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ECOLOGIA E CONSERVAÇÃO DO TUBARÃO GALHA-BRANCA OCEÂNICO (*Carcharhinus longimanus*, Poey 1861)

- ECOLOGY AND CONSERVATION OF THE OCEANIC WHITETIP SHARK-

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Centro de Tecnologia de Geociências
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Mariana Travassos Tolotti

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Tese aprovada em:
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Resumo

O objetivo principal da presente tese consistiu em agregar informações ao conhecimento sobre o tubarão galha-branca oceânico (*Carcharhinus longimanus*), principalmente no que se refere à sua distribuição, índices de abundância e preferências de habitat. Apesar de ser uma espécie muito capturada na pesca oceânica de atuns afins, informações acerca destes aspectos ecológicos são escassas e até mesmo ausentes na literatura relacionada à espécie. A tese é apresentada como um conjunto de capítulos autônomos, representando artigos científicos individuais. No primeiro capítulo-artigo foram discutidos os possíveis efeitos de medidas de manejo restritivas, implementadas recentemente por Organizações Regionais da Pesca Atuneira e que incluem algumas espécies de tubarões oceânicos. Medidas restritivas isoladas terão pouco impacto na redução da mortalidade de tubarões oceânicos. Um conjunto de medidas mitigadoras integradas será mais eficaz na conservação e recuperação das populações dessas espécies. No segundo capítulo-artigo foram analisados dados de captura e esforço de 14.835 lançamentos de espinhel pelágico realizados por embarcações arrendadas da frota atuneira brasileira, nos anos de 2004 a 2010. A CPUE nominal exibiu uma tendência de aumento gradual ao longo dos anos, variando de 0,04 em 2004 para 0,15 em 2010. A CPUE foi padronizada através de uma abordagem delta-GLM, entretanto, o índice de abundância padronizado não diferiu significativamente da CPUE nominal. Os modelos indicaram que as capturas de tubarões galha-branca são maiores para a estratégia de pesca espanhola, que se caracteriza pela utilização de anzóis em profundidades mais rasas. No terceiro capítulo-artigo, a interação entre tubarões galha-branca e a pesca de rede de cerco nos Oceanos Atlântico e Índico foi analisada, com o objetivo de investigar o potencial da utilização do banco de dados dessa pescaria para derivar índices de abundância e determinar tendências populacionais para a espécie. Dados de observadores de bordo da frota francesa combinados com dados históricos da União Soviética foram utilizados na análise. A série temporal combinada incluiu os anos entre 1986 e 2014. No Oceano Atlântico não foi possível determinar uma tendência populacional, uma vez que o índice de ocorrência foi muito baixo e não variou significativamente com o tempo. No Oceano Índico foi observada uma mudança bem-marcada no índice de ocorrência, oscilando em torno de 20%

entre meados dos anos 80 e 90 e caindo para menos de 10% a partir de 2005. No quarto capítulo-artigo, a vulnerabilidade do tubarão galha-branca à pesca de espinhel pelágico foi avaliada utilizando dados dependentes e independentes da pesca. Os dados dependentes incluíram informações de diários de bordo (1999-2011) e observadores embarcados (2004 a 2010), num total de 65.277 lançamentos de espinhel. Os dados independentes foram obtidos a partir de 8 tubarões marcados com marcas do tipo "*pop-up satellite archival tag*" na área onde a frota de espinhel operou. Locais de marcação e desprendimento das marcas foram relativamente próximos uns dos outros. Entretanto, os indivíduos marcados tenderam a viajar longas distâncias antes de retornar para a área de marcação. Foi observado um certo grau de filopatria à área. "*Hotspots*" de alta utilização dos tubarões marcados correspondeu à área sob forte pressão pesqueira. Todos os tubarões exibiram uma forte preferência por águas quentes e rasas da camada de mistura, gastando, em média, mais de 70% do tempo acima da termoclina e 95% acima de 120 m. Esse resultado justifica a maior capturabilidade da espécie em espinheis mais rasos. No quinto e último capítulo-artigo, os movimentos verticais dos tubarões marcados foram analisados em detalhe. Apesar da distribuição vertical restrita, os dados indicaram que o tubarão galha-branca apresenta padrões de movimento complexos, incluindo padrões de migrações circadianas distintos e mergulhos profundos. O padrão circadiano mais frequentemente observado é caracterizado de um deslocamento à superfície durante o nascer do sol e uma tendência a permanecer em profundidades mais baixas durante o dia. Os movimentos verticais também foram influenciados pela temperatura da superfície do mar, o que pode indicar a ocorrência de termoregulação para espécie. A integração dos resultados de cada capítulo-artigo proporcionou boas perspectivas para o desenvolvimento de medidas de mitigação. A evidência em relação à preferência do tubarão galha-branca por águas quentes e rasas é sólida, indicando que a remoção dos anzóis rasos do espinhel pode ser proposta para reduzir a captura incidental da espécie. O fato de variações na CPUE já terem sido observadas, sugere que esta pode ser uma medida eficaz. O comportamento filopátrico observado para o OCS também indica que a espécie pode se beneficiar com a criação de áreas marinhas protegidas.

