consumption, due to increased metabolic rates (Keeling *et al.*, 2010; Schmidtko *et al.*, 2017; Breitburg *et al.*, 2018; Levin, 2018). Thus, these areas are expected to continue expanding their ranges both horizontal and vertically, which emphasizes the importance of understanding how these two sharks, with different metabolic strategies and high commercial interest, interact with these on-growing areas in a changing ocean.

Eddies' Novel Insights

In contrast to the high productivity associated with CEs (McGillicuddy, 1998; Oschlies and Garçon, 1998), ACEs have long been considered as biological deserts (The Ring Group, 1981; Williams and Follows, 1998). However, new evidence provided by two recent studies suggests that apex predators such as white and blue sharks might be regularly using ACEs as foraging grounds (Gaube *et al.*, 2018; Braun *et al.*, 2019). Using the Mesoscale Eddy Trajectory Atlas, a recent product by AVISO (Archiving, Validation and Interpretation of Satellite Oceanographic data), which identifies and tracks eddies in daily maps of sea surface height (SSH) based on their sea level anomaly (SLA) signature, these authors compared eddy trajectories with the movements of satellite-tagged sharks. Surprisingly, both studies revealed a higher affinity with the warmer waters associated with ACEs' centres than with the expected highly productive, cold-core, CEs.

Furthermore, in both studies, sharks were double-tagged with both SPOT and PSAT tags, allowing the further recording of diving behaviour, which revealed these sharks to be performing numerous deep dives within the centre of the ACEs. These authors propose that these two predators might be taking advantage of the unusually warm waters at greater depths to explore on mesopelagic prey without being submitted to high physiological stress. In the case of the endothermic white shark, Gaube *et al.* (2018) suggested this behaviour to reduce the physiological costs associated with a long permanence in cold waters, whereas Braun *et al.* (2019) stressed the importance that such strategy might yield for the ectothermic blue shark in exploring upon deep mesopelagic prey for longer periods.

General Objectives

The purpose of the present study is to, using ARGOS PTTs, investigate the patterns of foraging space-use of blue and mako sharks in the North Atlantic and explore how these patterns might relate with two mesoscale physical processes: DO fronts and eddies. Moreover, I intend to contribute to a more complete picture of the spatial dynamics and habitat preferences of the two most caught pelagic shark species in the Atlantic Ocean, to better inform conservation and management strategies. More precisely, I aim to determine:

1. How sharp differences in DO concentrations across frontal systems may affect the foraging space-use of two pelagic predators with extensively different energetic requirements.
2. Whether blue and mako sharks foraging patterns are preferentially associated with CEs, as conventional wisdom suggests, or as recently proposed, if ACEs might be favoured by these predators, and if there are differences between them, given their distinct thermoregulatory strategies.

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The influence of oxygen fronts and mesoscale eddies on the foraging patterns and space-use of blue and mako sharks

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Abstract

Pelagic top predator populations worldwide have suffered sharp decreases in abundance over the last decades, with overfishing being the main cause of such declines. Blue (*Prionace glauca*) and mako sharks (*Isurus oxyrinchus*) are the two most caught pelagic shark species in the Atlantic Ocean, being classified, respectively, as “near-threatened” and “endangered” by the IUCN red list. However, their catches remain highly unregulated, unmonitored, and unreported. Identification of priority areas for pelagic top predators’ conservation is hampered by the high mobility of these animals and the consequent difficulty in determining aggregation areas, yet mesoscale dynamic features such as thermal fronts and eddies have been suggested to attract a variety of large apex predators while foraging.

In this study, the foraging movements of 34 blue and 24 mako sharks, satellite-tagged across 5 different locations in the North Atlantic Ocean, were analysed in relation to dissolved oxygen (DO) fronts, which until now had not been considered. The results presented here suggest that DO fronts might represent extensive foraging areas for these two species, but particularly for blue sharks. Two different DO front types were noticed to attract these species: strong, persistent, and vertically structured thermal-oxygen fronts, where high productivity creates important foraging opportunities; and oxygen-only fronts associated with hypoxic areas where the compression of prey in the more oxygenated surface waters results in higher predator-prey encounters. This study also reinforces the importance of eddies for pelagic predators foraging in oligotrophic waters. In addition, mako sharks revealed a clear preference for cyclonic eddies (CEs) while blue sharks showed a more balanced usage of CEs and anticyclonic eddies. These results strongly suggest the integration of DO fronts in conservation and management modelling, as they can substantially improve the identification of priority conservation areas for these two sharks and, possibly, many other pelagic top predators.

1. Introduction

Marine ecosystems and global fisheries are on the brink of collapse, due to decades of overfishing (Pauly *et al.*, 1998; Jackson *et al.*, 2001; Sethi *et al.*, 2010; Pinsky *et al.*, 2011; McCauley *et al.*, 2015). Large chondrichthyans, in particular, are of special concern because of their low resilience to exploitation, due to their slow life-history traits (Hutchings *et al.*, 2012), and their crucial function in the ecosystem as apex predators and consequent cascading effects associated with their removal (Myers *et al.*, 2007; Heithaus *et al.*, 2008; Ferretti *et al.*, 2010; Estes *et al.*, 2011). These trends have been reported for various large predatory sharks, such as blue (*Prionace glauca*) and mako (*Isurus oxyrinchus*) sharks, with many stocks being continuously fished over their rebounding capacities (Stevens *et al.*, 2000; Baum *et al.*, 2003; Baum and Myers, 2004; Worm *et al.*, 2013).

Longlines, in particular, are of extreme concern, as these fisheries alone comprise around 80% of all pelagic shark catches (Bonfil, 1994) and their overlap with pelagic sharks' foraging areas is exceptionally high (Queiroz *et al.*, 2016, 2019), exposing these species to great risk from fisheries. Blue and mako sharks are the two pelagic sharks at greater risk in the North Atlantic (Queiroz *et al.*, 2019). Blue sharks alone make up to ~80% of the total pelagic shark catches made by longlines, while makos are ranked second, with ~16% (Camhi *et al.*, 2008). Moreover, pelagic shark catches remain highly unregulated and poor reporting still occurs worldwide (Camhi *et al.*, 2008; Lack and Santa, 2011; Worm *et al.*, 2013), with stock assessments being often based on data with a high level of uncertainty (ICCAT SCRS, 2019), making necessary and effective management policies harder to determine.

Pelagic apex predators, such as blue and mako sharks, are regularly found in association with mesoscale (10s – 100s km) oceanographic features, such as fronts and eddies (Sims and Quayle, 1998; Worm *et al.*, 2003; Block *et al.*, 2011; Queiroz *et al.*, 2016, 2019; Scales *et al.*, 2018). This association is motivated by the regular upwelling of nutrient-rich waters promoted by the intense vertical circulation presented at these features, which sustains high levels of primary production, consequently, generating hotspots of marine fauna, where higher foraging opportunities for subsequently higher trophic level organisms ultimately draw the attention of marine top predators (Owen, 1981; Lutjeharms *et al.*, 1985; Le Fèvre, 1987; Franks, 1992; Olson *et al.*, 1994; Oschlies and Garçon, 1998; Mann and Lazier, 2013).

However, until now, most studies have focused only on thermal or chlorophyll-a fronts (exs: Belkin and O'Reilly, 2009; Queiroz *et al.*, 2016; Scales *et al.*, 2018). No studies have yet addressed the relationship of pelagic top predators with dissolved oxygen (DO) fronts. The concentration of DO in the ocean is greatly dependent on both physical and biological processes, such as air-sea fluxes, circulation, production and respiration (Bograd *et al.*, 2008). Thus, DO fronts can either occur in association with frontal thermal systems, as a consequence of the interdependence between water properties (Belkin *et al.*, 2009) or as a result of a combination of physical and biochemical factors that ultimately lead to the formation of hypoxic areas, as the case of oxygen minimum zones (OMZs). Such as regular fronts, OMZs have also been described to present higher foraging opportunities to pelagic top predators (Koslow *et al.*, 2011; Stewart *et al.*, 2013). In these areas, the hypoxic conditions lead to the aggregation of mesopelagic prey non-tolerant to hypoxia to the upper layers of the water column, where air-sea fluxes maintain DO at greater levels. Thus, providing large predators with high encounter rates with lethargic prey within unusually shallower depths.

Regarding eddies, their crucial role in providing nutrients within the oligotrophic waters of the open ocean has long been a matter of study (Owen, 1981; Falkowski *et al.*, 1991; McGillicuddy, 1998; Oschlies and Garçon, 1998). In this sense, cyclonic eddies (CEs), due to their counter-clockwise rotation, in the northern hemisphere, are usually associated with the upwelling of nutrient-rich cold waters and, for this reason, are considered to provide increased foraging opportunities to pelagic predators, in contrast to the low productive, warm core, anticyclonic eddies (ACEs), which has been confirmed for various species (Bailleul *et al.*, 2010a; Jaine *et al.*, 2014; Hsu *et al.*, 2015). Nonetheless, two recent studies described both white and blue sharks actively preferring ACEs instead of CEs while, presumably, foraging (Gaube *et al.*, 2018; Braun *et al.*, 2019). According to these authors, this behaviour might indicate an adaptive advantage of these sharks of foraging in ACEs, as they can take benefit from the anomalously warm waters at great depths to access mesopelagic prey while reducing the physiological stress associated with low temperatures.

In this study, satellite tags were deployed in blue and mako sharks across different locations in the North Atlantic Ocean to investigate the importance of oceanographic mesoscale processes in shaping the foraging movements of these large pelagic predators, namely, in what regards to DO gradients and ACEs as relevant foraging grounds. In addition, this research aimed to contribute towards a more complete picture of the spatial dynamics and habitat-use of the two most caught pelagic shark species in the Atlantic Ocean and, consequently, to provide further information for fisheries management and conservation strategies. Finally, the fact that this study considers two sharks with different metabolic strategies allows the extrapolation of the results obtained to other pelagic fishes, particularly those under high fishing pressure, as they allow to investigate how temperature and oxygen conditions may influence species with distinct thermoregulatory strategies and energetic requirements.

2. Material and Methods

2.1. Satellite Tagging and Spatial Analysis

2.1.1. Tagging Methods

Blue and mako sharks were tagged with ARGOS PTTs (Smart position-only tags, SPOT; model SPOT5, Wildlife Computers, Redmond, WA, USA) at five different locations in the North Atlantic between 2006 and 2017. These tags are affixed directly to the shark's first dorsal fin with stainless steel bolts, neoprene and steel washers, and steel screw-lock nuts. Blue sharks were tagged at two coastal locations in the North-eastern Atlantic (Southern England and Southern Portugal, respectively, n = 3 and n = 7) and two oceanic locations (off the Azores and Cape Verde Islands, n = 16 and n = 10). As for mako sharks, tagging occurred at the same oceanic locations (n = 13 and n = 4, respectively) and off the United States' east coast (east of Long Island, n = 7).

At coastal locations, sharks were captured by rod and line, measured, and tagged on-board. Differently, at oceanic locations, sharks were captured by longline commercial fishing vessels. Here, tagging was carried out with the sharks lifted in a vertical position and suspended alongside the vessel. All animal handling procedures undertaken were approved by institutional ethical review committees and completed by licensed, trained, and experienced personnel. Two of the tagged blue sharks, consisting of tracks with less than 7 days, were considered to be unrepresentative of sharks' environmental preferences due to tagging locations bias. Thus, all analyses in this study were limited to 34 blue and 24 mako sharks, together comprising a total of 4116 days of tracking data.

2.1.2. Tracking Processing

Given the nature of telemetry data and since sharks need to surface regularly and for enough time so that PTTs can communicate their position to satellite receivers, tracks must be manually corrected for possible errors. Therefore, failed attempts to obtain a position (location class Z data), and outliers (detected using a 3 m s^{-1} filter for all remaining positions) were removed from the dataset. Then, each track was interpolated to produce one single position per day using a continuous-time correlated random walk Kalman filter (CTCRW) (Jonsen *et al.*, 2005), implemented on the R-package "crawl" (Johnson *et al.*, 2018). In the case of temporal gaps greater than 20 days, the track would be split apart before the interpolation took place, to reduce unrepresentative position estimates (Block *et al.*, 2011).

2.2. Environmental Preferences

2.2.1. Space-Use Analysis

ArcGIS geographical information system (ESRI Inc., CA, USA) was used to identify areas of high and low space-use for each species separately. First, the mean days spent on each grid cell were calculated for all sharks. To do so, the density of daily positions within each grid cell was weighted by the number of individual id's tracked in each cell (Walli *et al.*, 2009). Then, a spatial hotspot analysis was conducted using the Hotspot Analysis tool (Getis-Ord Gi* statistic) from the Spatial Statistics toolbox of ArcGIS 10 (Robinson *et al.*, 2012). This tool compares the number of mean days in each grid cell with those of the surrounding cells, determining if there is a significant difference between them, and, this way, identifying areas of higher and lower utilization. Finally, and for interpretations purposes, the Kernel Density tool was also used. This tool calculates the density per-area of a given feature and uses a kernel function to produce a density raster for that same feature.

It is important to mention that, together with the above-stated re-weighting of the geolocated positions by the number of id's in each cell, both the deployment of tags in multiple locations across the North Atlantic and the removal of short tracks (less than a week; remaining tracks with an average of 71 days) contributed to reduce the potential hotspot spatial bias.

2.2.2. Environmental Data

All environmental variables were retrieved from CMEMS's (Copernicus Marine Environment Monitoring Service) Ocean Products. The global mole concentration of dissolved molecular oxygen (DO; mmol m−3), mass concentration of chlorophyll-a (CHL; mg m-3), mole concentration of phytoplankton, expressed as carbon, (PHYC; mmol m−3) and primary production of biomass, expressed as carbon per unit of volume (PP; mg m-3), in seawater, were retrieved from the Global Ocean Biochemistry Hindcast product (GLOBAL_REANALYSIS_BIO_001_029; from 1993-01-01 to 2019-12-23). SST (SST; ºC) was extracted from Global Ocean Ensemble Physics Reanalysis (GLOBAL_REANALYSIS_PHY_001_031; from 1993-01-01 to 2018-12-31). Ultimately, SLA, used to identify mesoscale eddy cores (Isern-Fontanet *et al.*, 2003), were extracted from Global Ocean Gridded L4 Sea Surface Heights and Derived Variables Reprocessed (SEALEVEL_GLO_PHY_L4_REP_OBSERVATIONS_008_047; from 1993-01-01 to 2019-10-15). SLAs consist of altimetry variations from the mean SSH of a particular region with respect to a 20-year mean reference period (1993-2012).

The first two products, derived from a combination of satellite-based, and surface and sub-surface buoys measurements, provide daily and monthly datasets of, respectively, biogeochemical and physical fields from the surface to 5500 m depth at a 0.25º x 0.25º grid-cell resolution. Whereas the last product displays monthly averages of SLA based on satellite altimetry measurements of SSH, also at a 0.25º x 0.25º grid-cell resolution. For this study, all variables were extracted from the surface, except for DO, which values were retrieved at 100 m depth, since this is the depth at which the North Atlantic's OMZ starts (Stramma *et al.*, 2011).

Furthermore, to determine the existence of DO and temperature fronts, monthly DO and SST maximum gradients between grid-cells (Δ mmol m^{-3} per ~25 km) were calculated, using geodetic-distance-corrected maximum gradients to produce horizontal maps of fronts (DO and SST Front). Finally, the distances (m) to each closest front (DO and SST FDist) were also calculated for 0.5 mmol m^{-3} and 0.5 ºC thresholds (Rivas and Pisoni, 2010), for DO and SST fronts respectively, and using the function "pointDistance" from the R-package "raster" (Hijmans *et al.*, 2020). The low thresholds are congruent with the idea that when variances are low, even small fluctuations of a given variable denote fronts (Podestá *et al.*, 1993).

2.2.3. Analysis

2.2.3.1. Area Restricted Search (ARS) Behaviour

The definition of ARS behaviour is grounded on the theory that predators, after capturing a prey, tend to restrict their foraging attention to the surrounding area before continuing their wider-range search (Kareiva and Odell, 1987). Thus, this behaviour is commonly used as a proxy for foraging movements. The area restriction is indicated by higher turning frequencies and lower speeds, since animals are expected to spend more time in areas of high prey density than in areas where resources are scarce (Fauchald and Tveraa, 2003). In addition to speed and turning frequency (hereafter referred to as straightness), another useful indicator of ARS behaviour, especially when working with telemetry data, is the first-passage time (FPT) (Pinaud, 2008). Therefore, and to increase robustness, all these three variables were combined to better infer where this behaviour is likely to have occurred.

The FPT is defined as the time required for an animal to cross a circle of a given radius (Fauchald and Tveraa, 2003). Thus, it is determined by calculating the time taken to travel from one geolocated position to the closest point (backward and forward) of the track where the straight distance to that geolocated position is given by radius r. This is calculated for each position along the track and repeated for increasing radius. The FPT´s relative variance, *S(r)*, is then calculated according to:

$$S(r) = var[\log(FPT)]$$

The radius corresponding to the highest variance in FPT is chosen as the spatial scale of the ARS behaviour (Fauchald and Tveraa, 2003; Pinaud, 2008). Note that the FPT is log-transformed, so that the variance is independent of the magnitude of the mean FPT (Fauchald and Tveraa, 2003). Finally, and since the FPT is a scale-dependent measure of search-effort, which will vary across different individuals, FPT was normalized for every individual to fall between 0 and 1, to be comparable within each species.

Areas associated with higher search effort will have higher tortuosity (and therefore, higher FPT) when compared to transiting only areas, where the movement is closer to a straight line. This way, it is possible to infer a measure of search effort for each point/location, except for the first and last positions, where the FPTs, backward and forward, are, respectively, unknown (Fauchald and Tveraa, 2003).

Speed and straightness were calculated using a custom-written R code, according to Sims (2010). In short, speed (km d^{-1}) was computed between every two positions five days apart, as well as the straightness, which was determined by dividing the straight distance between the two positions by the actual distance travelled in between them (dimensionless index, where 1 = straight line). Regarding the FPT, the function “fpt”, from the R-package “adehabitatLT” (Calenge *et al.*, 2020) was used. FPT (day^{-1}) was calculated for each interpolated location from radii 0.04 km to two times the maximum step length (i.e., the maximum distance between two consecutive locations) at increments of 0.1 times the maximum step length (Bradshaw *et al.*, 2007). While ARS scale for each shark was identified according to the FPT’s relative variance, that is, the spatial scale at which the sharks increased their search effort.

Considering that all three measures are related with tortuosity, a Spearman’s rank correlation matrix was performed to determine if there was any intercorrelation between them. As none of the measures exceeded a correlation of 0.75 (Žydelis *et al.*, 2011), all three were kept in the analysis.

For this study, speed and straightness were defined as low if they fell within the first quartile of their distribution in the whole sample. As for FPT, it was defined as high if it fell within the fourth quartile. Thus, if, at least, two of these three parameters were met, ARS behaviour was considered to occur, in opposition to a regular transiting movement.

Additionally, ARS behaviour was plotted against DO Fronts, DO and SLAs in ArcGIS to further explore shark-environment relationships, as well as to identify preferred foraging areas.

2.2.3.2. Exploratory Analysis

To investigate whether the foraging patterns and space-use of these two species are affected by eddies and/or differences in DO concentration across frontal systems, the R software v.4.0.2 (R Core Team, 2020) was used to test their relation to a combination of environmental variables: DO, DO Fronts, DO FDist, SLA, PHYC, CHL, PP, SST, SST Fronts and SST FDist.

All variables were plotted against the three ARS parameters – speed, straightness and FPT – to examine their relation, which were then verified through Spearman's rank correlation tests. Furthermore, all variables were tested for correlation using a Spearman's rank correlation matrix, with those exceeding a correlation of 0.75 being removed (Žydelis *et al.*, 2011). The whole analysis was performed separately for the two species.

2.2.3.3. Resource Selection Probability Function (RSPF) Models

To further explore the tendencies suggested by the exploratory analysis, RSPF (Boyce and McDonald, 1999; Manly *et al.*, 2002; Lele and Keim, 2006; Lele, 2009) models were used. After the removal of all correlated variables and those for which relation to foraging movements was not suggested by the exploratory analysis, the environmental variables underlining the subsets of the tracks where the sharks displayed ARS behaviour were compared against those where this behaviour was not found to occur, in order to determine which variables best explained the observed ARS behaviours.

The RSPF is a function that quantitatively describes the probability that an individual animal has of using a particular resource, defined by a combination of environmental variables, that can be either categorical (as long as not all) or continuous (Lele and Keim, 2006). It is considered that a species will select the resources that best fit its life requirements. However, since resources are not evenly distributed in nature, species' resource selection may differ according to their availability. For this reason, RSPF models take into consideration the whole extent of available habitat and compare it to the fraction of that habitat that was actually used. Here, usage refers to the portion of the resource utilized by the animal within a certain period of time, whereas availability indicates the amount of that same resource that was accessible to the animal during that time. When the relation between the "used" and "available" resources is disproportional, the use is considered to be selective (Manly *et al.*, 2002).

Thus, if a particular habitat is visited more often, we could say that it is used preferentially. However, and given the nature of telemetry data, every location is assumed to be "used" (Lele and Keim, 2006), when, in reality, that location might only illustrate a transiting movement, without any type of usage. For this reason, and to increase the likeliness of those locations having actually been used, the subset of the tracks where foraging patterns were identified (as ARS) was compared against the subsets where no ARS was observed.

When unused locations are unknown, only relative probabilities of use are possible to infer. Yet, when a use-availability design is possible (i.e., when it is known both the resource units that were available and those that were actually used), as is the case with telemetry data, RSPFs can render the absolute probability of a particular resource being used (Lele and Keim, 2006). The use of logistic regression to estimate habitat selection models has become one of the most common statistical approaches under a use-availability design (Hebblewhite *et al,* 2005). Moreover, the association of RSPFs with geographical information systems (GIS) facilitates the analysis and use of remotely sensed environmental features to help understanding potential patterns of resource usage (Boyce and McDonald, 1999). To estimate the logistic RSPF model, the "rspf" function, from the R-package "ResourceSelection" (Lele *et al.*, 2019) was used. Let $\pi(x;\beta)$ denote the probability of a particular area/resource being used, given the values of the explanatory variables x present in that area ($P[Y = 1 \mid X = x]$). This model is given by:

$$\pi(x;\beta) = \frac{\exp(x\beta)}{1+\exp(x\beta)}$$

$$\text{where,} \quad x\beta = \beta_0 + \beta_1 x_1 + \ldots + \beta_p x_p\,,$$

β_0 represents the intercept and the other parameters denote the coefficients associated with the considered environmental variables. As for any probabilistic model, Y (or $\pi(x;\beta)$) is a binary variable represented by "1" or "0". The "1" refers to the used resource units, or in this case, to the area where ARS behaviour occurred, and the "0" to the available, but unused, units, here represented by the units where the sharks could have displayed ARS behaviour, but did not.