Palavras-chave: fauna acompanhante, pesca atuneira, dados de observadores de bordo, taxas de capturas, índice de abundância, marcas eletrônicas, padrões de movimento, comportamento, medidas mitigadoras.

Abstract

The ultimate goal of this thesis was to generate knowledge regarding the ecology of the oceanic whitetip shark (*Carcharhinus longimanus*) and contribute for an ecosystem-based fishery management. The work focuses on the interactions between tuna fisheries and the species and its habitat preferences. Despite being frequently caught on high-sea fisheries, there are wide knowledge gaps regarding the ecology of the oceanic whitetip shark. The thesis is presented as a set of self-contained standalone chapters, constructed as individual research articles. The first article-chapter provides a discussion concerning pelagic sharks and the recent species-specific banning measures implemented by Regional Fishery Management Organizations (RFMOs) in charge of tuna fisheries. It is unlikely that banning measures alone can reduce the high level of fishing mortality and recover pelagic shark's depleted populations. Managers should be fully aware that the development and implementation of mitigation measures are critical for a more effective conservation strategy. In the second article-chapter, catch and effort data from 14,835 longline sets conducted by foreign tuna longline vessels chartered by Brazil, from 2004 to 2010, were analyzed. The nominal catch per unit of effort (CPUE) exhibited a gradual increase, varying from 0.04 sharks/1000 hooks in 2004 to 0.15 in 2010. A CPUE standardization was performed using a delta-GLM approach, but the standardized index of abundance did not differ significantly from the nominal CPUE. The models indicated that the catches of oceanic whitetip sharks are higher for the Spanish fishing strategy, which is characterized by the deployment of hooks at shallower depths. In the third article-chapter, the interaction between oceanic whitetip sharks and the purse seine fishery in the eastern Atlantic and western Indian oceans was analyzed, in order to investigate the potential of using this fishery's database to derive abundance indexes and determine population trends for the species. Observer data from the French purse seine fleet combined with a historic database from the Soviet Union were used in the analyses. The combined time series spanned from 1986 to 2014. The occurrence index was very low for Atlantic Ocean and no marked temporal trend was observed. For the Indian Ocean a well-marked change on the occurrence index was observed, fluctuating around 20% from mid 80's to mid 90's and dropping to less than 10% as from 2005. In the fourth article-chapter, a combination of fisheries dependent and independent data was used to assess the vulnerability of the oceanic whitetip shark to pelagic longline fisheries. Fisheries dependent data included information from logbooks (from 1999 to 2011) and on-board observers (2004 to 2010), totaling 65,277 pelagic longline sets. Fisheries independent data were obtained from 8 oceanic whitetip sharks tagged with pop-up satellite archival tags in the area where longline fleet operated. Tagging and pop-up sites were relatively close to each other, although individuals tended to travel long distances before returning to the tagging area. Some degree of philopatry was observed. High utilization hotspots of tagged sharks fell inside the area under strongest fishing pressure. All sharks exhibited a strong preference for the warm and shallow waters of the mixed layer, spending on average more than 70% of the time above the thermocline and 95% above 120 m. This result explains the higher catchability of the species on shallow longline gear. In the fifth and last article-chapter, the vertical movements of tagged oceanic whitetip sharks were analyzed in detail. Despite its restricted vertical distribution, the analyses reveled that oceanic whitetips perform complex movement patterns, including distinct diel patterns and deep diving behavior. A correlation between vertical movements and sea surface temperature was also observed, suggesting the occurrence of thermoregulation for the species. The combined results of each article-chapter have provided good insights towards the development of mitigation measures. The evidence regarding oceanic whitetip shark's preference for warm and shallow waters is solid and this information suggests that the removal of the shallow hooks from the longline gear could be proposed as a technique to reduce OCS bycatch. The fact that CPUE variations were already observed suggests that this might be an effective measure. The philopatric behavior observed for the OCS also indicates that the species could benefit from time-area closure measures.

Keywords: bycatch, tuna fisheries, observer data, catch rates, abundance index, electronic tagging, movement patterns, behavior, mitigation measures.