Briefly, to fit the model, a use-availability framework was built, consisting of a list of the available units, followed by the values of the considered explanatory variables and the response variable column labelled as "1" or "0". Models are estimated based on maximum likelihood methods and the best model is chosen using Bayesian information criteria (BIC). The output consists of the estimates of these parameters, that is the statistical contribution of each variable for the model (Lele, 2009).

3. Results

3.1. Space-Use Analysis

Between 2006 and 2017, 36 blue and 24 mako sharks were tagged in five different locations across the North Atlantic Ocean (Figs. 3.1 and 3.2). After the removal of two blue shark tracks, considered to be location biased, the results presented here refer to the analyses resultant from a total of 2141 (average track time: 62.97 d^{-1}; range: 9 – 233 d^{-1}) and 1975 (82.29 d^{-1}; 12 - 326 d^{-1}) days of horizontal tracking data of blue and mako sharks, respectively.

Hotspot analysis revealed three essential high use areas for mako sharks (Fig. 3.2), in contrast with a more continuous habitat for blue sharks (Fig. 3.1), though both species showed the expected broad distribution. Generally, blue sharks performed more extensive movements, whereas mako sharks' tracking tended to take place in areas closer to that of tagging location. Including the longest of all tracks (shark #38), which remained near the coastline of the United States' east coast for 326 days, with only one small excursion to offshore waters, towards the Gulf Stream, during the winter season (Annex A, Fig. A2). In addition, no transequatorial movements were observed for either of these sharks.

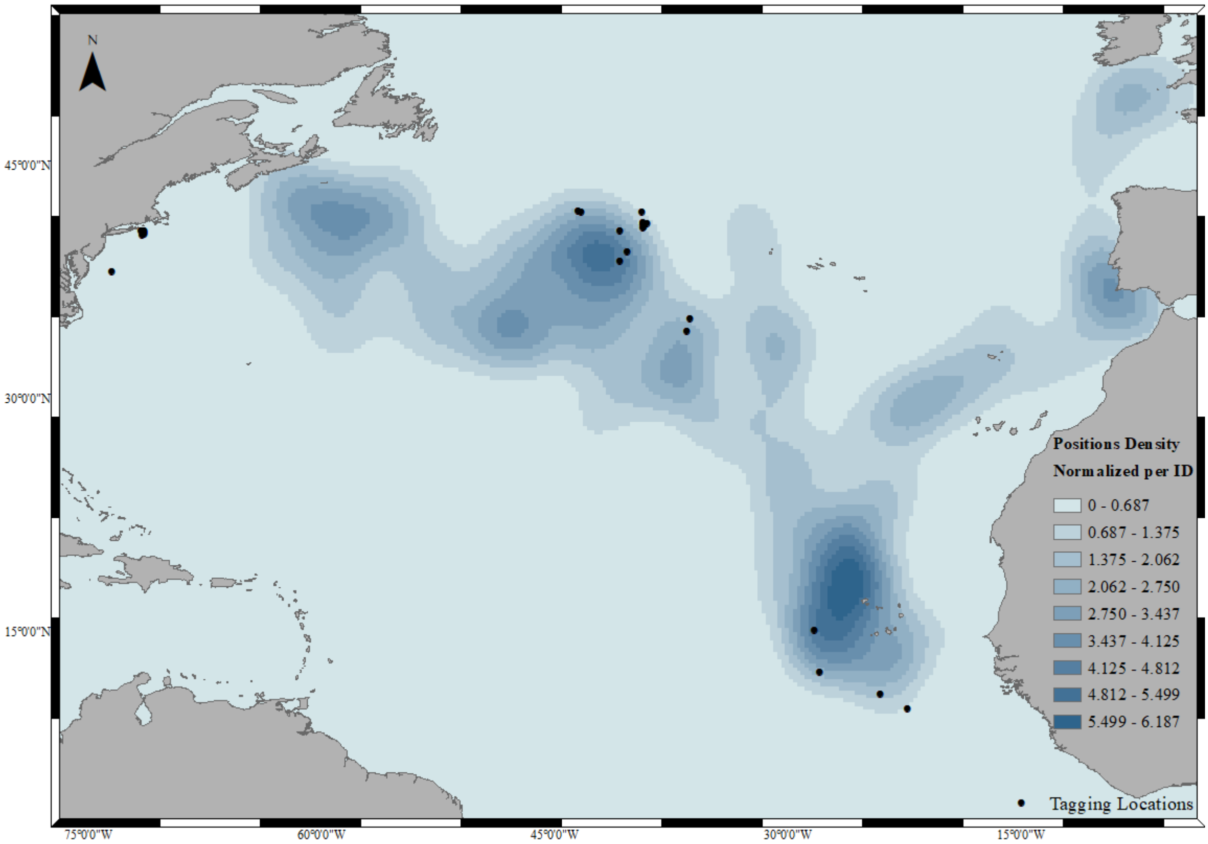

Figure 3. 1 - Map of tagging locations and calculated high and low used habitats of tracked blue sharks.

Both species occupied a similar latitudinal range (between 8° and 51°), inclusive some overlap was observed, essentially in the central North Atlantic, one of the two tagging locations where both species were tagged. Here, aggregation was observed west of the Azorean Islands. Yet, blue shark movements stretched more westward, reaching the shore of Nova Scotia, whereas mako sharks generally did not cross the 50th meridian west. Differently, in Cape Verde, blue and mako sharks showed different predominant movements. Blue sharks tended to move northward after tagging, with an intensively used area detected north of Cape Verde Islands. Contrarily, mako sharks showed a preference for moving slightly southward and more inshore.

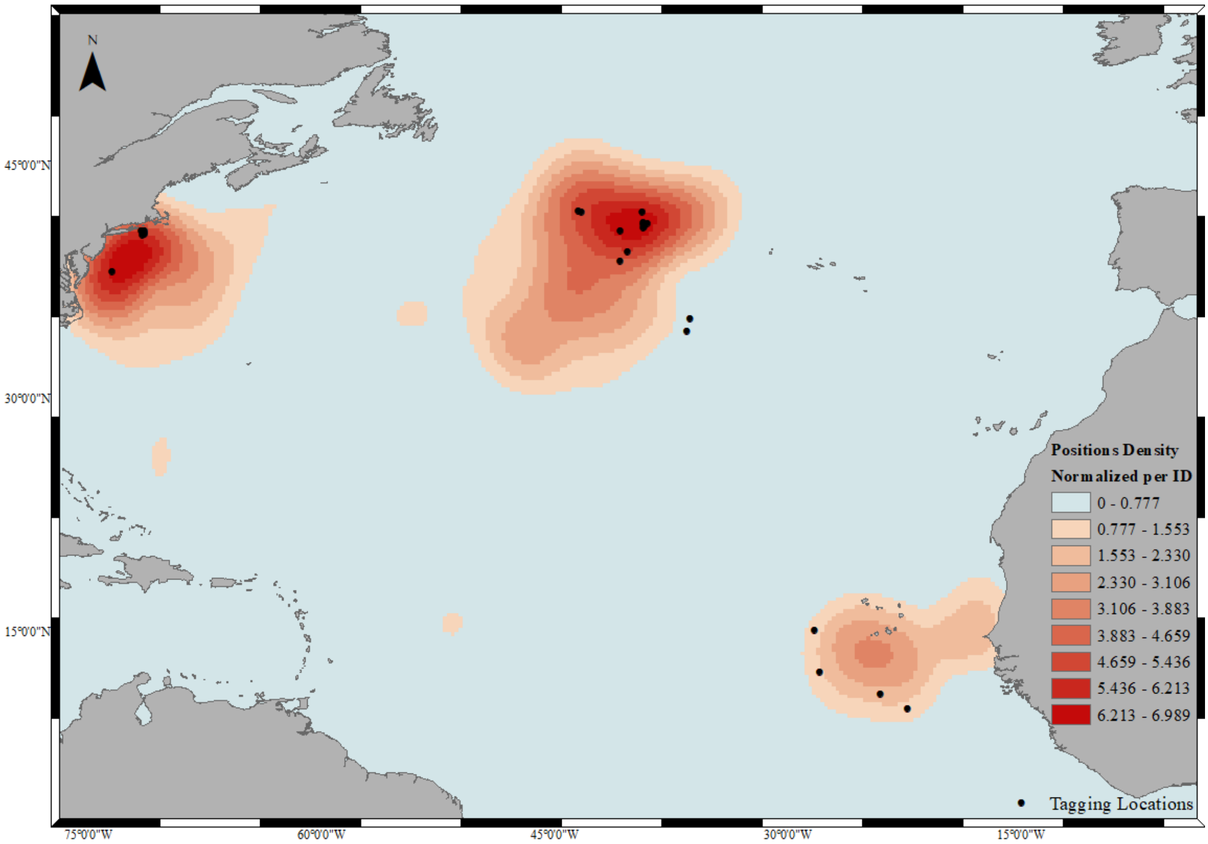

Figure 3. 2 - Map of tagging locations and calculated high and low used habitats of tracked mako sharks.

Regarding coastal tagging sites where only one species was tagged, mako sharks tagged off the United States' east coast revealed a high affinity with the continental shelf from the south of Nova Scotia to Cape Hatteras. Likewise, blue sharks tagged off western Europe also exhibited a general preference for more inshore areas around both Southwest England and Portugal.

3.2. ARS Behaviour

To quantify ARS behaviour, three metrics were used: speed, straightness and FPT. For blue sharks, average speed was 39.32 km d^{-1}, straightness 0.7 and FPT (prior to normalization)

5.01 d^{-1}. While mako sharks had an average speed of 44.59 km d^{-1}, 0.6 of straightness and 9.27 d^{-1} of FPT. Probably due to the great differences in tracking periods (especially in mako sharks) and the scale dependency of this method, FPT greatly varied among individuals, ranging from near 0 to 70.32 d^{-1} and near 0 to 247.93 d^{-1} in blue and mako sharks, respectively. Similarly, FPT radius ranged from 4 276.9 to 252 446.5 m and 4 450.4 to 565 022.6 m, for blue and mako sharks, respectively.

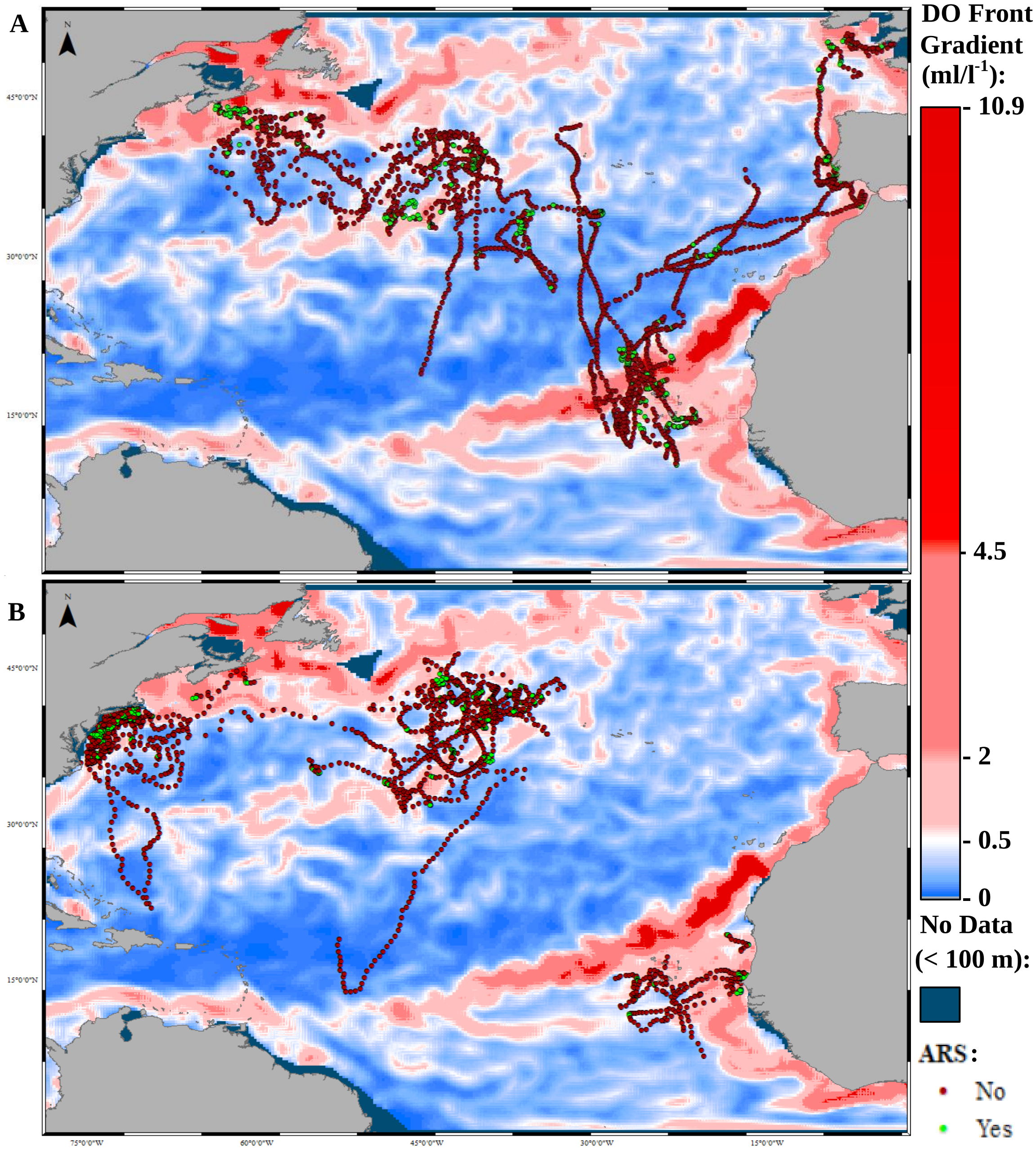

Figure 3. 3 - ARS behaviour (green circles) of tracked blue (A) and mako (B) sharks in relation to mean DO frontal gradients at 100 m depth for the years 2006 to 2017.

ARS behaviour was then assessed from a combination of these three metrics, as previously mentioned. A total of 422 (~19.7%; Figs. 3.3 to 3.6, A) positions with foraging activity were estimated for blue sharks, whereas mako sharks' analysis indicated 358 (~18.1%; Fig. 3.3 to 3.6, B). Blue sharks revealed four primary areas of foraging (Fig. 3.1): north of Cape Verde (30.3%); the southwest coast of Portugal (23%); the central North Atlantic, west of the Azorean Islands (22.3%) and west of the Grand Banks, from south of Newfoundland to the coastline of Nova Scotia (16.8%). In addition, some meaningful foraging behaviour was also observed southwest of England (4.5%) and northwest of the Canary Islands (2.8%). On the other hand, mako sharks exhibited foraging behaviour almost exclusively in three central areas (Fig. 3.2): from south of Long Island to Cape Hatteras (53.1%); in the central North Atlantic, west of the Azorean Islands (34.6%) and east of Cape Verde (8.1%). Plus, some residual ARS behaviour was noticed southwest of Cape Verde (3.1%) and south of Nova Scotia (1.1%).

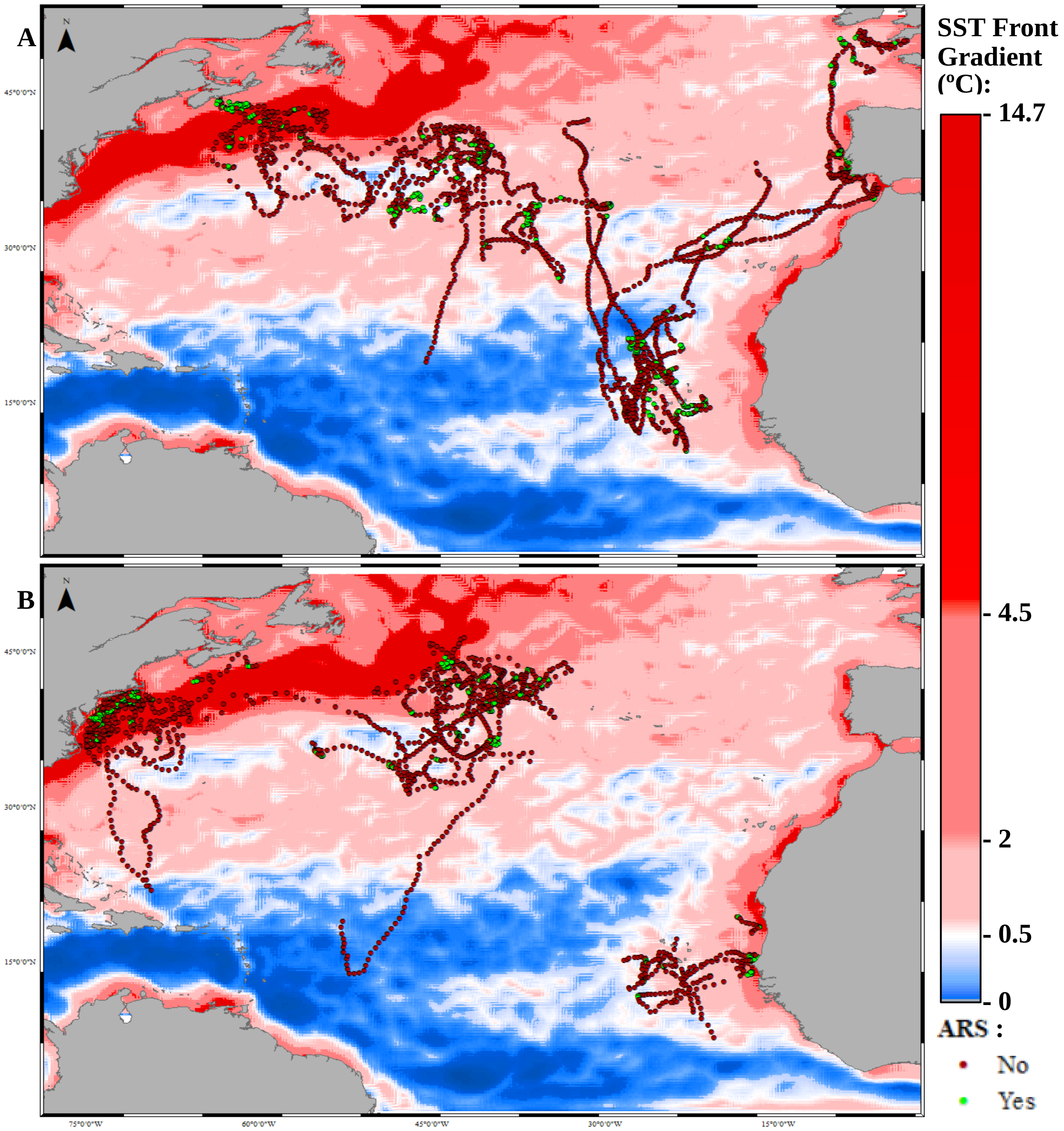

Figure 3. 4 - ARS behaviour (green circles) of tracked blue (A) and mako (B) sharks in relation to mean SST frontal gradients for the years 2006 to 2017.

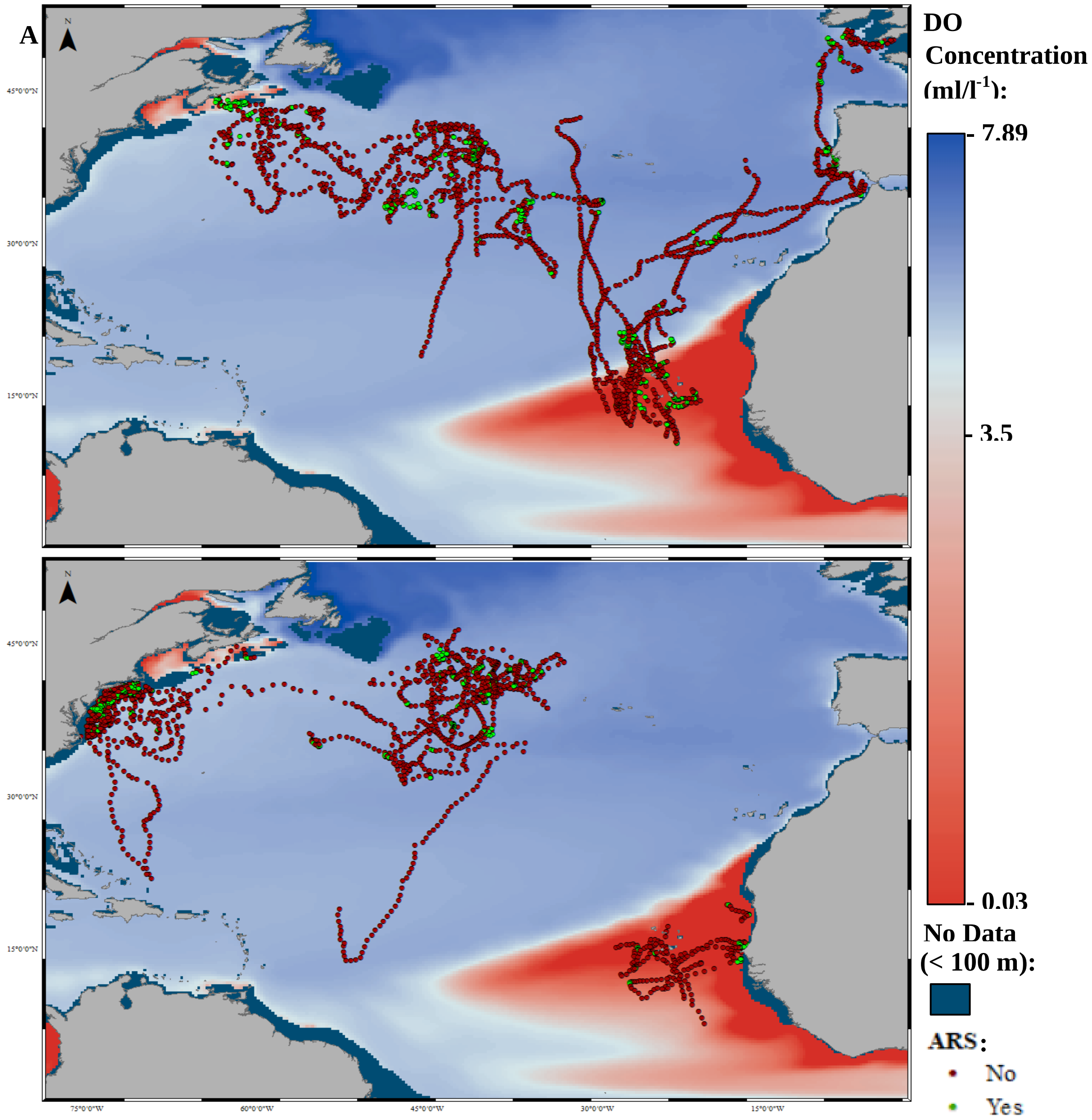

Figure 3. 5 - ARS behaviour (green circles) of tracked blue (A) and mako (B) sharks in relation to mean DO concentration for the years 2006 to 2017.