Table of contents

Chapters published in peer-reviewed journals

Chapter 2

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

Chapter 3

Tolotti, M.T., Travassos, P., Frédou, F.L., Wor, C., Andrade, H.A., Hazin, F. 2013. Size, distribution and catch rates of the oceanic whitetip shark caught by the Brazilian tuna longline fleet. Fisheries Research, 143: 136–142. doi:10.1016/j.fishres.2013.01.014

Chapter 5

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Note:

Chapter 4 was partially presented as a working paper during the Ecosystem and bycatch meeting of the Indian Ocean Tuna Commission (IOTC), held at Olhão – Portugal, between September 7th and 11th of 2015.

Tolotti, M.T., Bach, P., Romanov, E., Dagorn, L. 2015. Interactions of oceanic whitetip sharks with the tuna purse seine fishery in the Indian Ocean. IOTC-2015-WPEB11-29.

Chapter 1

General introduction

1. Context of the thesis

1.1. Global

The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) has, on its latest meeting on March 2013, moved the oceanic whitetip shark (*Carcharhinus longimanus*, FAO 3 alpha code = OCS) from appendix III to II (CoP16 Prop. 42). CITES is an international agreement between governments aiming to ensure that international trade of wild fauna and flora does not threaten their survival. Species listed on appendix II are considered threatened and their international trade must be closely controlled in order to avoid utilization incompatible with their survival. The inclusion of the OCS on appendix II was proposed by Brazil, Colombia and the United States. The approval of this proposal is a result of the widespread increase of public awareness regarding the conservation status of this shark species.

Concerns regarding the conservation of the oceanic whitetip shark started to rise substantially from 2006 when the species was classified as vulnerable by the IUCN red list of threatened species worldwide and critically endangered in the northwest and western central Atlantic Ocean. This status was mainly defined due to increasing fishing pressure throughout the species range and due to lack of knowledge and adequate monitoring (Baum et al., 2006). In 2010, the International Commission for the Conservation of Atlantic Tunas (ICCAT) decided to ban landings, storing, and selling of the OCS in the Atlantic Ocean (Rec. 10-07). Following this resolution, similar measures were adopted in the Eastern and Western Pacific and Indian oceans, by their respective Regional Fishery Management Organizations (RFMO): the Inter American Tropical Tuna Commission on January 1st 2012 (IATTC Rec. C-11-10), the Western and Central Pacific Fisheries Commission on January 1st 2013 (WCPFC CMM 11-04) and the Indian Ocean Tuna Commission on January 1st 2014 (IOTC Res. 13–06).

All of these conservation measures, including the recent listing on CITES appendix II, were taken under the precautionary approach concept and represent a first step towards the preservation of oceanic whitetip sharks worldwide. Knowledge gaps concerning the species ecology and biology are still wide, imposing a barrier on the development of mitigation measures for fisheries and accurate stock assessments. To bridge these gaps, scientific research is now greatly encouraged.

1.2. National – Brazil

In 2008, around 550,000 tons of tuna and tuna-like species were caught in the Atlantic Ocean by both artisanal and industrial fisheries (ICCAT, 2010). These species included yellowfin (*Thunnus albacares*), bigeye (*Thunnus obesus*) and skipjack tunas (*Katsuwonus pelamis*), swordfish (*Xiphias gladius*) and other teleost fishes and several species of pelagic sharks (*Prionace glauca*, *Carcharhinus* sp.). During the same year, the Brazilian fleet caught 35,000 t of large pelagic fishes, or the equivalent of 6% from the whole Atlantic Ocean catches. Skipjack tuna represents almost two thirds of the Brazilian catches and has the lower commercial value when compared to other tuna species and the swordfish. From an economic point of view, those numbers reflect in sub-optimal revenue (Hazin, 2010). Brazil is strategically located in relation to the main migration routes of tuna and tuna-like stocks in the South Atlantic (Hazin and Travassos, 2006). Taking into account the great extension of Brazil's coastline, with approximately 8,500 km, and its proximity with major fishing grounds, it is clear that the position currently occupied by the country in the scenario of open ocean fisheries is not justified (CGEE, 2008). While fishing vessels operating from Brazilian ports reach areas of occurrence of tuna schools within hours of navigation, long distance fishing fleets from countries with consolidated fishing tradition, such as Japan, Taiwan, Korea, Spain and Portugal, are required, in some cases, to navigate more than 20,000 km to reach the same fishing grounds. The Brazilian government has been strongly investing to develop its fishery sector and due to the depletion of most coastal stocks (Dias-Neto, 2003) and to the high commercial value of tuna species, open ocean fisheries have become a priority (Hazin and Travassos, 2006). Investments on the Brazilian fishery sectors include many fronts with great focus being put into research, including biology and ecology of target and bycatch species as well as oceanography, development of new technology and qualification of manpower.