The comparison of sharks' ARS behaviour locations against DO Fronts all years mean (Fig. 3.3) suggests an apparent relation between foraging activity and DO Fronts. Particularly for blue sharks, for which most ARS behaviour seems to occur in waters characterized by medium to high DO gradients, whereas low to near zero DO gradient waters appear to be mostly used for transiting movements. Mako sharks ARS behaviour also appears to be related to DO Fronts, however, the difference between foraging and transiting movements is not so clear, as almost all movements are within regions characterized by some DO gradient. In addition, DO concentration (Fig. 3.5) was also plotted in order to identify which DO Fronts referred to hypoxic areas (< 3.5 ml l^{-1}; Stramma *et al.*, 2011). Similarly to DO Fronts, SST

Front all years mean (Fig. 3.4) also indicated a general higher preference of mako sharks for these features when compared to blue sharks.

In what regards to mesoscale eddies (Fig. 3.6), a clear association of foraging movements with these features seems to prevail, however, eventual preferences for CEs or ACEs are difficult to infer based on descriptive analysis only.

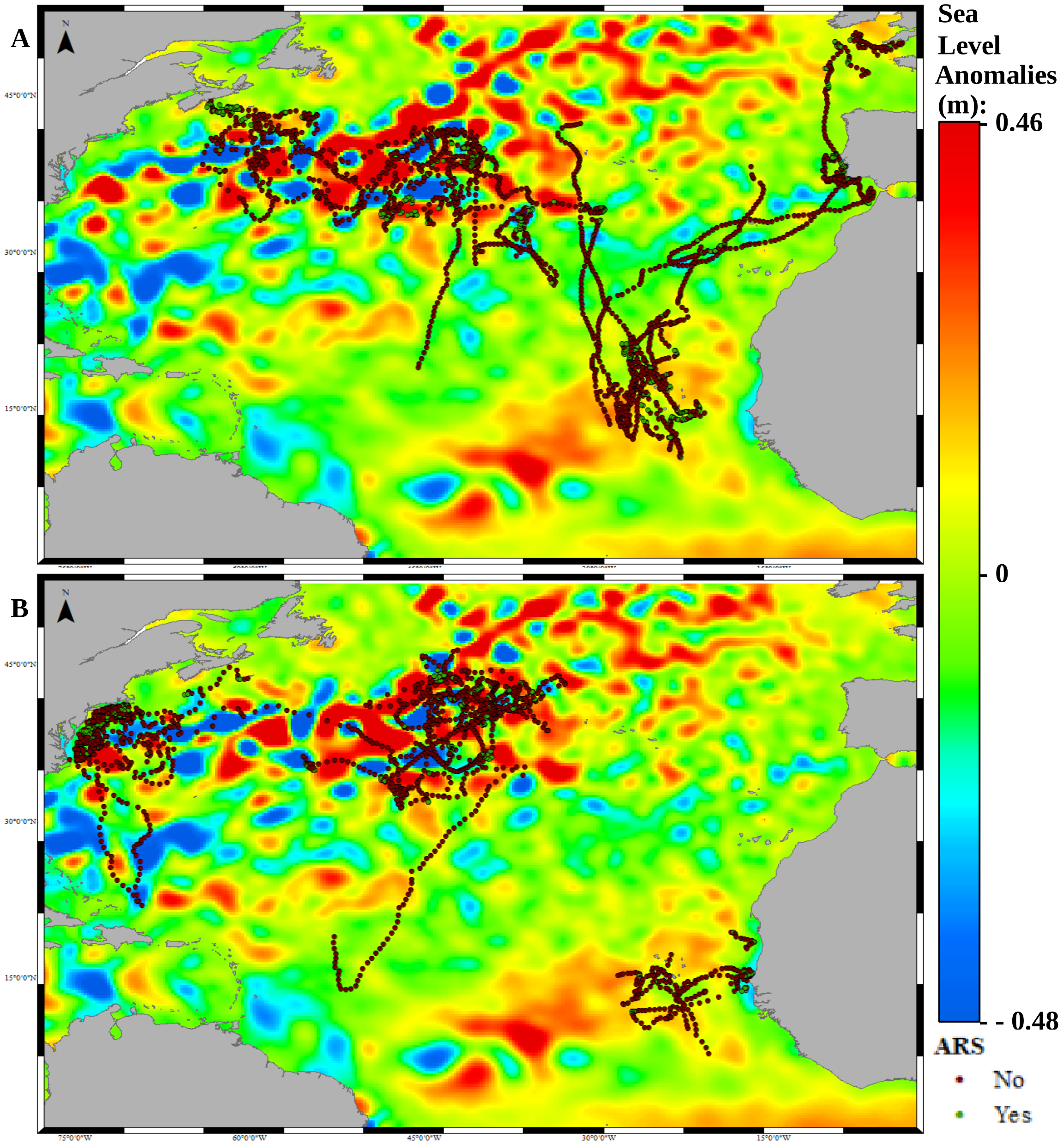

Figure 3. 6 - ARS behaviour (green circles) of tracked blue (A) and mako (B) sharks in relation to mean SLA of SSH for the years 2006 to 2017.

3.3. Exploratory Analysis

Blue and mako sharks seemed to respond to the presence of DO fronts in a similar way. Although not strongly correlated, both species increased their ARS behaviour, characterized by low speeds and straightness and high FPT, with increasing front intensity (Fig. 3.8). While as distance to front increased, this behaviour appeared to diminish (Fig. 3.9). In addition, this tendency was further supported by a negative correlation between shark's distance to the front and front intensity (- 0.51 for blue and - 0.3 for mako sharks, at significance level α = 0.001), with the former decreasing as the latter increases (Fig. 3.7), suggesting a general preference for areas of higher DO front intensity. Similarly, both species behaved in the same manner to SLA, suggesting a preference for negative SSH while foraging, that is, for CEs (Fig. 3.10). Yet, this preference was far more evident in mako sharks, which might indicate that blue sharks, although displaying a minor preference for CEs, may often forage at ACEs too. All these tendencies were additionally corroborated by Spearman's correlation coefficients, with all being significant, except for the relation between FPT and DO FDist in mako sharks (Table 1). For ARS behaviour relationship with other variables see Annex B.

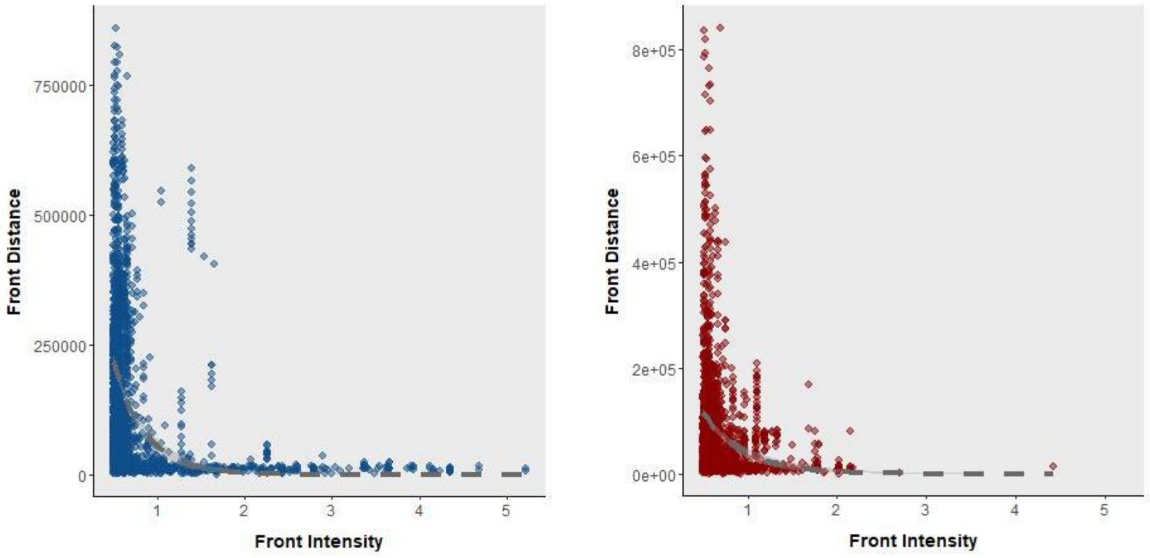

Figure 3. 7 - Relationship between distance to DO Front and front intensity of tracked blue (left) and mako (right) sharks.

	Blue Sharks			Mako Sharks		
	Speed	Straightness	FPT	Speed	Straightness	FPT
DO Front	*** - 0.2	*** - 0.16	*** 0.09	*** - 0.1	*** - 0.25	* 0.06
DO FDist	*** 0.22	*** 0.18	*** - 0.13	** 0.06	*** 0.15	0.01
SST Front	*** - 0.19	*** - 0.16	*** 0.1	** - 0.07	*** - 0.42	*** 0.11
SST FDist	*** 0.11	*** 0.09	** - 0.07	* 0.05	*** 0.12	0.02
SLA	*** 0.1	*** 0.09	*** - 0.09	*** 0.13	*** 0.48	*** - 0.26

Table 3. 1 - Spearman's correlation coefficients between ARS behaviour and environmental variables and correspondent significance level: *** for significant at α < 0.001, ** at α < 0.01, * at α < 0.05 and no star if not significant.

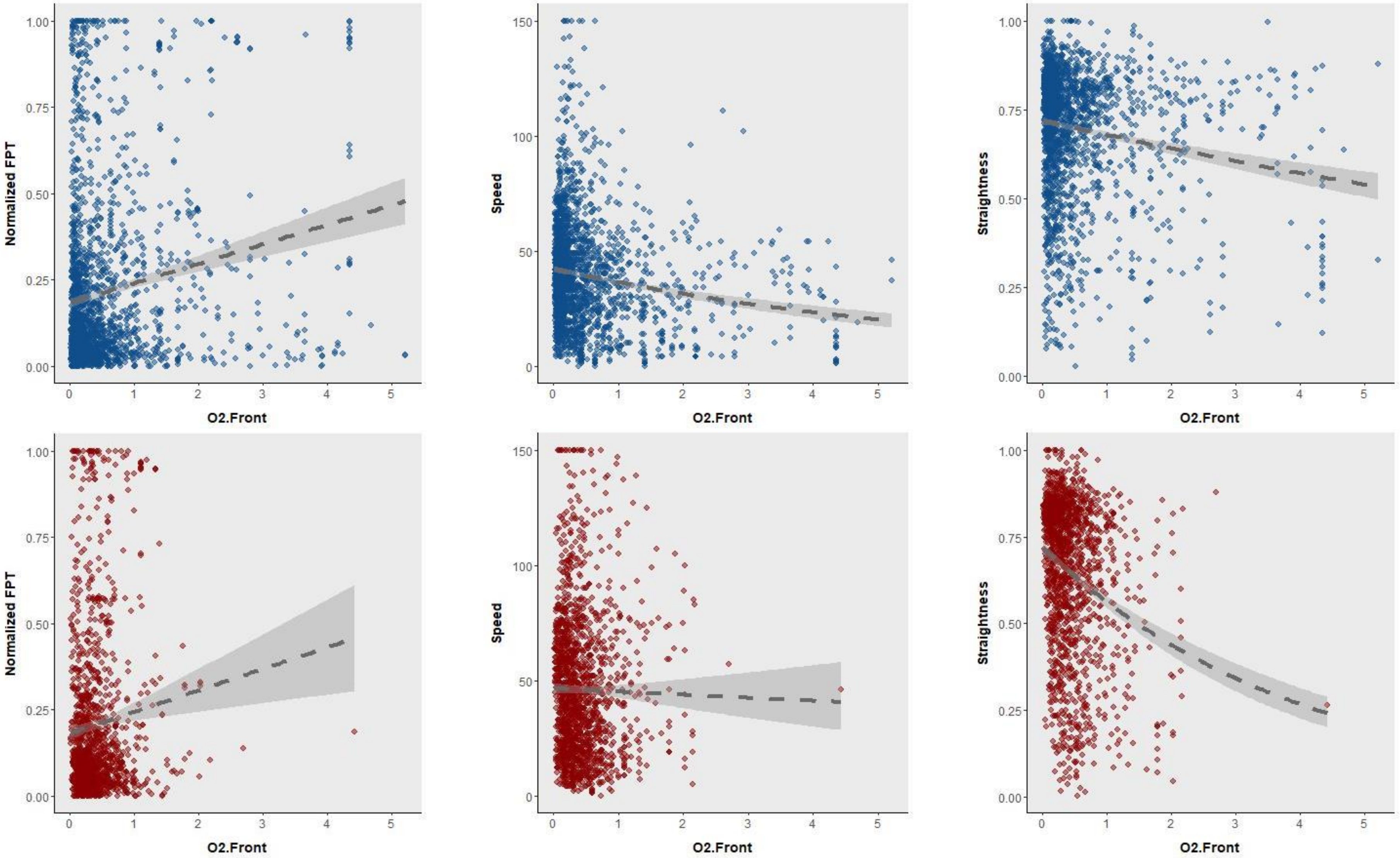

Figure 3. 8 - Relationship of DO Front intensity at 100 m depth with FPT, speed and straightness for blue (blue graphs) and mako (red graphs) sharks.

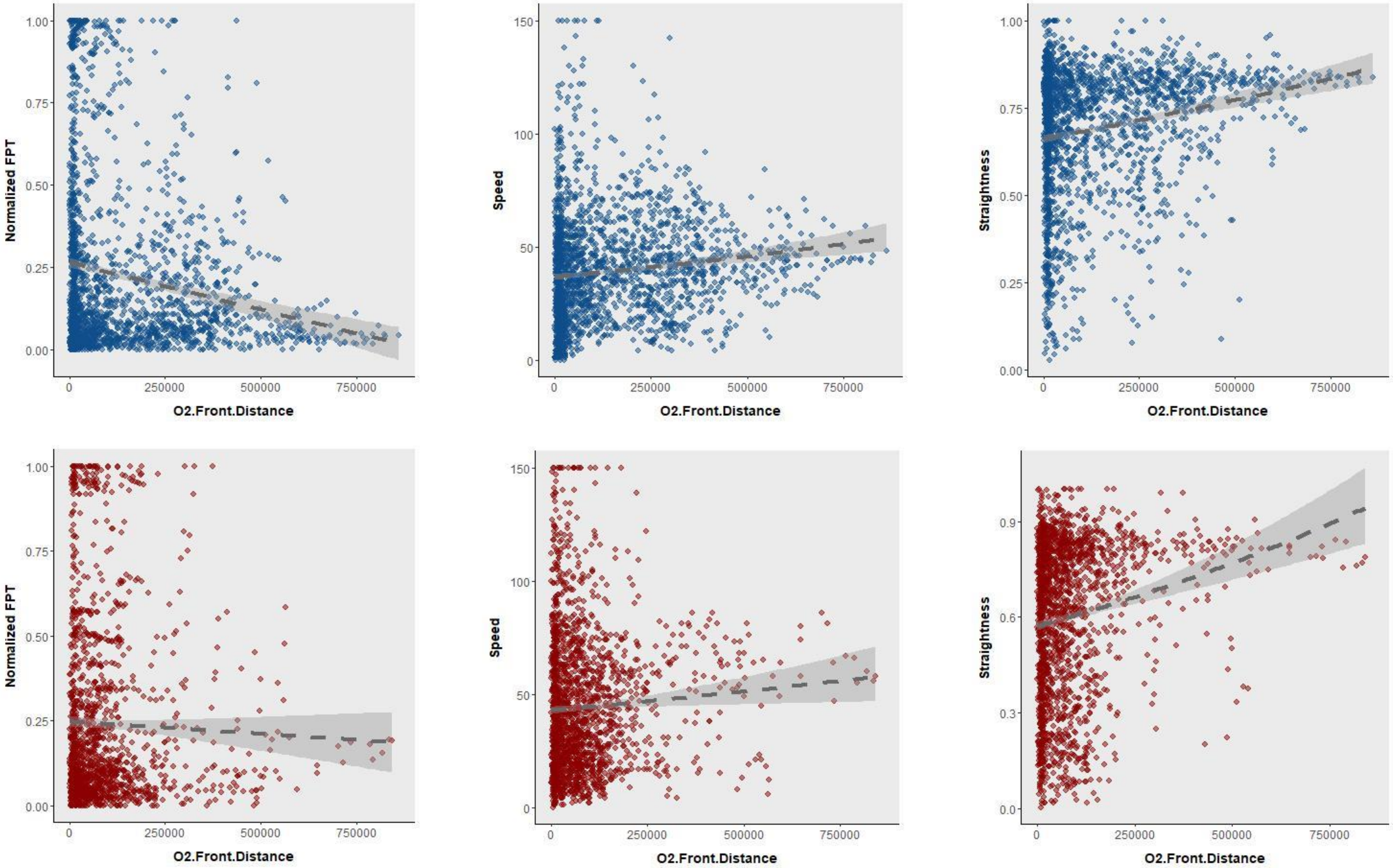

Figure 3. 9 - Relationship of distance to DO Front at 100 m depth with FPT, speed and straightness for blue (blue graphs) and mako (red graphs) sharks.

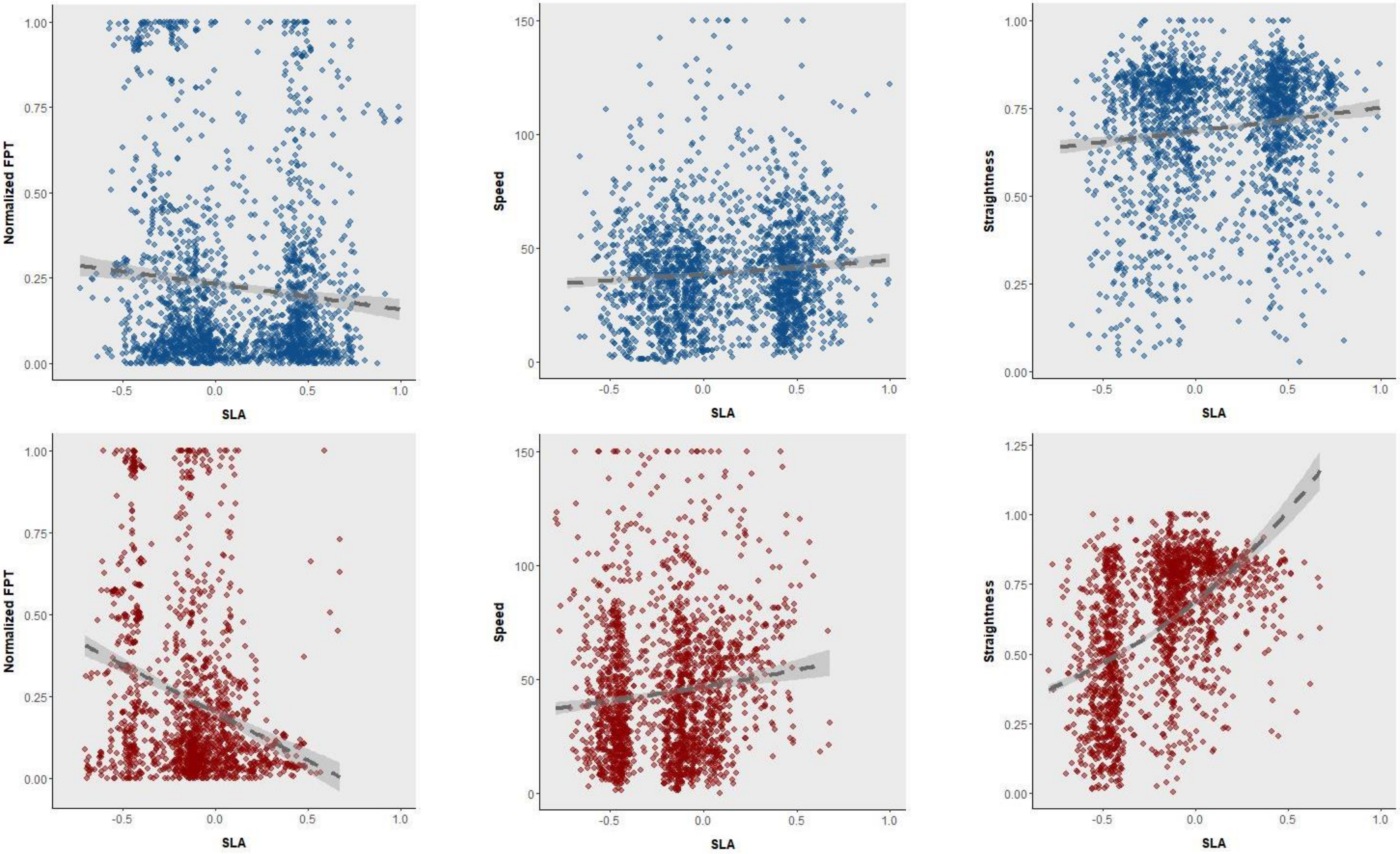

Figure 3. 10 - Relationship of SLA of SSH with FPT, speed and straightness for blue (blue graphs) and mako (red graphs) sharks.

3.4. RSPF Models

For blue sharks, RSPF models' output followed the tendencies suggested by the exploratory analysis, increasing their ARS behaviour in the presence of both DO Fronts and CEs (Table 2). On the other hand, mako sharks did not respond significantly to the presence of DO fronts or its distance, but, likewise, increased their foraging behaviour with decreasing SLA (Table 3). Furthermore, important differences could be noted regarding the influence of mesoscale eddies in both species, as these features revealed a substantially higher contribution for mako sharks' model.

PP and CHL were removed from both analyses due to the strong correlation with PHYC (Annex C, Figs. C1 and C2), as the latter showed an overall higher correlation with ARS metrics. Similarly, DO Front and DO FDist showed a strong negative correlation (Annex C, Figs. C1 and C2). For this reason, only one of these variables was used for each model.

Coefficients (cloglog link):	**Estimate**	**Std. Error**	**z value**	**Pr (> | z |)**
(Intercept)	- 24.11964	3.89798	- 6.188	*** < 2 e-10
DO	0.10935	0.05552	1.970	* 0.0489
PHYC	0.58890	0.10179	5.785	*** 7.23 e-09
SST	0.18782	0.03179	5.908	*** 3.47 e-09
DO Front	0.34702	0.05442	6.376	*** 1.81 e-10
SLA	- 1.10402	0.25027	- 4.411	*** 1.03 e-05
				BIC = 3998

Table 3. 2 - Summary of final model results for blue sharks: Estimated parameters from the final RSPF models; Standard errors and the value of the log-likelihood function at the estimated parameters.

Coefficients (logit link):	**Estimate**	**Std. Error**	**z value**	**Pr (> | z |)**
(Intercept)	7.71670	1.59526	4.837	*** 1.32 e-06
SST	0.38105	0.06809	5.597	*** 2.19 e-08
SST Front	0.03987	0.04806	0.830	0.407
SLA	- 5.00942	1.16925	- 4.284	*** 1.83 e-05
				BIC = 5189

Table 3. 3 - Summary of final model results for mako sharks: Estimated parameters from the final RSPF models; Standard errors and the value of the log-likelihood function at the estimated parameters.

4. Discussion

The present study uses a combination of descriptive and processed-based techniques to analyse the foraging patterns of 34 blue and 24 mako sharks, satellite-tagged in 5 different locations across the North Atlantic Ocean, and their relationship with DO fronts and mesoscale eddies.

Mesoscale oceanographic features, such as fronts and eddies, have been shown to greatly influence the movements of marine apex predators, due to enhanced foraging opportunities presented by the higher biologic productivity available at these features (Sims and Quayle, 1998; Worm *et al.*, 2003; Block *et al.*, 2011). For instance, Pade *et al.* (2009) reported porbeagle sharks (*Lamna nasus*) spending over a month in persistent thermal fronts, where schooling fishes such as Atlantic mackerel (*Scomber scombrus*), a common porbeagle shark prey, attracted by zooplankton assemblages aggregated. Likewise, Hsu *et al.* (2015), using 13 years of U.S. longline fisheries data and employing multivariate statistical model analysis, described a different association with mesoscale eddies for three different tuna species, with bluefin tuna (*Thunnus thynnus*) catches higher in ACEs, in contrast to yellowfin (*Thunnus albacares*) and bigeye tunas (*Thunnus obesus*) for which catches were higher in CEs.

The results of this study suggest that the foraging behaviour of blue and mako sharks might relate with DO fronts in a similar way as it is known to be associated with thermal fronts. Furthermore, evidence was found of a preference for CEs in relation to ACEs, particularly for mako sharks.

4.1. Frontal Systems

Both blue and mako sharks showed a positive correlation with frontal systems characterized not only by steep SST gradients, as expected, but also steep DO gradients. In fact, analysis of blue shark tracks indicated an even greater correlation between foraging movements and DO fronts than with thermal fronts, with Spearman’s correlation coefficients being slightly higher (Table 1) and RSPF analysis not including thermal fronts as one of the most explicative variables, in contrast to the inclusion of DO fronts (Table 2). Differently, mako sharks revealed a higher affinity to thermal fronts than to DO fronts, as shown by both higher correlations (Table 1) and its inclusion on the best explanatory model, in contrast to DO fronts (Table 3). Note that, although not significant in the best model, the inclusion of SST Front returned a better BIC value. Moreover, in the absence of SLA, the model revealed SST Front to be highly significant (Annex C, Table C6), which might suggest an over preference for this feature as it will be further explored.

4.1.1. Foraging in highly productive Thermal-Oxygen Frontal Systems

As mentioned, and given the interdependence between water properties (Belkin *et al.*, 2009), strong and persistent fronts are likely to, simultaneously, present sharp gradients of different properties, such as temperature and DO. In fact, this is also suggested by the mean frontal gradients of both DO and SST along the years under analysis (Figs. 3.3 and 3.4), which mostly coincide in regions of strong gradients. Moreover, subsurface foragers, such as blue and mako sharks, in contrast to surface foragers like many seabird species, are usually found associated with stronger, vertically structured, fronts (Begg and Reid, 1997). For these reasons, the foraging effects of these two variables on the stronger, most used, frontal systems, are probably interrelated and, therefore, hard to distinguish.

Based on descriptive analysis, it can be observed that notably strong foraging associations with both DO and SST fronts occur in the Northwest Atlantic (Figs. 3.3 and 3.4), especially between Cape Hatteras and Cape Cod for makos sharks and south of Nova Scotia for blue sharks. This whole area, from Cape Hatteras to southeast of Newfoundland, is deeply shaped by the seasonally persistent frontal zone resultant from the encounter of two extremely different water masses, the cold, low saline and highly oxygenized subarctic and coastal waters, and the warmer, high saline and less oxygenized subtropical waters associated with the Gulf Stream and the North Atlantic Current (Bersch, 2002; Holbrook *et al.*, 2003). In addition, another seasonally persistent frontal zone, the so-called shelf-break front, is observed in this region along the 100/200 m isobath (Ryan *et al*., 1999; Ullman and Cornillon, 1999). This front is driven by bottom topography, more exactly, by the well-delineated shelf-break and the topographic deflection along the steep continental slope (Belkin *et al.*, 2009). Furthermore, both chlorophyll-a and phytoplankton enhancement have been widely described along this front as a result of a combination between upwelled, nutrient-rich, waters and a well-lighted water column (Marra *et al.*, 1990; Ryan *et al.*, 1999). Finally, tidal mixing fronts around Georges Banks and Gulf of Maine (Loder *et al.*, 1993), fronts associated with the Eastern Maine Coastal Current (Townsend *et al.*, 1987) and river plumes resultant from river runoff (Ullman and Cornillon, 1999) also contribute for making this continental shelf one of the most productive in the world (O'Reilly and Busch, 1984). In this regard, a great diversity of predators has been known to explore these waters while foraging, such as baleen whales (Whitehead, H. and Carscadden, 1985), harp seals (Lawson, J.W. *et al.*, 1998), marine birds (Garthe *et al.*, 2003), swordfish and tunas (Hsu *et al.*, 2015) and sharks (Stillwell and Kohler, 1982; Joyce *et al.*, 2002; Campana *et al.*, 2011).

Similarly, some foraging association with near-shore fronts of both DO (Fig. 3.3 A) and SST (Fig. 3.4 A) were observed for blue sharks tagged off western Europe, more exactly around the southwestern coast of Portugal and southwest of England. Southwest of England, sharks were found associated with shelf-break and tidal mixing fronts, namely the Ushant and Celtic Sea tidal fronts (Pingree and Griffiths, 1978). As discussed, shelf-edge fronts are characterized by strong gradients and tend to persist all year long (Scales *et al.*, 2014). Likewise, tidal fronts in this region can persist for the whole year, though frontal strength is known to vary seasonally (Pingree *et al.*, 1974). By increasing both light and nutrient availability (Pingree *et al.*, 1975), these fronts have been shown to enhance phytoplankton production, as well as to enclose substantial concentrations of zooplankton and young fish (Pingree *et al.*, 1974). In addition, extensive descriptions of large predators' association with these fronts can be found in the literature, inclusive for blue sharks (Pade *et al.*, 2009; Queiroz *et al.*, 2012; Miller *et al.*, 2015).

Regarding the foraging association with the Portuguese coast, this is probably related with a wind-driven upwelling front, as the Portuguese west coast corresponds to the northern limit of the Eastern North Atlantic Upwelling System (Wooster *et al.*, 1976; Chavez and Messié, 2009). In accordance, Peliz *et al.* (2002), described a double-upwelling system, with the main upwelling front closely following the 100 m isobath. However, this front is only seasonal, with upwelling usually starting in late May and prevailing until early October (Haynes *et al.*, 1993). Interestingly, all shark positions in this region were observed within the upwelling season, except for shark #7, with its last position within this region being recorded on the 2nd of November. Yet, since zooplankton is known to have a time lag of several weeks relative to phytoplankton bloom (Longhurst, 2007), and given that blue sharks are preying upon mesopelagic prey targeting zooplankton assemblages, it is possible that, although the upwelling event had already ceased by the time the shark was located in the region, enhanced foraging opportunities provided by the still higher concentrations of zooplankton and fish might prevail in early November in this area.

Concerning the foraging activity observed in the central North Atlantic, it might be related to a possible topographic deflection of the current system southeast of the Grand Banks (Mann, 1967) along the Mid Atlantic Ridge. However, the foraging behaviour in this area is more likely to be related to the intense eddy activity (Fig. 3.6), as will be further discussed.

Finally, the foraging behaviour around the Cape Verde Islands was found to be related with two different front types. Mako sharks, although tagged off Cape Verde Islands were mostly found performing ARS behaviour near the continental shelf, associated with convergent fronts between the, colder and well-mixed, upwelled waters of the western Sahara upwelling system (Wooster *et al.*, 1976; Chavez and Messié, 2009; Marchesiello and Estrade, 2009) and the warmer offshore waters. This region is characterized by year-round upwelling, marked by a strong seasonal maximum during spring (Lathuilière *et al.*, 2008), and intense biological activity (Chavez and Messié, 2009). Differently, blue sharks were not found in association with this intense upwelling front. Instead, they were found to prefer foraging around the intense DO front found along the borders of the North Atlantic OMZ.

4.1.2. OMZs' DO fronts as important foraging grounds for large predators

In OMZs, the combination of high productivity, resultant from upwelling phenomena, little wind-driven ventilation and poor oxygen deliver produces hypoxic zones, where little oxygen is available (Helly and Levin, 2004; Breitburg *et al.*, 2018; Levin, 2018). The sharp differences encountered across both vertical and horizontal OMZ borders add physiological constraints to the distribution of marine biota, since biodiversity is known to drop abruptly as oxygen levels decline to less than 1.4 ml l^{-1} (Portner *et al.*, 2014), while higher oxygen levels (as long as below air saturation) can still trigger stress responses in several organisms (Gilly *et al.*, 2013).

Previous studies have described not only a restriction to waters above the OMZ for hypoxic non-tolerant species but also vertical displacements of hypoxia-tolerant species to shallower depths (Childress and Seibel, 1998). For instance, squids, a common prey of blue and mako sharks, have been described to spend most of the daytime moving in and out of the upper OMZ and to significantly reduce their vertical velocities, while reducing their metabolic activity, in comparison to more oxygenated depths (Rosa and Seibel, 2010; Gilly *et al.*, 2012). In addition, sperm whales *(Physeter macrocephalus)* in the Gulf of California, Mexico, have been suggested to target OMZs in the fall, presumably to take advantage of lethargic squids with impaired escaping mechanisms compromised by hypoxia conditions (Davis *et al.*, 2007). The usage of oxygen-limited layers by squids has been suggested as a refuge during daylight conditions since these waters are hostile to most pelagic predatory fish (Gilly *et al.*, 2006; Bertrand *et al.*, 2010; Rosa and Seibel, 2010). However, the vertical displacement to the euphotic layer observed in many organisms, especially for those intolerant to hypoxia, is likely to render them more vulnerable to visual predators, resulting in more foraging opportunities for pelagic predators (Koslow *et al.*, 2011; Stewart *et al.*, 2013).

Contrarily to sperm whales, which can hold their breath for about 45 minutes (Whitehead, 2018), most pelagic top predators have high physiological demands for oxygen (Payne *et al.*, 2015). Nonetheless, several studies have described a wide usage of OMZ surface waters by sharks, tunas and billfishes (Prince and Goodyear, 2006; Jorgensen *et al.*, 2009; Nasby-Lucas *et al.*, 2009; Stramma *et al.*, 2011). Interestingly, these authors have proposed an adaptative advantage of foraging in these areas, due to the enhanced foraging opportunities derived from the habitat compression of both prey and predator to the upper layers of the water column.

The deep scattering layer (DSL) is a mid-depth zone composed of a dense assemblage of mesopelagic organisms which undergo daily vertical migrations between dusk and dawn (Barham, 1966). In normoxic conditions, DSL depth is essentially dependent on light intensity and turbidity, in order to avoid visual predators (Koslow *et al.*, 2011; Bianchi and Mislan, 2016). Yet, when oxygen is limited, as in OMZs, the shoaling of the hypoxic boundary layer is reflected in the consequent upward movement of the DSL, due to oxygen-related physiological demands, leaving these organisms more vulnerable to predation (Bianchi and Mislan, 2016; Klevjer *et al.*, 2016). Vertical diving patterns of many pelagic fish, including sharks, have been proposed to be related to foraging in the vertically migrating DSL (Carey and Robison, 1981; Dagorn *et al.*, 2000; Nakano *et al.*, 2003; Nasby-Lucas *et al.*, 2009).

At 100 m depth, in the North Atlantic OMZ, DO concentration averages approximately 3.5 ml l^{-1} (Prince and Goodyear, 2006; Stramma *et al.*, 2011). Mako sharks have been described to have a lower DO concentration thresholds of about 3 ml l^{-1} (Abascal *et al.*, 2011), although they have been documented at concentrations as low as 1.25 ml l^{-1} while preying squids on the Eastern Tropical Pacific OMZ (Vetter *et al.*, 2008). Similarly, blue sharks have recently been reported to tolerate hypoxic conditions as low as 1.2 ml l^{-1}, precisely in the North Atlantic OMZ, though their average threshold should lie between 2.5 and 3 ml l^{-1} (Vedor *et al.*, 2021). Thus, the apparently tolerated extreme hypoxic conditions, coupled with the vertical and horizontal habitat compression of potential prey, strongly suggest that in the presence of strong DO fronts, as in OMZs, these two large predators might be taking advantage of the shoaling DSL to prey upon high densities of, more lethargic, mesopelagic prey feeding within it.

Last but not least, a small seasonally persistent hypoxic/near-hypoxic region (less than ~ 1.5 ml l^{-1}; Portner *et al.*, 2014), to the extent of my knowledge still absent in the literature, was identified just south of Nova Scotia and in the Gulf of Maine (Fig. 3.5). It is likely that processes similar to those described for the OMZ might happen in this region, as a result of the intense biological productivity observed in the area, though these effects are probably minimized by the greater mesoscale dynamics and consequent water recirculation, compared with the OMZ. In addition, substantial inputs of riverine nitrogen in this region, mostly from agricultural sources (Boyer *et al.*, 2002), cause eutrophication and algal blooms (Anderson *et* *al.*, 2008) which also promote higher rates of oxygen consumption. The observation of these conditions within an area of intense foraging activity of blue shark and where mako sharks were also observed performing some foraging behaviour suggests that similar biological responses as those described for the OMZ may occur in this region, resulting in higher predator-prey encounters. Hence, these findings strongly reinforce the idea that DO fronts might play an important role in shaping the foraging activity of these two large predators, especially the blue shark.

4.1.3. Species differences and energetic and metabolic traits involved

In the present study, blue sharks showed a higher preference for regions marked by strong DO gradients than mako sharks (Tables 1 to 3). Moreover, mako sharks presented higher correlations with SST Fronts than with DO Fronts (Table 1) and were observed to actively prefer thermal-oxygen fronts in opposition to the oxygen-only fronts associated with the OMZ. Although both species were found to perform foraging movements within the OMZ, differences were observed regarding the region of the OMZ utilized. While blue sharks generally foraged inside the OMZ and around its borders, mako sharks' foraging behaviour was markedly associated with the western Sahara upwelling frontal system, as suggested by the observed ARS behaviour in close association to this feature, performed by 3 out of 4 mako sharks (Figs. 3.3 and 3.4, B).

Considering the different metabolic strategies of these two large predators, these results were, somehow, expected. Blue sharks, as ectotherms, have a significantly lower metabolic scope than mako sharks (Bernal *et al.*, 2003). This means that their metabolic rates do not vary much and, therefore, neither do their oxygen demands (Fry, 1947), expanding their tolerance to momentary decreases in oxygen availability. Moreover, the affinity of haemoglobin with oxygen ($Hb - O_2$) usually increases with decreasing water temperature (Skomal and Bernal, 2010). This might be an important advantage for blue sharks in these regions, considering that during their deeper dives within the OMZ, as the water temperature decreases, their $Hb - O_2$ increases, eventually aiding tolerance to the hypoxic conditions. In addition, blue sharks are known to endure extreme and rapid variations in water temperatures of up to 19ºC (Carey and Scharold, 1990) during their deep dives, which suggests an important ability to cope with induced physiological stress, as well as to explore highly productive waters across thermal front systems. However, is likely that the combination of oxidative and temperature-induced stress in strong hypoxic regions might be too exhaustive and, for this reason, these sharks avoid thermal fronts while in the OMZ.

On the other hand, the elevated temperatures maintained by the endothermic mako shark coupled with the intense swimming activity, result in a substantially higher metabolic scope (Bernal *et al.*, 2003). Thus, in order to maintain the high metabolic rates, it should be expected for this species to require minimal DO concentrations higher than those needed by blue sharks. However, mako sharks within the OMZ were found substantially further inshore than blue sharks, where DO concentrations are lowest (Fig. 3.5). Nevertheless, endothermic sharks have also evolved physiological mechanisms that may contribute to a higher resilience to low oxygen conditions. The rapid temperature changes to which these sharks are exposed during their deep dives should markedly alter Hb – O_2 affinity. Yet, their ability to maintain a more stable body temperature is likely to also provide them with a higher capacity to protect their Hb – O_2 equilibrium (Skomal and Bernal, 2010). In this sense, a recent study concluded that, although both blue and mako sharks utilize OMZ waters as foraging grounds, blue sharks were performing substantially deeper dives and more regular dives than mako sharks (Vedor, unpublished data). Thus, and although an overall higher relation between blue sharks and DO fronts is suggested, it is possible that the absence of DO Fronts as an explanatory variable for the mako shark RSPF models may be related to both the great number of positions within depths above 100 m (i.e. no data for DO at 100 m) and the lesser extent of transiting movements between foraging grounds observed by mako sharks, which place ARS and non-ARS behaviours more enclosed to the same areas, and therefore, within approximately the same range of variables' values.

Furthermore, both these species can, in case of a stress event, rapidly synthesise heat shock proteins (HSP). These proteins prevent cells' genetic material, along with several other cellular proteins, from irreversible conformational changes and, this way, allow them to preserve their functions under stress events (Skomal and Bernal, 2010). Furthermore, these proteins have also been shown to maintain the functional structure of Hb, safeguarding its binding affinity with oxygen and, thus, the adequate oxygen delivery to aerobically working tissues (Kihm *et al.*, 2002). Yet, a study carried out by Bernal *et al.* (unpublished data in: Skomal and Bernal, 2010) comparing both species showed that, in case of a sudden increase in arterial blood temperature, blue sharks Hb – O_2 affinity considerably diminished while it had virtually no effect on mako sharks. Thus, these characteristics may also explain mako sharks' higher correlation with thermal fronts and the different preferences observed within the OMZ, as mako sharks are more capable to maintain their aerobic performance in abrupt temperature changing environments, as previously observed by Queiroz *et al.* (2016).

In summary, the results from this study suggest that blue and mako sharks increase their foraging activity in the presence of thermal-oxygen fronts, where they take advantage of the high productivity that characterizes these systems and consequent prey aggregation, as well as oxygen-only fronts associated with OMZs, where they benefit from both vertical and horizontal habitat compression of usually deeper mesopelagic prey. Moreover, these two large predators seem to possess physiological mechanisms that allow them to endure temporary hypoxic conditions and abrupt temperature changes, thus permitting them to explore and forage upon more densely aggregated prey patches within abruptly changing waters as are frontal systems.

4.2. Eddies

In what concerns the foraging relationship of these two species with mesoscale eddies, the results from the present study suggest an overall preference for CEs (Tables 1 to 3). Noteworthy, and in contrast to mako sharks, which exhibited a clear preference for CEs, blue sharks' preference for CE at the expense of ACEs was not so evident, resulting in only a slight preference for this type of eddies.

4.2.1. Eddies as important foraging areas for large predators

In contrast to the well-mixed waters of high latitudes or close to the continental shelf, at the mid-latitudes of the North Atlantic Ocean, the lack of nutrient input by wind-induced upwelling generally results in very low levels of phytoplankton primary production (Williams and Follows, 1998). In this so-called "ocean desert" the low primary productivity still observed is strongly dependent on mesoscale eddy activity for nutrient supply (Oschlies and Garçon, 1998). In this area, most eddies are formed along the Atlantic Polar Front from extending meanders that, due to front instability, pinch off from the main water mass and are shed as eddies. If shed southeast of the front, into the Sargasso Sea, a CE will be formed, transporting high near-surface chlorophyll waters into this otherwise low productive region. On the other hand, if shed northwest, ACEs will be formed, transferring the low productive waters of the Sargasso Sea into the generally higher productive waters north of the front (Owen, 1981; Gaube *et al.*, 2014).

The higher productivity associated with CEs is essentially due to two distinct mechanisms: the trapping of cold, nutrient-rich waters with high biological activity, during eddy formation; and the nutrient upwelling occurring within the eddy, resultant from the Coriolis effect on the counter-clockwise rotation of CEs. In contrast, the ACEs lower productivity is largely dictated by the enclosing of warm, nutrient-depleted waters, with low phytoplankton concentrations (Gaube *et al.*, 2014). Furthermore, being one of the world's region with the highest energetic eddies (Chelton *et al.*, 2011), the relevance of eddy related productivity in the oligotrophic waters of the North Atlantic open ocean is emphasized, being accounted for about one-third of the nutrient input into the euphotic zone in these waters (McGillicuddy, 1998; Oschlies and Garçon, 1998). The observed higher correlation with CEs was, thus, expected for these two large predators, since higher productivity associated with these features is predicted to present higher foraging opportunities than the surrounding oligotrophic waters. Moreover, similar associations with CEs have already been described for other large predators such as yellowfin and bigeye tunas (Hsu *et al.*, 2015), southern elephant seals (Bailleul *et al.*, 2010a) or manta rays (Jaine *et al.*, 2014).

4.2.2. Differences between blue and mako sharks

Blue sharks, although revealing an apparent preference for CEs, showed important differences regarding eddy preferences compared to mako sharks. As observed in the exploratory analysis (Fig. 10; Table 1), blue sharks' preference for CEs is not as evident as for mako sharks. Interestingly, analogous trends have been suggested for some species concerning this, supposedly low productive features. For instance, king penguins (*Aptenodytes patagonicus)* (Cotté *et al.*, 2007) and loggerhead sea turtles (*Caretta caretta*) (Polovina *et al.*, 2006; Gaube *et al.*, 2017) have been shown to forage on both CEs and ACEs, while bluefin tuna has been suggested to actively prefer foraging within ACEs (Hsu *et al.*, 2015). Two central evidence might help to understand this otherwise contradictory association: 1) an apparent adaptive strategy, recently proposed, of foraging in ACEs; and 2) a third type of eddies, the so-called mode-water eddies.

Gaube *et al.* (2018) and Braun *et al.* (2019) have suggested an adaptive advantage of foraging in regular ACEs. By comparing eddy trajectories with the movements performed by, double-tagged, white and blue sharks, respectively, these authors found higher predator correlations with warm-core ACEs than with the expected cold-core CEs, which contradicted the well-established conception that these unproductive regions were biological deserts (The Ring Group, 1981; Williams and Follows, 1998; Gaube *et al.*, 2014). Yet, deep-diving information provided by PSAT tags showed that these sharks were performing frequent dives to great depths which, they propose, might indicate a possible advantage in utilizing unusually warm waters to dive deeper and for longer periods into the mesopelagic, where they can more easily access prey while reducing energetic costs.