As highly migratory species, tuna stocks are managed by RFMOs. In the case of the Atlantic Ocean ICCAT is the entity responsible, from which Brazil is a member since its foundation at Rio de Janeiro in 1966. Since then, being able to comply with ICCAT recommendations and resolutions is one of the basic principles for Brazil. Conservation issues have always been included in Brazil's agenda, specially regarding the vulnerable group of pelagic sharks species. Brazil was one of the first countries to adopt a legislation to ban the shark finning practice already in 1998 (IBAMA decree, N° 121, August 24 of 1998). A national plan of action for the conservation and management of sharks (NPOA Shark) was proposed in 2011 and is currently being implemented (Dias-Neto, 2011). The oceanic whitetip shark is relatively common in the catches of the Brazilian tuna longline fleet (Frédou et al., 2015) and due to the strong signs of depletion regarding its population status Brazil has actively acted on the behalf of its conservation. The ICCAT banning recommendation (Rec. 10-07) was supported by biological studies conducted by Brazil and (Tambourgi et al., 2013), as mentioned in the previous item, Brazil was also one of the head countries proposing the listing of the OCS on CITES appendix II. Following the approval of CITES proposal, Brazil also adopted a national banning law for the species (Ministry of Fisheries and Aquaculture–MPA and Ministry of the Environment-MMA normative instruction, N°1, March 12 of 2013).

2. State of the art

The Chondrichthyans, or cartilaginous fish, form a relative small group with approximately 1,115 described species, including sharks, rays and chimaeras (Compagno et al., 2005). Pelagic species represent 6% of this group and of those roughly 30 inhabit oceanic regions (Camhi, 2009). The also called elasmobranchs are known for their k-strategist life cycle, which is characterized by slow growth, high longevity, late sexual maturity and low fecundity (Hoenig and Gruber, 1990). Due to these characteristics, elasmobranch species exhibit low population growth rates (Cortés, 2000), which makes them much more vulnerable to overfishing when compared to teleost fish (Frisk et al., 2005; Musick et al., 2000).

In recent years, there has been increasing concern about the deteriorating status of the world's pelagic shark populations (Cortés et al., 2010; Dulvy et al., 2008; Worm et al., 2013). Whereas there is some uncertainty about the precise status of these species, there is no doubt that shark populations have declined significantly (Baum and Blanchard, 2010; Baum and Myers, 2004; Baum et al., 2003; Simpfendorfer et al., 2008). It is, therefore, important that management measures are in place to ensure the future sustainability and prevent further population collapse. Open ocean sharks and rays are relatively numerous and play an important role in the food webs of the high seas, but, as wide-ranging animals that spend most of their lives far from land these species have received less research attention than their coastal relatives (Pikitch et al., 2008).

Most of the world's shark catches are incidental, constituting bycatch that is either discarded at sea or landed for sale. Within the fishing methods with the upmost incidence of elasmobranchs are high-seas pelagic longlines, gillnets and purse seines targeting mainly tuna and/or swordfish (Bonfil, 1994; Camhi et al., 2008). The historically low economic value of shark products compared to the target species has resulted in fewer incentives for research and conservation (Barker and

Schluessel, 2005). Global concern on this matter, however, has been growing over the past decade (Pikitch and Camhi, 2003). Although statistics concerning shark's catches are very scarce, it is noteworthy that representatives of the Carcharhinidae family are amongst the most commonly captured species. These pelagic shark species include the oceanic whitetip (*C. longimanus*), silky (*C. falciformis*), and blue sharks (*P. glauca*), which are also considered the most abundant ones within their group (Compagno, 1984).

The oceanic whitetip shark is easily distinguishable from the other species of the Carcharhinidae family by the round shape of its long pectoral and dorsal fins, as well as by the white stains in their margins (Compagno, 1984). Their large fins are highly valued in international trade making them an important target of this market (Camhi, 2009; Clarke et al., 2006). Once considered amongst the most abundant oceanic sharks, the oceanic whitetip is now commonly perceived as rare. Inadequate monitoring makes the estimates of their populations very difficult but there is a scientific general consensus that populations are decreasing (Baum et al., 2006).