Also, pycnoclines are usually raised within CEs and lowered within ACEs. However, a third type of eddy has been described, where the main pycnocline is lowered, but the seasonal pycnocline is raised due to the presence of a dense water mass between them (Fig. 4.1) (McGillicuddy *et al.*, 2007; Gaube *et al.*, 2014). These mode-water eddies have been reported to sustain important plankton blooms as a result of eddy-wind interactions, which produce divergent water flows, and consequent upwelling, in the eddy centre (McGillicuddy *et al.*, 2007). Nonetheless, since the lowering of the main pycnocline dictates geostrophic velocities, mode-water eddies have the same rotating direction as ACEs (McGillicuddy *et al.*, 2007) and, therefore, cannot be distinguished based on satellite observations of SSH/SLA, due to their equally higher SSH (Gaube *et al.*, 2014). Thus, according to the current analysis, both mode-water eddies and regular ACEs would be characterized as ACEs, meaning that important phytoplankton blooms might be mistaken by low productive areas.

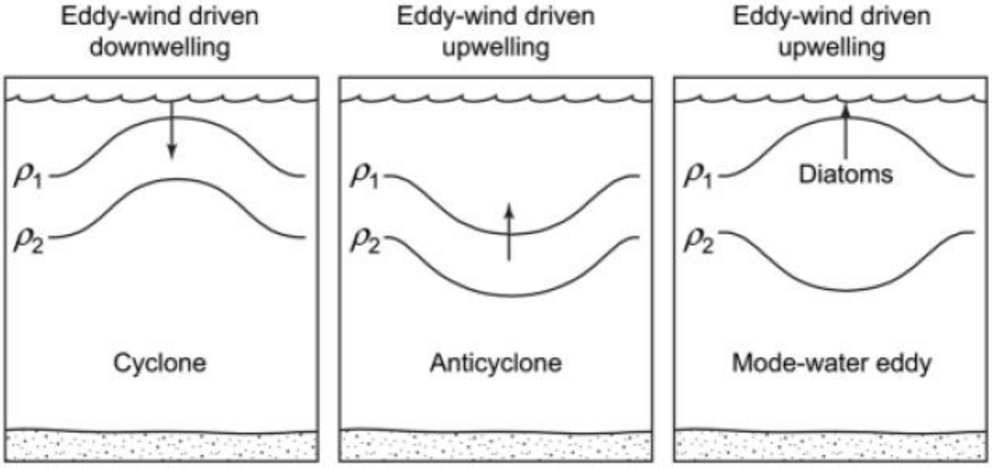

Figure 4. 1 - Isopycnal displacements associated with three types of eddies. Two density surfaces are depicted: one in the seasonal thermocline ρ1 and one in the main thermocline ρ2. Arrows indicate the sense of the vertical velocity arising from the interaction of the wind with the underlying eddy-driven flow, which is upward in anticyclones and mode-water eddies and downward in cyclones. This eddy/wind interaction stimulates diatom blooms in mode-water eddies.

Source: Fig. 1A, page 1022, McGillicuddy, D. J. *et al.* (2007).

Thus, it is possible that blue sharks more equitable relation with general eddy activity observed in this study might be ascribed to either taking advantage of similar conditions as those provided by CEs, the exploitation of warmer than usual waters to explore on deep mesopelagic prey or even a combination of the two. Blue sharks' higher relation with these features, when compared to mako sharks, might reflect their lower ability to explore the deep waters of the mesopelagic for extended periods (Bernal *et al.*, 2012), as a result of their ectothermic condition. The deep warmer waters presented within the ACEs might, therefore, allow blue sharks to spend more time at depth, while foraging upon cephalopods, their favourite prey (Cortés, 1999), within two of the three richest squid stocks in the North Atlantic Ocean (Rosa *et al.*, 2008). Furthermore, although Gaube *et al.* (2018) reported this same behaviour in the endothermic white shark (*Carcharodon carcharias*), the results from the present study clearly indicate that mako sharks' foraging activity was substantially reduced in the vicinity of ACEs. These differences could be driven by different feeding habitats and strategies, as makos are known not only not to regularly dive as deep as blue (Stevens *et al.*, 2010) and white sharks (Skomal *et al.*, 2017), but also for their striking speeds (Díez *et al.*, 2015) and ambush-like predatory behaviour, characteristics that make mako sharks specialists in surface hunting.

Finally, the noticed lack of a significant statistical contribution of SST Front for the mako sharks' final model could suggest an over preference of mako sharks for these mesoscale features, since before the inclusion of SLA variable in the model, the SST Front revealed a highly significant statistical contribution for the model (Annex C, Table C9). Although frontal systems are recognized to present considerably more energetic and highly localized vertical displacement of water masses than eddies (Owen, 1981), it is possible that the nutrient enriching effects of an upwelling CE along an already highly productive frontal system would result in an even greater biological production within these features, and therefore, to the preference for CEs over SST Fronts when both are presented within the same area.

Moreover, the extreme energy of these features within the Northwest Atlantic Ocean (Chelton *et al.*, 2011), coupled with the increasing low productivity observed in the open ocean (Polovina *et al.*, 2008), where broad populations of large predators are known to occur, likely reflects the extreme importance of eddies, and especially of CEs pumping (Falkowski *et al.*, 1991), for the foraging movements of apex migratory predators, such as blue and mako sharks, in these oligotrophic waters.

4.3. Fisheries and conservation in face of climate change

The current results highlight the importance of both thermal-oxygen fronts and oxygen-only fronts associated with OMZs as important foraging habitats, essentially at coastal and near-coastal locations, for the two most caught pelagic shark species in the Atlantic Ocean. Furthermore, mesoscale eddies revealed great importance by providing foraging opportunities in the oligotrophic waters of the open ocean. These oceanographic features, however, are also heavily targeted by longline fishing vessels because of the high fish densities presented in these regions (Queiroz *et al.*, 2016, 2019).

Fronts and eddies are known to attract a great variety of large predators, and sharks in particular (Tittensor *et al.*, 2010; Queiroz *et al.*, 2016, 2019; Scales *et al.*, 2018), and have inclusive been suggested as priority conservation areas for oceanic marine predators (Scales *et al.*, 2014). However, no previous studies have addressed the potential role of DO fronts in shaping the foraging patterns of large pelagic predators. Building on this knowledge, this study suggests a higher probability of these sharks performing foraging movements on or near DO fronts, especially blue sharks. Thus, yielding new information on the influence of these oceanographic mesoscale features on the spatial dynamics and habitat-use of these two large predators that could be used to better inform spatially dynamic fisheries management actions.

Moreover, in face of the present climate change scenario, the necessity of valuable insights to inform decisions on the implementation of better and more reasoned conservation and management actions becomes even more urgent (Heller and Zavaleta, 2009; Robinson *et al.*, 2009). The consistently rising temperatures observed during the last decades have caused rearrangements of species distribution due to temperature-related physiological impairments, as well as sharp declines in zooplankton in some highly productive areas due to the increased stratification of the water column and consequent decrease in upwelling intensity (Hughes, 2000). Concurrently, oceans have been losing oxygen at concerning rates, especially within OMZs (Schmidtko *et al.*, 2017), and are expected to continue doing so as long as global warming persists (Keeling *et al.*, 2010). The expansion of OMZs, however, will increase areas of higher foraging opportunities for large apex predators but, on the other hand, will also increase their encounter rate with longline hooks, thus, probably resulting in increased mortality (Prince *et al.*, 2010; Vedor *et al.*, 2021). Furthermore, near-shore coastal regions have also experienced declines in oxygen levels as a result of eutrophication caused by the intensification of the usage of agriculture fertilizers rich in nitrogen (Seitzinger *et al.*, 2010).

Besides the urgent implementation of sustainable catch limits for mako sharks and a more confident stock assessment on blue sharks, other strategies should be enforced. In this sense, marine protected areas (MPAs) arise as the most consensual approach (Hyrenbach *et al.*, 2000; Game *et al.*, 2009; Edgar *et al.*, 2014). Hence, biological hotspots associated with persistent fronts should be areas of first concern (Scales *et al.*, 2014) and have been included in MPAs in both the UK shelf-sea (Miller and Christodoulou, 2014) and the Mediterranean sea (Panigada *et al.*, 2008). Analogous replication in the open ocean raises additional constraints, essentially because of their logistic and economic feasibility and due to the highly dynamic physical processes. Yet, they are crucial for the protection of highly mobile species, such as blue and mako sharks, even more due to the general lack of regulations of the "high-seas", out of national jurisdictions (Game *et al.*, 2009). A possible solution to this problem is dynamic ocean management (DOM), or real-time fishery closures. DOM uses near real-time shifts in biotic and abiotic features to adapt management actions according to species-specific habitat-use, permitting temporary closure of ecologically critical areas (Dunn *et al.*, 2011; Hobday *et al.*, 2014). For instance, to minimize longline by-catch of the southern bluefin tuna (SBT;

Thunnus maccoyii), a quota-limited species, habitat preference models based on satellite tagging data and subject to continued ocean reanalysis have been used to predict real-time SBT distribution maps since 2003. This information is then used to restrict access of non-quota holders to these areas (Hobday and Hartmann, 2006; Hobday *et al.*, 2011). Notwithstanding, and given the extensive movements performed by blue and mako sharks, the establishment of large-scale MPA networks, with individual MPAs being enforced in critical areas of their distribution, such as known foraging and breeding areas is even more important (Gaines *et al.*, 2010; Block *et al.*, 2011).

Furthermore, additional management actions such as gear modifications that increase selectivity and decrease non-target species by-catch, or the assignment of catch shares to individual fisherman instead of industry-wide quotas have proven successful in several cases (Worm *et al.*, 2009). For instance, the banning of wire leaders in pelagic longline fisheries has been proved successful in reducing shark catches while increasing the targeted bigeye tuna catch rates (Ward *et al.*, 2008). Likewise, the deployment of hooks farther from sharks preferred depths, especially within hypoxic regions, has been suggested to reduce hook encounter rates (Queiroz *et al.*, 2016). On the other hand, the implementation of catch shares has shown promising results in incentivising fisherman to entail in more sustainable practices to rebuild fishery stocks, as once they are secured on a share of the quota they are less prompt to "race to fish" in order to outcompete their direct competitors (Costello *et al.*, 2008).

4.4. Future Work

Notwithstanding, some adjustments are suggested in order to increase the robustness of the analyses and, thus, to strengthen the confidence in the obtained results. A possible weakness of the present analyses has to do with the low volume of ARS behaviour positions in comparison to transiting-only positions which, therefore, reduces the information provided to the model on the conditions in which ARS behaviour happens. Several approaches that could be explored to improve this aspect are suggested for future research.

One hypothesis would be to split between ARS and non-ARS behaviour on a grid basis. That is, instead of considering all geolocated positions, each pixel would be characterized as ARS-occurring if, at least, one position characterized by ARS behaviour was present within it. This would substantially diminish the number of no-ARS positions, resulting in more balanced ARS/no-ARS areas and, therefore, better inform RSPF analysis, as there would be a more discrete separation between areas where this behaviour occurred and where it did not.

Similarly, an alternative approach would be to reconsider the method of ARS identification. Here, it was considered that ARS behaviour occurred if, at least, two of the three metrics used indicated so. However, and although this approach would increase the confidence in the positions where this behaviour occurred, this method would substantially decrease the total number of ARS positions in comparison to a single metric approach. An alternative hypothesis would be a combination with the first hypothesis, i.e., if two of the three metrics indicated ARS behaviour within the same grid-cell, though not necessarily through the same position, then, that grid-cell would be accounted as ARS occurring behaviour. This way, confidence in the behaviour identification would still prevail but, again, the ARS/no-ARS balance would improve.

Also, a more thorough reformulation of this method would be the integration of simulated random-walks of model sharks in the RSPF analysis, as is often done with this kind of analysis (Thurfjell *et al.*, 2014; Queiroz *et al.*, 2016). However, the disadvantage of the standard RSPF methodology is that it uses equally all geolocated and randomly simulated positions to compare between used and unused habitat. Hence, it does not distinguish between foraging-related and transiting-only behaviours. A possible solution for this problem would be to "teach" the random-walks to perform ARS behaviour. That is, and revising the theory of ARS behaviour (Kareiva and Odell, 1987), every time a simulated (shark) walk would randomly engage on ARS-like behaviour (characterized by higher than average tortuosity), the algorithm would assume a prey had been caught and, consequently, the shark should now restrict its foraging attention to its vicinities before leaving the area. This way, ARS behaviour would be identified in both geolocated and randomly simulated positions, permitting the comparison between used and unused area for foraging. In addition, simultaneously adopting one of the previously proposed alternatives, or adding more satellite-tracked sharks to the analysis would increase robustness even more, since more real ARS positions would be used for comparison. Added sharks would be especially meaningful in those regions where species representation is either absent or not optimal. Fundamentally, more mako sharks in both around Cape Verde and Southwest Europe and blue sharks off the US coast would substantially improve the confidence in the results.

Finally, focusing on a single age class or sex and taking into account seasonal variability would further strengthen the results, as these factors are known to affect resource selection (Manly *et al.*, 2002). Additionally, double-tagging of individuals with both SPOT and PSAT tags could provide three-dimensional information on their relation with these mesoscale features while maintaining the higher accuracy in location estimation (Hueter *et al.*, 2013).

Similarly, the integration of accelerometers could also contribute to a three-dimensional picture of their movement ecology and even with information on prey-capture success (Watanabe and Takahashi, 2013). In this sense, it could be interesting to explore the novel technique proposed by (Bailleul *et al.*, 2010b) the SFPT (spherical first-passage time), as well as the volume-restricted search (VRS; Adachi *et al.*, 2017). Both approaches are, essentially, respective extensions of FPT and ARS behaviour to a three-dimensional environment.

5. Conclusions

The present study reinforces the importance of mesoscale oceanographic features to the movement ecology and, in particular, to the foraging patterns of the two most caught pelagic shark species in the Atlantic Ocean (Queiroz *et al.*, 2016). Besides the widely studied thermal fronts, the obtained results emphasize the importance of DO fronts in the foraging behaviour of these sharks, especially for blue sharks, for which the relationship with DO fronts was even greater than that with thermal fronts. DO fronts were shown to influence shark behaviour both through strong, persistent, and vertically structured thermal-oxygen fronts, which create high foraging opportunities due to the great productivity available, or through oxygen-only fronts associated with hypoxic regions, where the consequent prey-compression to the surface layers results in the foraging advantage of higher predator-prey encounters. In addition, the crucial role of mesoscale eddies, but especially CEs, in the oligotrophic waters of the open ocean was confirmed by their substantial relationship with foraging activity in the central North Atlantic. In this sense, mako sharks showed a substantial preference for CEs, while blue sharks presented a more balanced usage of CEs and ACEs, partially corroborating the previous work developed by Braun *et al.* (2019).

These results suggest that the integration of DO fronts in conservation and management modelling could help better identification of crucial areas for the protection of these sharks. Furthermore, integration of this information in real-time distribution mapping and demarcation of stock management measures accordingly, as it has been done in Australia (Dunn *et al.*, 2011; Hobday *et al.*, 2014), could significantly improve the management and conservation of these and other large pelagic predators with high commercial interest. This is even more urgent given the present climate change scenario and rapid environmental changes associated with it, especially regarding both temperature and DO conditions (Hughes, 2000; Keeling *et al.*, 2010).

In conclusion, this study emphasizes the importance of, fisheries-independent, biotelemetry studies and their integration with oceanography data and fisheries management, to collect vital information on the ecological patterns of wide-ranging large predators, which can then be used to further inform more reasoned conservation and stock management plans. The advent of electronic tagging techniques has, and continues to provide, crucial insights on large, highly mobile pelagic predators, adding new information on the temporal and spatial scales of their movements and on the seasonal significance of particular areas, as well as their overlap with fisheries. Thus, studies on this subject are still needed in order to promote more sustainable and efficient management and conservation of highly migratory predators, even more in times of rapid climate change. Improved understanding of these species' ecological patterns, such as the identification of ecologically important areas, as well as the environmental drivers behind their association, is crucial for preventing biodiversity loss and ecosystems disruption.

6. Bibliography

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Annexes

Annex A: Shark Data

Table A1 - Summary data for satellite tagged sharks; F – female; M – male; AZ – Azores; CV – Cape Verde; LI – Long Island; SE – Southern England; SP - Southern Portugal

Shark ID	PTT ID	Species	Sex	Length (cm)	Tag Type	Tagging Date	Tagging Latitude	Tagging Longitude	Region	Days-at-Liberty
Shark 1	40390	*Prionace glauca*	F	210	SPOT5	28/08/2011	31.5	-36.4	AZ	48
Shark 2	66951	*Prionace glauca*	F	186	SPOT5	15/08/2006	50.03	-4.09	SE	9
Shark 3	66952	*Prionace glauca*	F	170	SPOT5	18/08/2006	50.02	-4	SE	15
Shark 4	66954	*Prionace glauca*	F	160	SPOT5	31/08/2007	50	-4.26	SE	21
Shark 5	66955	*Prionace glauca*	F	145	SPOT5	01/06/2009	36.98	-8.65	SP	24
Shark 6	66957	*Prionace glauca*	M	220	SPOT5	01/06/2009	36.98	-8.63	SP	103
Shark 7	66963	*Prionace glauca*	M	85	SPOT5	10/10/2006	36.99	-8.64	SP	24
Shark 8	66967	*Prionace glauca*	F	130	SPOT5	06/06/2008	37.01	-8.67	SP	77
Shark 9	66969	*Prionace glauca*	M	130	SPOT5	13/06/2008	37.02	-8.64	SP	113
Shark 10	66970	*Prionace glauca*	F	125	SPOT5	26/05/2009	36.99	-8.69	SP	23
Shark 11	84174	*Prionace glauca*	F	190	SPOT5	30/08/2011	31.07	-36.58	AZ	19
Shark 12	84175	*Prionace glauca*	F	220	SPOT5	02/09/2011	34.02	-36.44	AZ	34
Shark 13	132044	*Prionace glauca*	F	120	SPOT5	20/05/2015	37.01	-7.71	SP	40
Shark 14	133669	*Prionace glauca*	M	205	SPOT5	04/06/2014	41.28	-42.36	AZ	219

Shark ID	PTT ID	Species	Sex	Length (cm)	Tag Type	Tagging Date	Tagging Latitude	Tagging Longitude	Region	Days-at-Liberty
Shark 15	133670	*Prionace glauca*	M	240	SPOT5	05/06/2014	41.42	-42.1	AZ	233
Shark 16	135925	*Prionace glauca*	F	220	SPOT5	05/06/2014	41.4	-42.31	AZ	43
Shark 17	135926	*Prionace glauca*	F	220	SPOT5	05/06/2014	41.39	-42.48	AZ	94
Shark 18	135927	*Prionace glauca*	F	230	SPOT5	05/06/2014	41.38	-42.57	AZ	11
Shark 19	135928	*Prionace glauca*	F	215	SPOT5	07/06/2014	41.23	-44.01	AZ	28
Shark 20	135929	*Prionace glauca*	F	210	SPOT5	07/06/2014	41.22	-44.01	AZ	16
Shark 21	135929a	*Prionace glauca*	F	190	SPOT5	31/08/2015	39.29	-40.44	AZ	22
Shark 22	135930	*Prionace glauca*	F	190	SPOT5	07/06/2014	41.44	-44.01	AZ	11
Shark 23	135931a	*Prionace glauca*	F	220	SPOT5	09/06/2014	41.57	-43.23	AZ	57
Shark 24	135932a	*Prionace glauca*	F	220	SPOT5	11/06/2014	41.53	-43.42	AZ	43
Shark 25	160252	*Prionace glauca*	F	220	SPOT5	16/01/2017	11.02	-24.03	CV	73
Shark 26	160253	*Prionace glauca*	M	230	SPOT5	17/01/2017	10.32	-23.07	CV	40
Shark 27	160254	*Prionace glauca*	F	195	SPOT5	17/01/2017	10.34	-23.09	CV	23
Shark 28	160255	*Prionace glauca*	M	270	SPOT5	19/01/2017	12.05	-27.16	CV	84
Shark 29	160256	*Prionace glauca*	F	225	SPOT5	19/01/2017	12.04	-27.15	CV	25
Shark 30	160385	*Prionace glauca*	F	230	SPOT5	20/01/2017	12.42	-27.55	CV	109

Shark ID	PTT ID	Species	Sex	Length (cm)	Tag Type	Tagging Date	Tagging Latitude	Tagging Longitude	Region	Days-at-Liberty
Shark 31	160386	*Prionace glauca*	M	220	SPOT5	26/01/2017	14.08	-28.42	CV	89
Shark 32	160387	*Prionace glauca*	F	210	SPOT5	22/01/2017	13.24	-28.23	CV	125
Shark 33	160388	*Prionace glauca*	M	225	SPOT5	26/01/2017	14.17	-28.4	CV	172
Shark 34	160389	*Prionace glauca*	F	230	SPOT5	25/01/2017	13.49	-29.14	CV	103
Shark 35	40392	*Isurus oxyrinchus*	F	210	SPOT5	05/09/2011	34.37	-36.58	AZ	59
Shark 36	40393	*Isurus oxyrinchus*	M	200	SPOT5	08/09/2011	35.21	-36.41	AZ	51
Shark 37	132343	*Isurus oxyrinchus*	F	152	SPOT5	27/07/2013	40.85	-71.72	LI	38
Shark 38	132344	*Isurus oxyrinchus*	M	152	SPOT5	27/07/2013	38.21	-73.6	LI	326
Shark 39	132345	*Isurus oxyrinchus*	F	152	SPOT5	28/07/2013	40.84	-71.52	LI	186
Shark 40	141194	*Isurus oxyrinchus*	M	160	SPOT5	12/07/2014	40.69	-71.51	AZ	12
Shark 41	141197	*Isurus oxyrinchus*	F	183	SPOT5	13/07/2014	40.66	-71.51	AZ	30
Shark 42	141198	*Isurus oxyrinchus*	F	198	SPOT5	13/07/2014	40.6	-71.62	AZ	302
Shark 43	141198a	*Isurus oxyrinchus*	F	206	SPOT5	18/07/2015	40.79	-71.54	AZ	41
Shark 44	135931	*Isurus oxyrinchus*	M	185	SPOT5	23/08/2015	42.02	-39.49	LI	40
Shark 45	135932	*Isurus oxyrinchus*	F	195	SPOT5	23/08/2015	41.36	-39.43	LI	226
Shark 46	135933	*Isurus oxyrinchus*	F	160	SPOT5	09/06/2014	42.03	-43.4	LI	67

Shark ID	PTT ID	Species	Sex	Length (cm)	Tag Type	Tagging Date	Tagging Latitude	Tagging Longitude	Region	Days-at-Liberty
Shark 47	135934	*Isurus oxyrinchus*	M	180	SPOT5	09/06/2014	42.11	-43.58	AZ	55
Shark 48	149238	*Isurus oxyrinchus*	M	140	SPOT5	27/08/2015	41.32	-39.14	AZ	37
Shark 49	149240	*Isurus oxyrinchus*	F	160	SPOT5	27/08/2015	41.26	-39.42	AZ	103
Shark 50	149242	*Isurus oxyrinchus*	F	170	SPOT5	28/08/2015	41.11	-39.38	AZ	192
Shark 51	149243	*Isurus oxyrinchus*	M	160	SPOT5	28/08/2015	41.02	-39.41	AZ	34
Shark 52	149244	*Isurus oxyrinchus*	M	150	SPOT5	30/08/2015	39.47	-40.43	AZ	104
Shark 53	149245	*Isurus oxyrinchus*	F	170	SPOT5	03/10/2015	40.83	-40.94	AZ	24
Shark 54	149246	*Isurus oxyrinchus*	F	210	SPOT5	26/12/2015	38.87	-40.93	CV	78
Shark 55	160390	*Isurus oxyrinchus*	M	220	SPOT5	16/01/2017	11.07	-24.13	CV	88
Shark 56	160391	*Isurus oxyrinchus*	F	210	SPOT5	17/01/2017	10.13	-22.42	CV	33
Shark 57	160392	*Isurus oxyrinchus*	F	160	SPOT5	20/01/2017	12.47	-28.03	CV	62
Shark 58	160393	*Isurus oxyrinchus*	F	150	SPOT5	28/01/2017	15.15	-28.41	LI	70

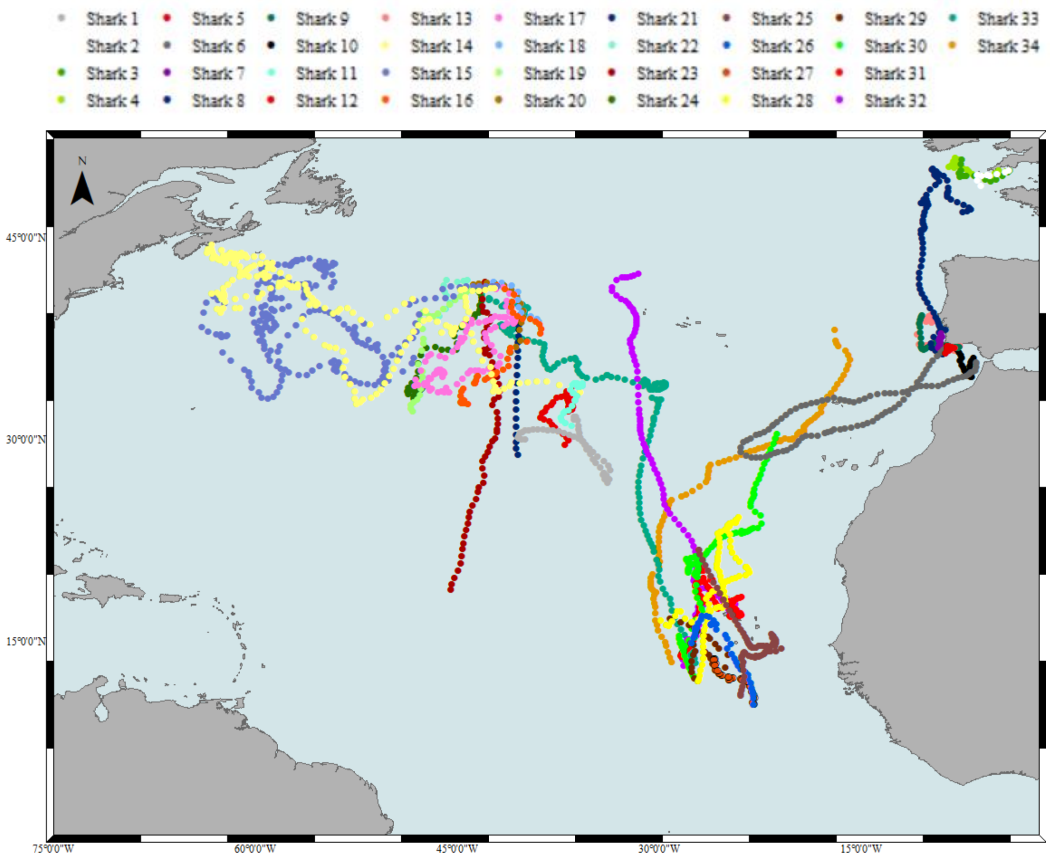


Figure A2 - Daily locations, estimated from locations obtained via satellite transmitters of the 34 blue sharks.

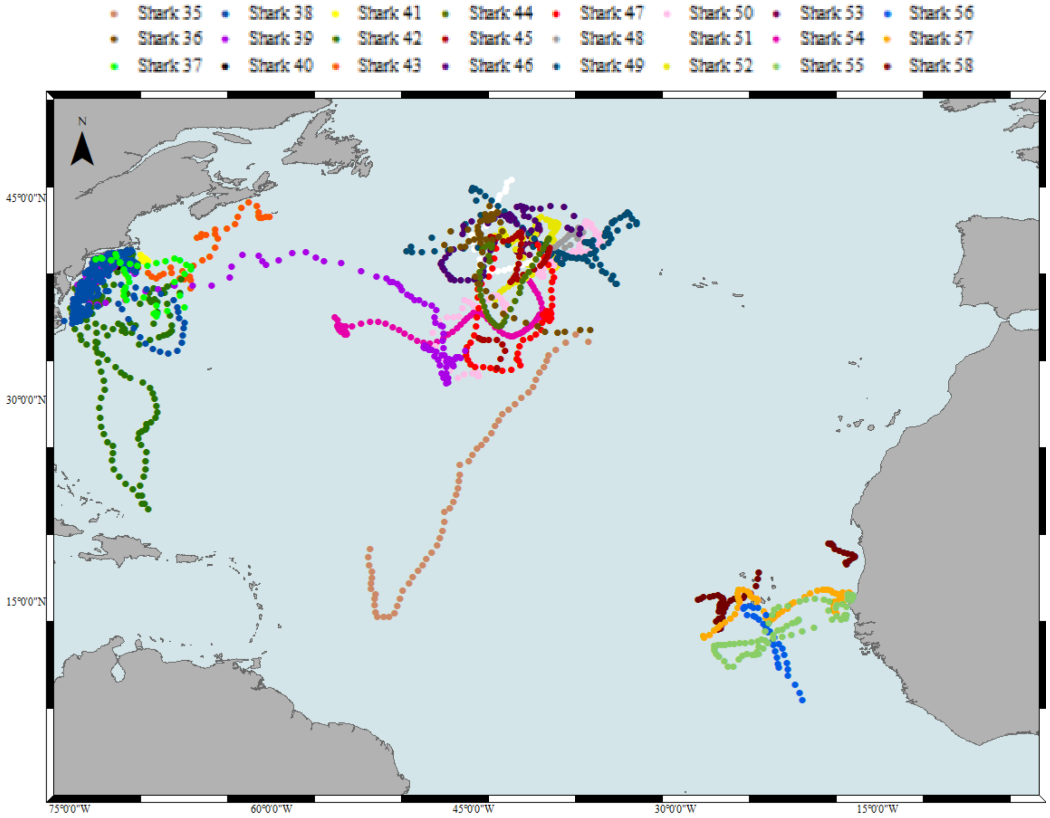


Figure A1 - Daily locations, estimated from locations obtained via satellite transmitters of the 24 mako sharks.

Annex B: Relationship between ARS behaviour metrics and environmental variables

a) Blue vs Mako Sharks

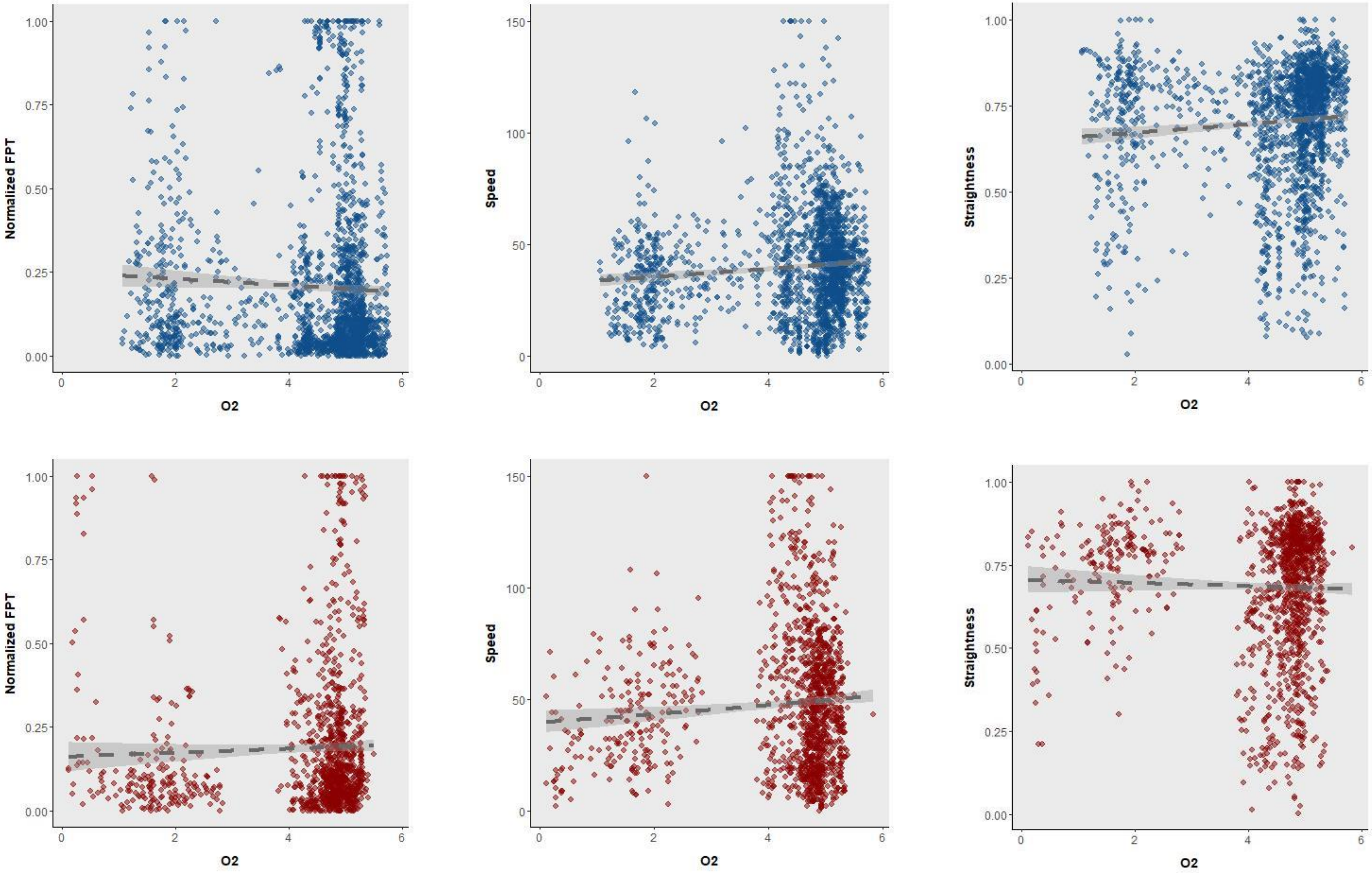


Figure B1 - Relationship of DO at 100 m depth with FPT, speed and straightness for blue (blue graphs) and mako (red graphs) sharks.

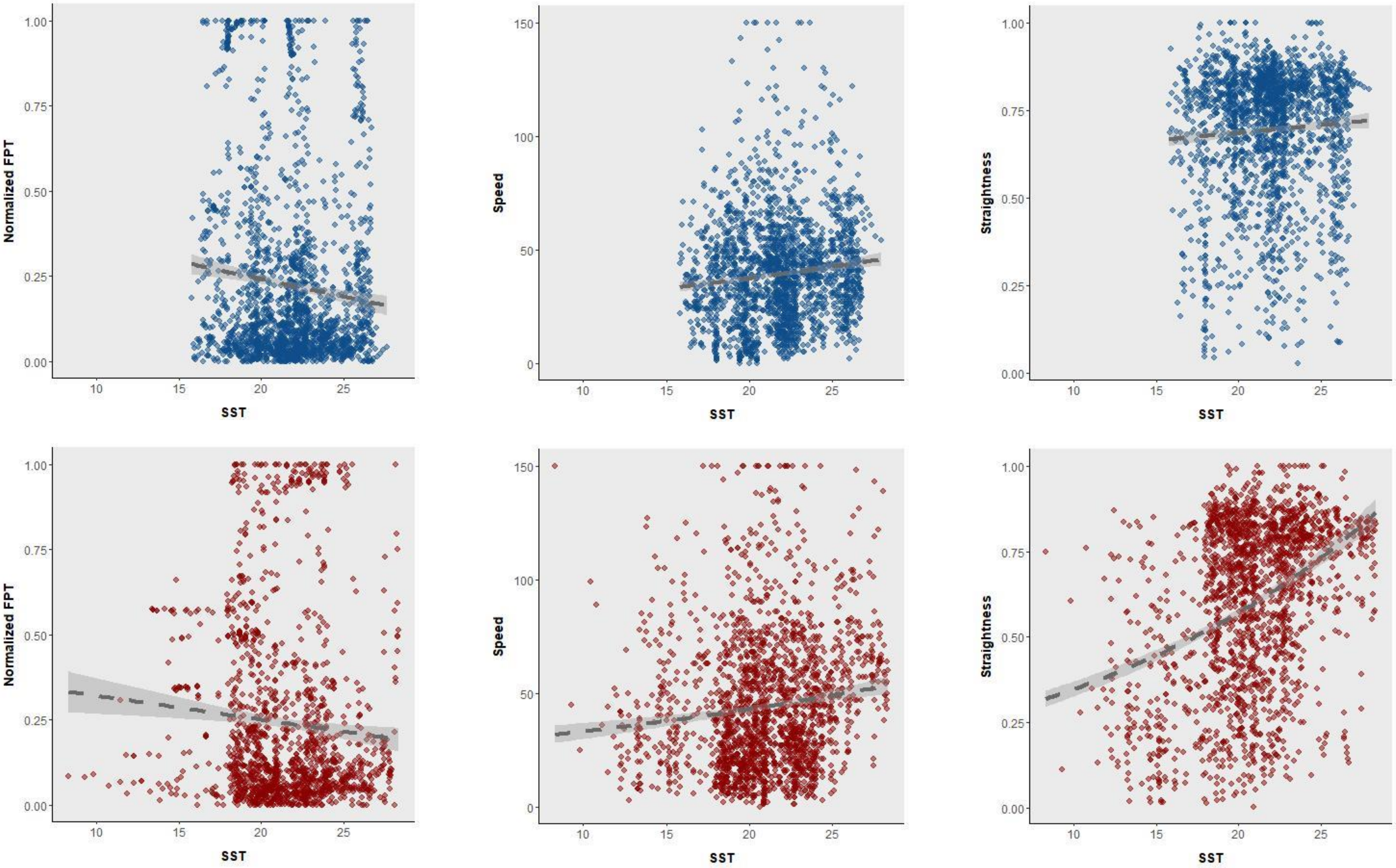


Figure B2 - Relationship of SST with FPT, speed and straightness for blue (blue graphs) and mako (red graphs) sharks.

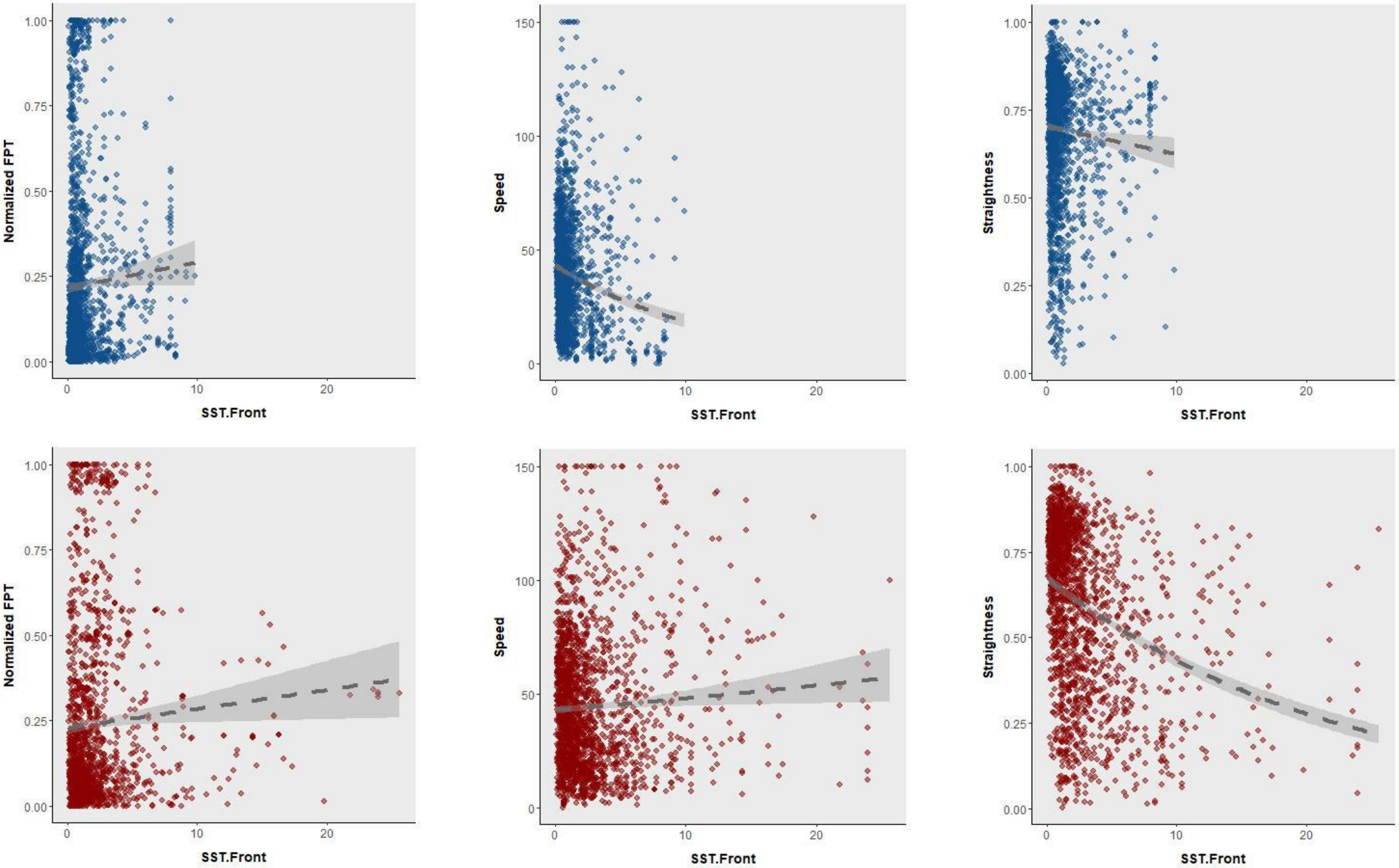


Figure B3 - Relationship of SST front intensity with FPT, speed and straightness for blue (blue graphs) and mako (red graphs) sharks.

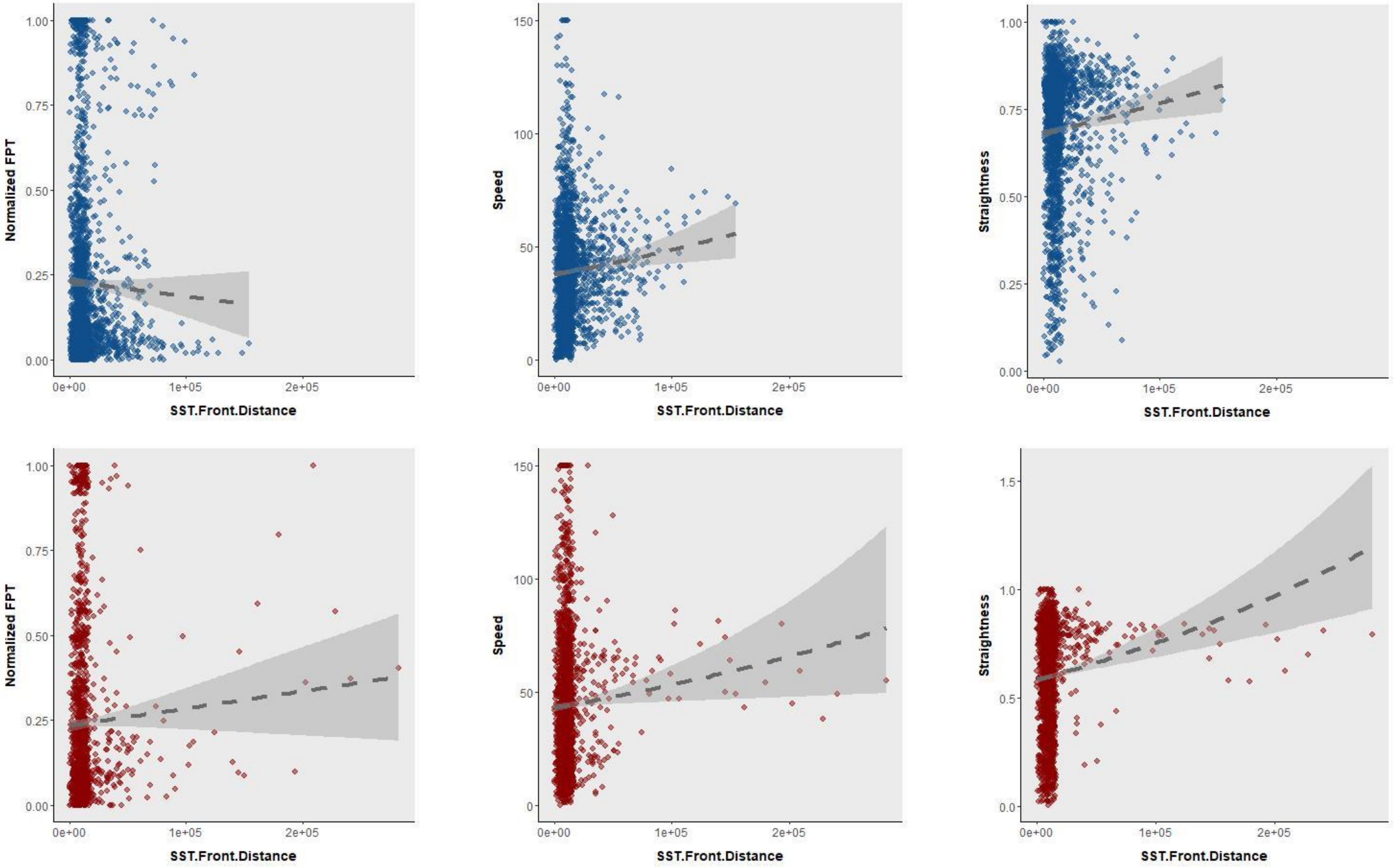


Figure B4 - Relationship of distance to SST Front with FPT, speed and straightness for blue (blue graphs) and mako (red graphs) sharks.

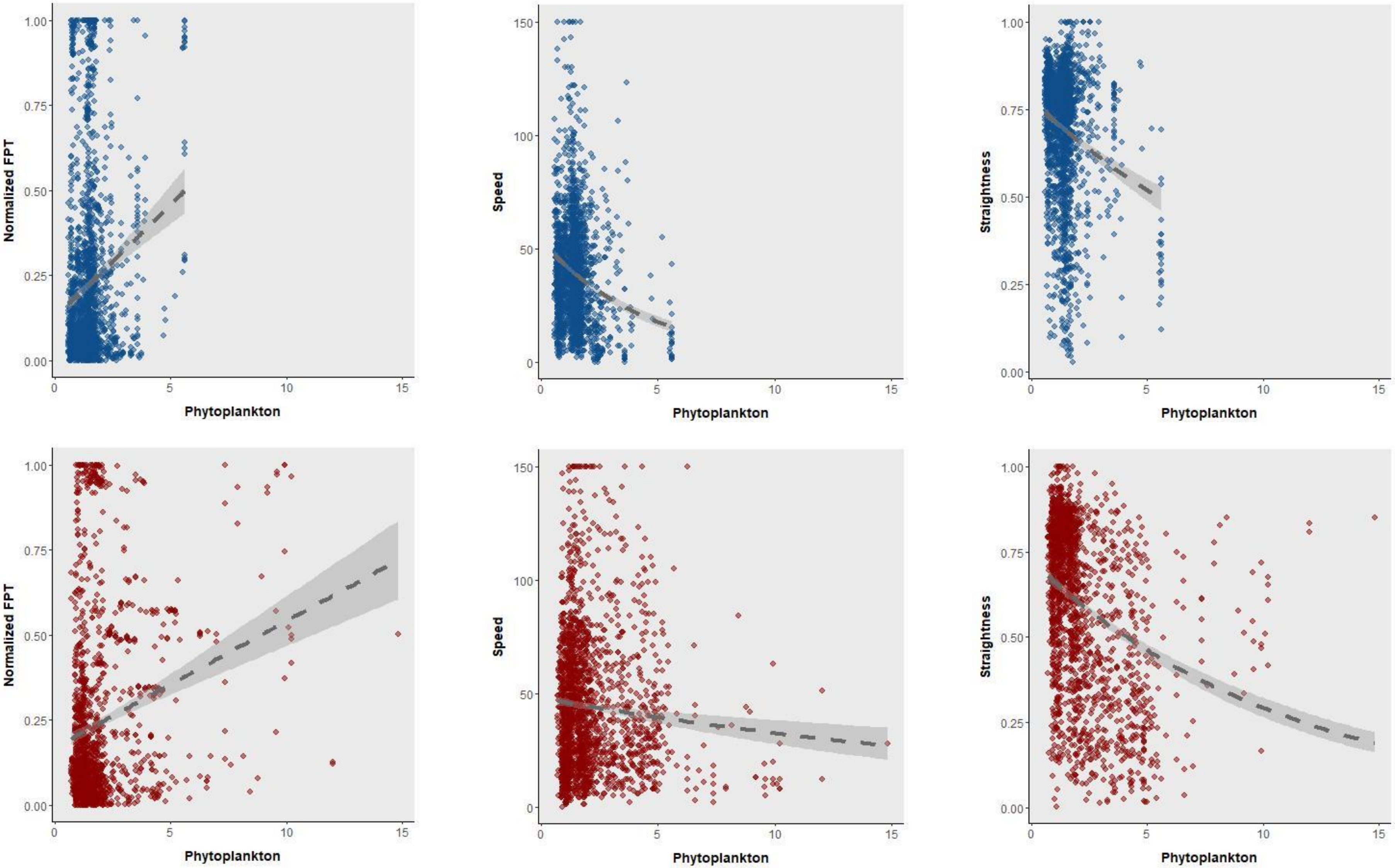


Figure B5 - Relationship of phytoplankton with FPT, speed and straightness for blue (blue graphs) and mako (red graphs) sharks.

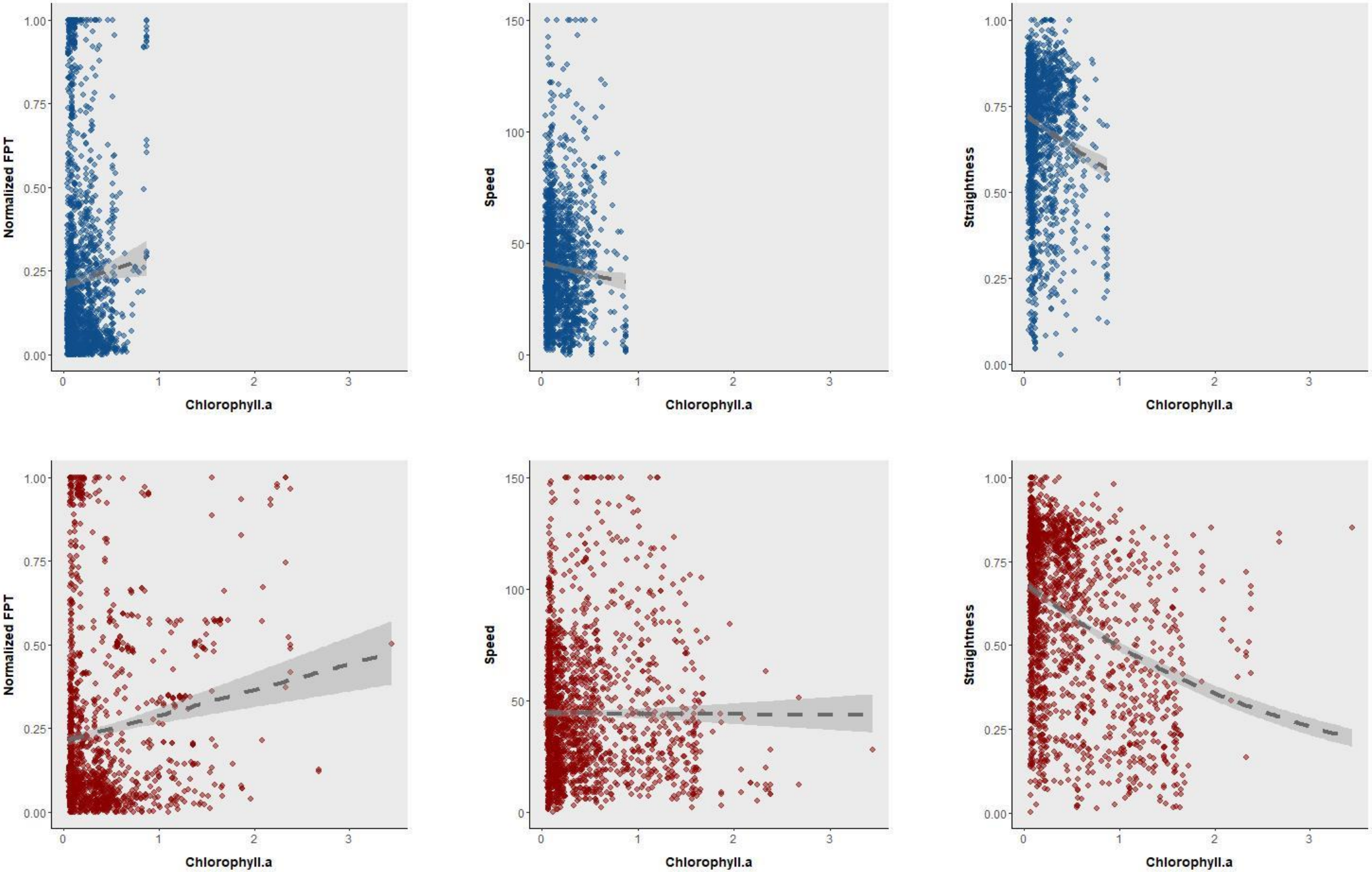


Figure B6 - Relationship of chlorophyll-a with FPT, speed and straightness for blue (blue graphs) and mako (red graphs) sharks.

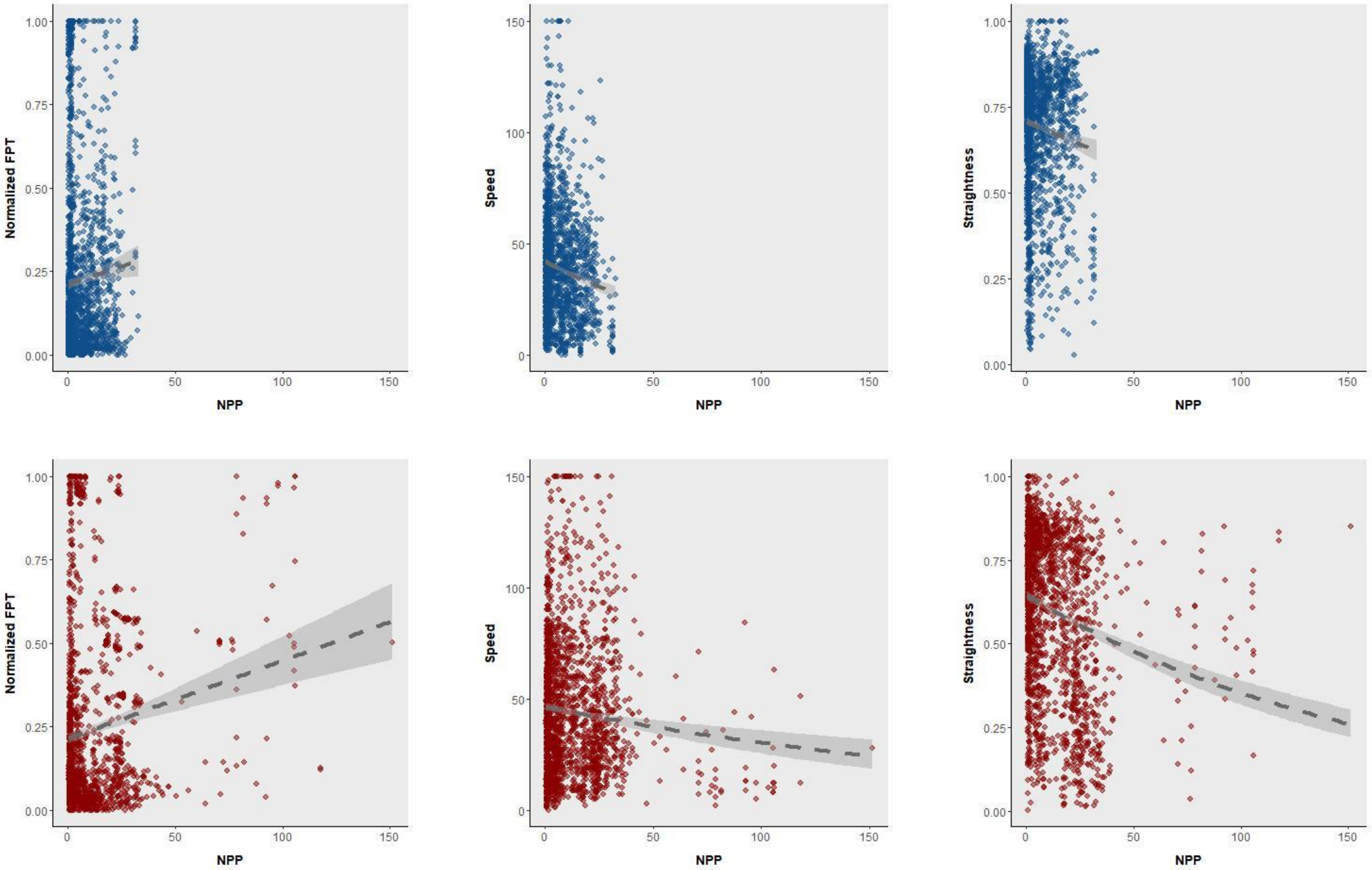


Figure B7 - Relationship of primary production with FPT, speed and straightness for blue (blue graphs) and mako (red graphs) sharks.

	Blue Sharks			Mako Sharks		
	Speed	Straightness	FPT	Speed	Straightness	FPT
DO	*** 0.07	*** 0.18	*** - 0.09	- 0.02	** 0.08	** 0.09
SST	*** 0.12	0.04	** 0.07	*** 0.17	*** 0.32	*** - 0.11
SST Front	*** - 0.19	*** - 0.16	*** 0.1	** - 0.07	*** - 0.42	*** 0.11
SST FDist	*** 0.11	*** 0.09	** - 0.07	* 0.05	*** 0.12	0.02
PHYC	*** - 0.16	*** - 0.13	*** 0.18	- 0.02	*** - 0.41	*** 0.11
CHL	*** - 0.01	*** - 0.15	** 0.06	- 0.01	*** - 0.33	0.03
PP	*** - 0.11	*** - 0.14	*** 0.08	- 0.02	*** - 0.32	0.03

Table B1 - Spearman's correlation coefficients between ARS behaviour and environmental variables and correspondent significance level: *** for significant at α < 0.001, ** at α < 0.01, * at α < 0.05 and no star if not significant.

b) Zoomed relationship

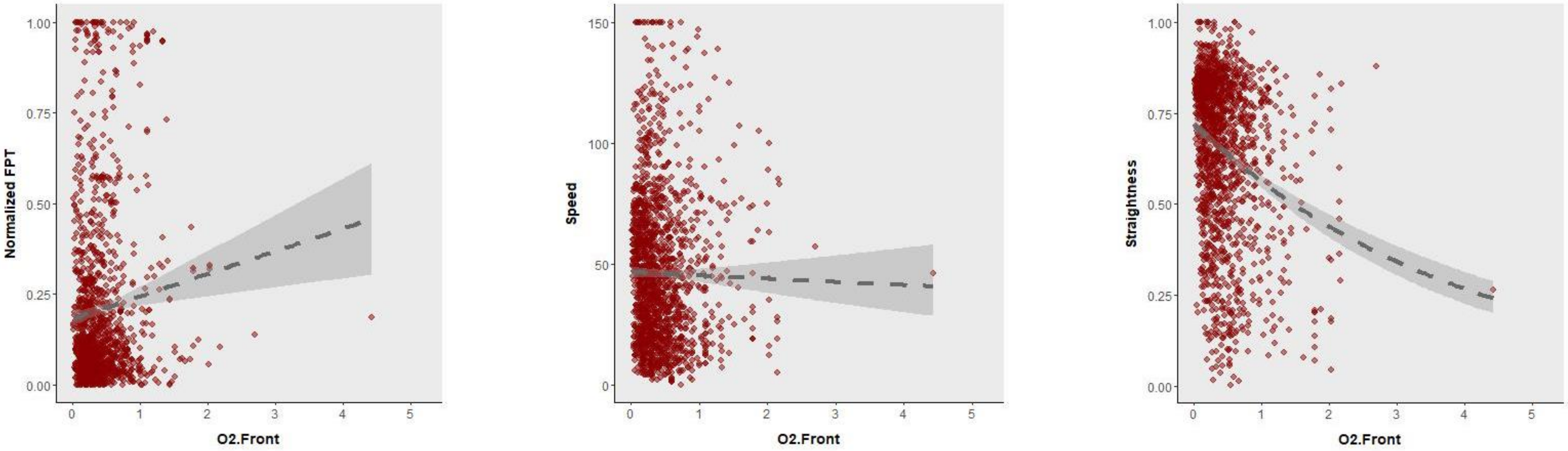


Figure B8 - Zoomed relationship of DO Front intensity at 100 m depth with FPT, speed and straightness for and mako sharks.

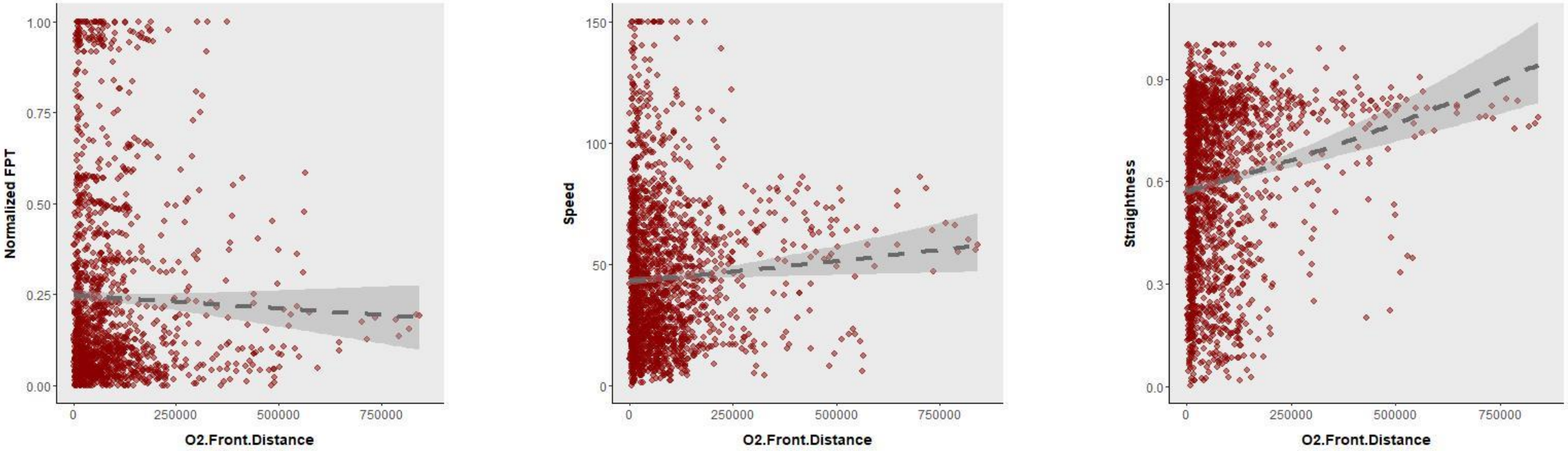


Figure B9 - Zoomed relationship of distance to DO Front at 100 m depth with FPT, speed and straightness for mako sharks.

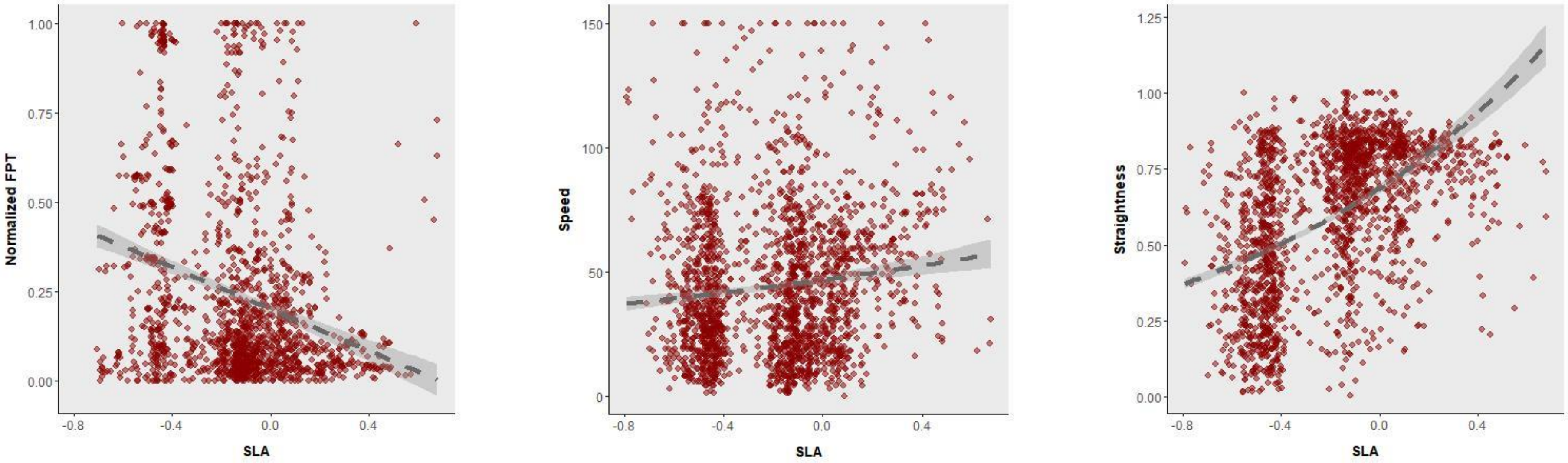


Figure B10 - Zoomed relationship of SLA of SSH with FPT, speed and straightness for mako sharks.

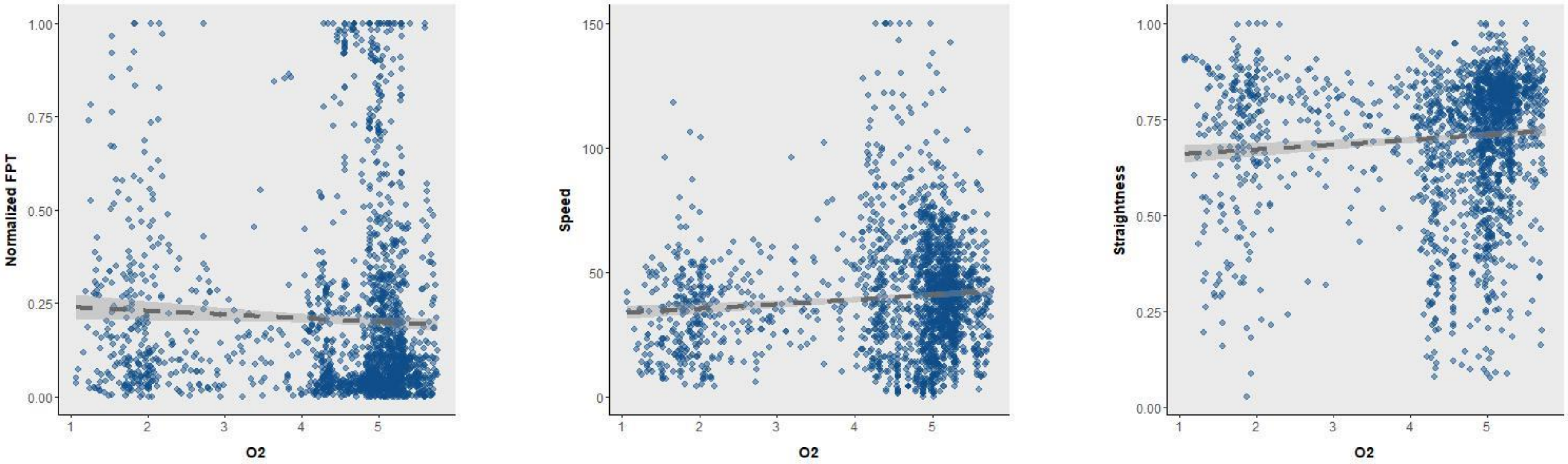


Figure B11 - Zoomed relationship of DO at 100 m depth with FPT, speed and straightness for blue sharks

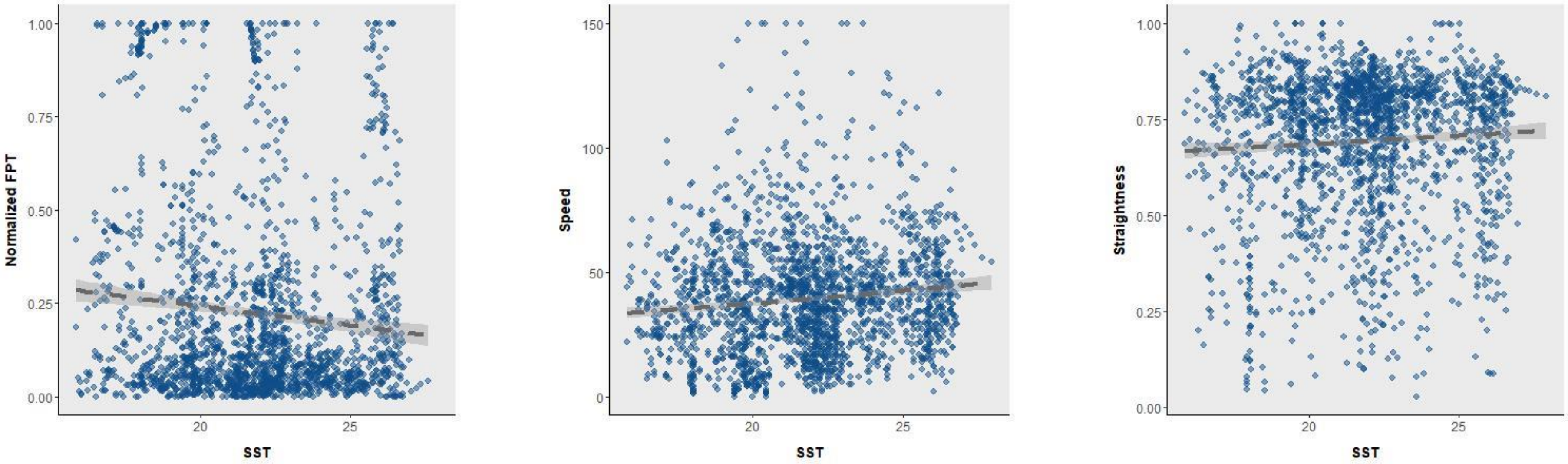


Figure B12 - Zoomed relationship of SST with FPT, speed and straightness for blue sharks.

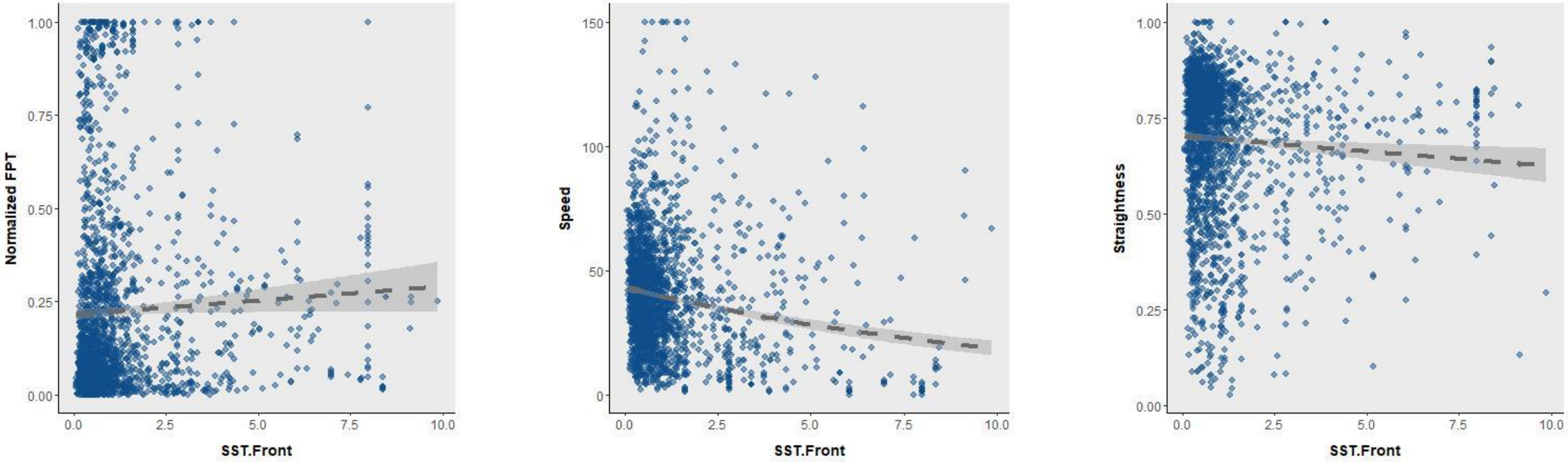


Figure B13 - Zoomed relationship of SST Front intensity with FPT, speed and straightness for blue sharks.

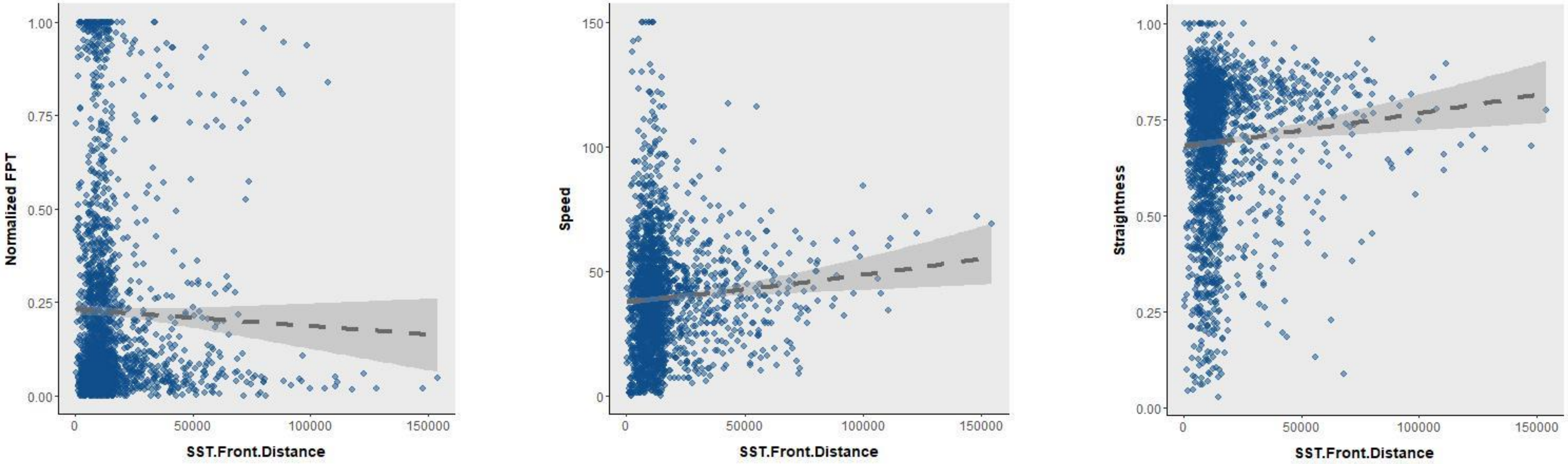


Figure B14 - Zoomed relationship of distance to SST Front with FPT, speed and straightness for blue sharks.

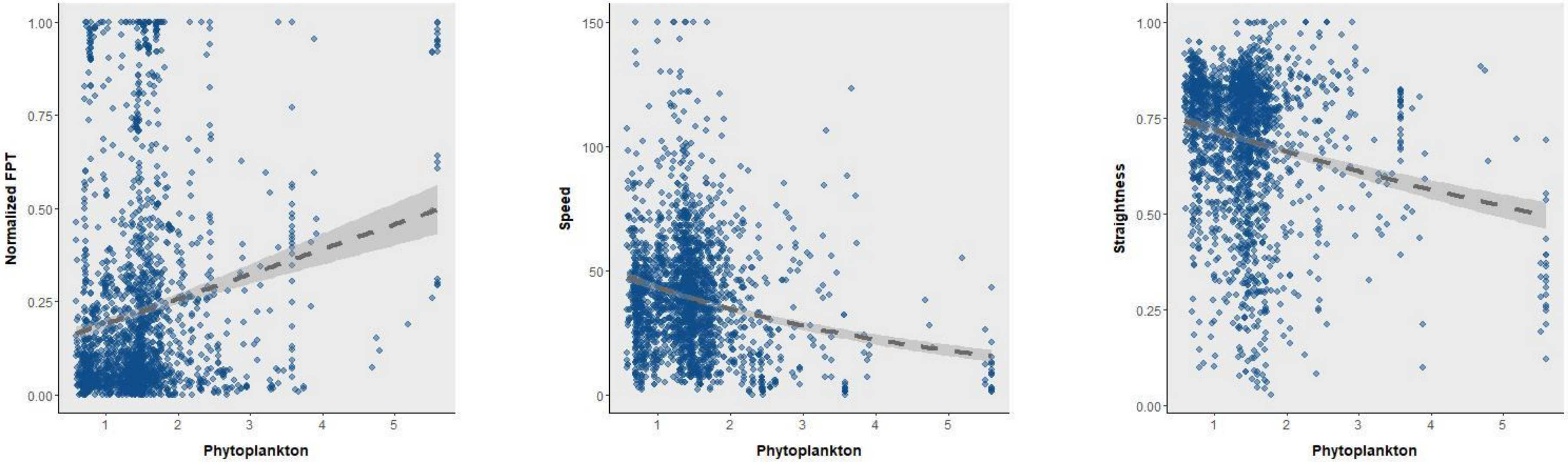


Figure B15 - Zoomed relationship of phytoplankton with FPT, speed and straightness for blue sharks.

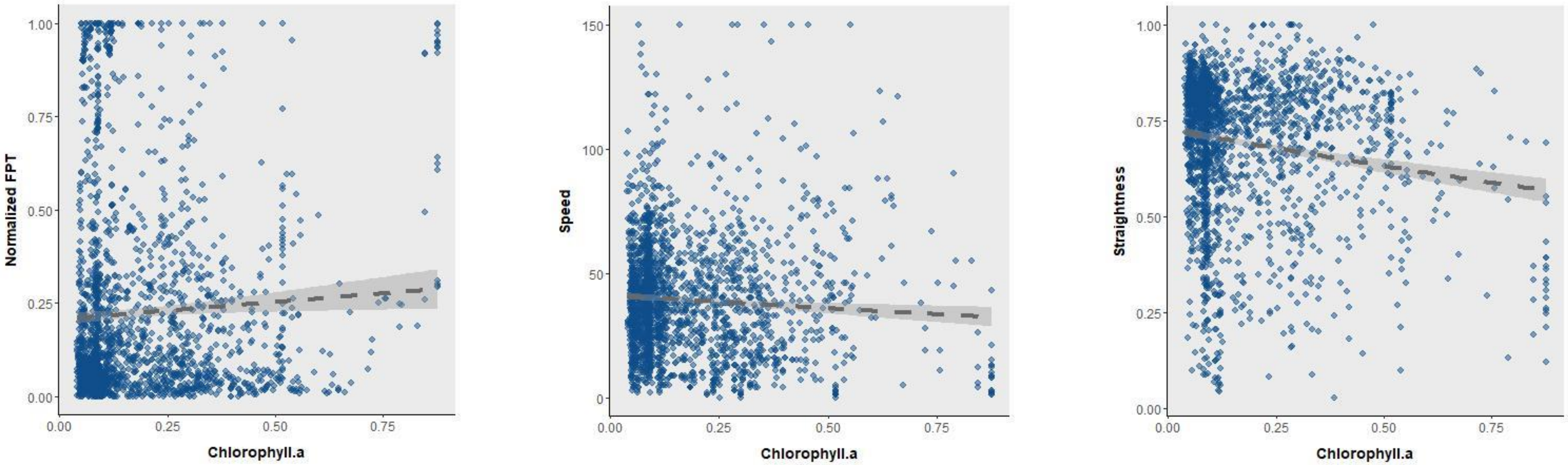


Figure B166 - Zoomed relationship of chlorophyll-a with FPT, speed and straightness for blue sharks.

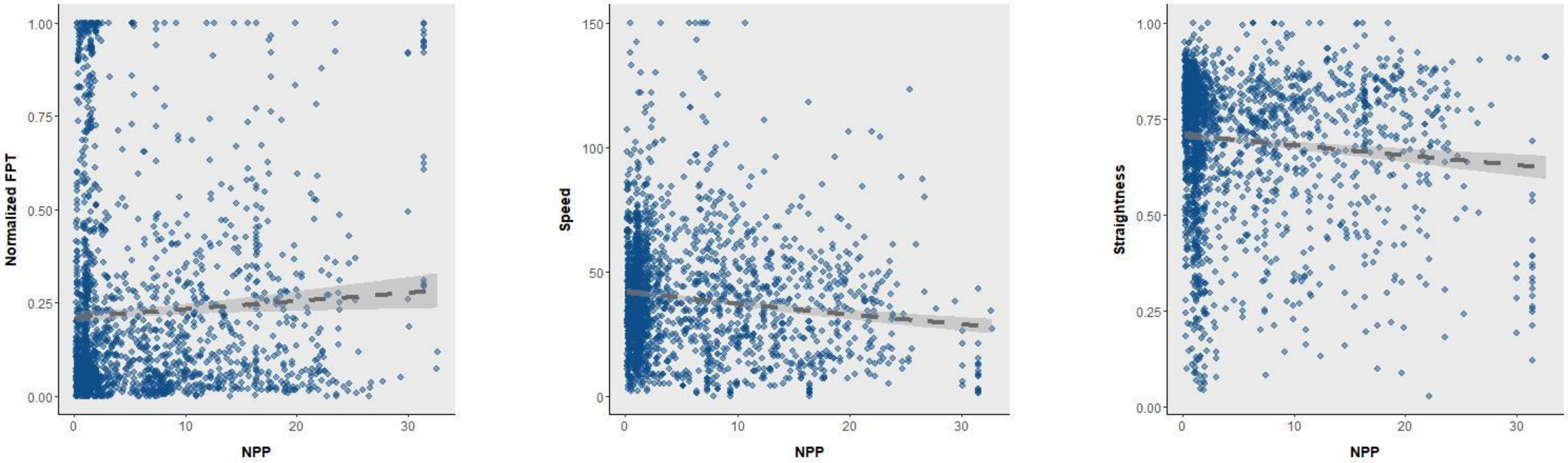


Figure B17 - Zoomed relationship of primary production with FPT, speed and straightness for blue sharks.

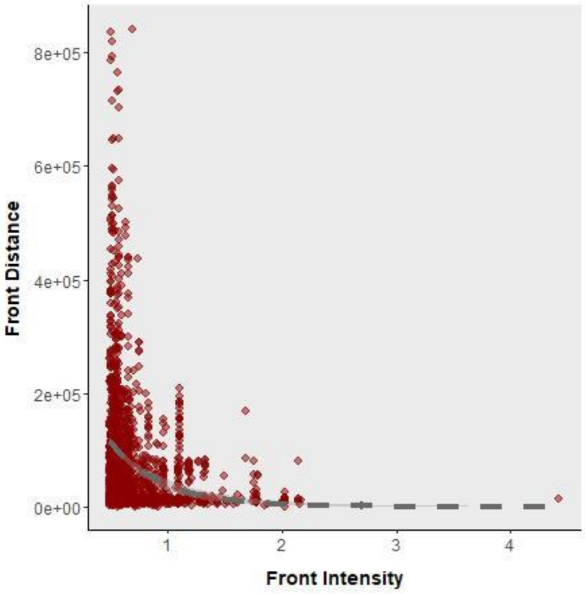


Figure B17 - Zoomed relationship between distance to DO Front and front intensity (from left to right, at 0.5, 1.5 and 2.5 thresholds) for mako sharks.

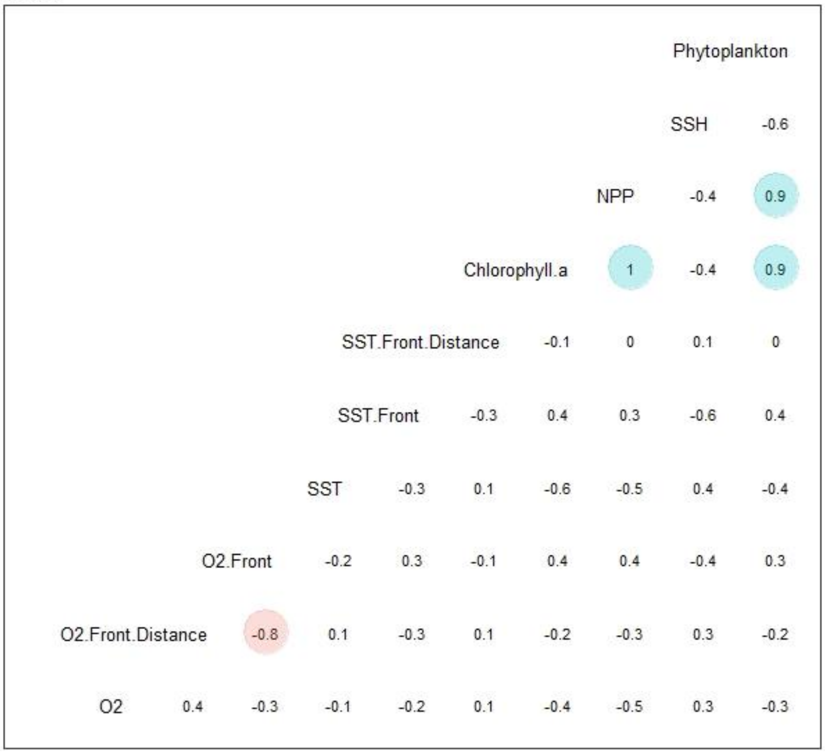
Annex C: RSPF Exploratory Models

BLUE

									Phytoplankton
								SSH	-0.4
							NPP	-0.2	0.8
						Chlorophyll.a	1	-0.2	0.8
					SST.Front.Distance	-0.2	-0.1	0.3	-0.2
				SST.Front	-0.6	0.3	0.3	-0.5	0.3
			SST	-0.4	0.3	-0.2	-0.1	0.6	-0.2
		O2.Front	-0.1	0.2	-0.1	0.4	0.4	-0.3	0.2
	O2.Front.Distance	-0.8	0.1	-0.2	0.1	-0.4	-0.4	0.3	-0.2
O2	0.6	-0.5	-0.3	-0.1	-0.1	-0.5	-0.6	-0.1	-0.2

Figure C1 - Spearman's rank correlation matrix for blue shark environmental variables.

MAKO



									Phytoplankton
								SSH	-0.6
							NPP	-0.4	0.9
						Chlorophyll.a	1	-0.4	0.9
					SST.Front.Distance	-0.1	0	0.1	0
				SST.Front	-0.3	0.4	0.3	-0.6	0.4
			SST	-0.3	0.1	-0.6	-0.5	0.4	-0.4
		O2.Front	-0.2	0.3	-0.1	0.4	0.4	-0.4	0.3
	O2.Front.Distance	-0.8	0.1	-0.3	0.1	-0.2	-0.3	0.3	-0.2
O2	0.4	-0.3	-0.1	-0.2	0.1	-0.4	-0.5	0.3	-0.3

Figure C2 - Spearman's rank correlation matrix for mako shark environmental variables.

Coefficients (cloglog link):	**Estimate**	**Std. Error**	**z value**	**Pr (> | z |)**
(Intercept)	- 1.086	0.7485	- 1.451	0.146829
DO	0.5977	0.1591	3.756	*** 0.000173
				BIC = 4094

Table C1 - Summary of first model results for blue sharks: Estimated parameters from the final RSPF models; Standard errors and the value of the log-likelihood function at the estimated parameters.

Coefficients (cloglog link):	**Estimate**	**Std. Error**	**z value**	**Pr (> | z |)**
(Intercept)	- 15.15614	0.6293	- 24.084	*** < 2 e-16
DO	0.02866	0.04683	0.612	0.54
PHYC	0.56459	0.12215	4.622	*** 3.8 e-06
				BIC = 4058

Table C2 - Summary of second model results for blue sharks: Estimated parameters from the final RSPF models; Standard errors and the value of the log-likelihood function at the estimated parameters.

Coefficients (cloglog link):	**Estimate**	**Std. Error**	**z value**	**Pr (> | z |)**
(Intercept)	- 18.63195	0.77854	- 23.932	*** < 2 e-16
DO	0.09635	0.04357	2.211	* 0.027
PHYC	0.75577	0.11747	6.434	*** 1.25 e-10
SST	0.13214	0.02779	4.756	*** 1.98 e-06
				BIC = 4038

Table C3 - Summary of third model results for blue sharks: Estimated parameters from the final RSPF models; Standard errors and the value of the log-likelihood function at the estimated parameters.

Coefficients (cloglog link):	**Estimate**	**Std. Error**	**z value**	**Pr (> | z |)**
(Intercept)	- 17.45225	0.8027	- 21.742	*** < 2 e-16
DO	0.18167	0.05502	3.302	*** 0.00096
PHYC	0.67362	0.10645	6.328	*** 2.49 e-10
SST	0.14785	0.02971	4.976	*** 6.50 e-07
DO Front	0.33505	0.0428	7.828	*** 4.96 e-15
				BIC = 4022

Table C4 - Summary of forth model results for blue sharks: Estimated parameters from the final RSPF models; Standard errors and the value of the log-likelihood function at the estimated parameters.

Coefficients (logit link):	Estimate	Std. Error	z value	Pr (> | z |)
(Intercept)	9.53583	1.97145	4.837	*** 1.32 e-06
SST	0.43332	0.07537	5.749	*** 8.97 e-09
				BIC = 5234

Table C5 - Summary of first model results for mako sharks: Estimated parameters from the final RSPF models; Standard errors and the value of the log-likelihood function at the estimated parameters.

Coefficients (logit link):	Estimate	Std. Error	z value	Pr (> | z |)
(Intercept)	7.66275	1.30844	5.856	*** 4.73 e-09
SST	0.39761	0.05556	7.156	*** 8.32 e-13
SST Front	0.94945	0.33024	2.875	** 0.00404
				BIC = 5225

Table C6 - Summary of second model results for mako sharks: Estimated parameters from the final RSPF models; Standard errors and the value of the log-likelihood function at the estimated parameters.