Despite its worldwide distribution and frequent catches on most high seas pelagic fisheries, little has been published on the biology and ecology of the oceanic whitetip shark. The first few studies were conducted more than 50 years ago, in the western North Atlantic and in the eastern Pacific Ocean, including general information on diet, reproduction and behavior (Backus et al., 1956; Strasburg, 1958). Since then, however, very little was added until the past decade when more detailed biological studies were published (Lessa et al., 1999a, 1999b; Seki et al., 1998). It was not until very recent that new information regarding oceanic whitetip shark's started to become available again, these included movement patterns, temperature preferences and biology studies (Howey-Jordan et al., 2013; Madigan et al., 2015; Musyl et al., 2011; Tambourgi et al., 2013).

In the past year, a first stock assessment was conducted for the oceanic whitetip shark in the Pacific Ocean (Rice and Harley, 2012). It was concluded that either overfishing is occurring or the stock is overfished and the greatest impact on the stock was attributed to bycatch from the longline fishery, with lesser impacts from purse seining. Considering the bycatch nature of fishery impacts, it was advised that mitigation measures could provide the best opportunity to improve the status of the oceanic whitetip population, as it has being suggested for shark species in general (Gilman et al., 2008). The development of new research regarding stock structure, behavior, post-release survival, female maturity, improvement of basic catch and effort data, among others, was also advised. The deficiency of such information prevented similar analyses for being conducted for the Atlantic (Cortés et al., 2010) and Indian Ocean stocks.

3. Thesis outline

This work is product of an international research cooperation between France, through the *Institut de recherche pour le développement* (IRD) and Brazil, through the *Departamento de Pesca e Aquicultura* of the *Universidade Federal Rural de Pernambuco* (UFRPE). The aim of this international cooperation is to mitigate the adverse ecological impacts caused by open ocean fisheries in the Atlantic and Indian oceans, with focus on the bycatch issue of tuna fisheries.

The thesis is presented as a set of self-contained standalone chapters, constructed as individual research articles. Consequently, styles might vary and references, as well as other components, may occasionally be repeated to accommodate the styles of different journals. Following this first introductory chapter, five article-chapters are presented. These chapters address ecological and conservation issues regarding the oceanic whitetip shark. The ultimate goal was to generate knowledge and contribute for an ecosystem-based fishery management (Gilman et al., 2014; Pikitch et al., 2004). A closing chapter, integrating the main findings of each article-chapter is also presented. An overview of each article-chapter is given below.

Chapter 2 provides a discussion concerning pelagic sharks and the recent species-specific banning measures implemented by Regional Fishery Management Organizations (RFMOs) in charge of tuna fisheries. These measures include retention bans, finning bans and trading bans. The positive and negative aspects of such measures are analyzed inside of two distinct scenarios: one where pelagic sharks are the targeted species and other where they represent the bycatch component. The main objective was to alert managers that banning measures are not the final step towards the conservation of pelagic sharks, but rather the initial one.

In Chapter 3, catch and effort data from the Brazilian tuna longline fleet were analyzed. This chapter provides information on size, distribution and catch rates of the oceanic whitetip sharks caught by this fishery. Data was analyzed with regards to year, season and fishing strategy. Little is known in relation to the spatial distribution and relative abundance of the species. Understanding how oceanic whitetip sharks interact with the fishery will help on the development of mitigation measures to prevent their capture.

Following the idea behind Chapter 3, Chapter 4 provides an analysis of the interaction between oceanic whitetip sharks and the tuna purse seine fishery. Catch and effort data form the French fleet operating in the eastern Atlantic and western Indian oceans were available for this analysis. Additional historic data from the Soviet Union in the Indian Ocean was also included. The main objective was to investigate the potential of using this fishery's database to derive abundance indexes and determine population trends for the species.

In Chapter 5, a combination of fisheries dependent and independent data was used to assess the vulnerability of the oceanic whitetip shark to pelagic longline fisheries. Fisheries independent data consisted on information collected with the use pop-up satellite archival tags. These tags provide information on depth, water temperature and ambient light level (for estimation of geolocation) experienced by the tagged individuals. Sharks were tagged in the same area where the Brazilian longline operates, thus the fisheries dependent data comes from this fishery. Vulnerability was assessed with regards to both spatial dynamics (horizontal) and depth distribution (vertical) of both shark and longline gear, taking into consideration seasonality and strategies in the fishery. The overall goal was to provide information to aid in the design of mitigation measures and improve conservation efforts for the species.

Finally, Chapter 6 provides a detailed analysis of the vertical movements of the tagged oceanic whitetip sharks. Most of the recently published information describing depth and temperature preferences for the species consisted on general summaries only (Howey-Jordan et al., 2013; Musyl et al., 2011). Vertical movements were not explored in detail. The aim of this chapter was to describe potential diel cycles, highlighting similar and contrasting patterns amongst individuals. An analysis of the species vertical occupation with regards to environmental variables, especially the temperature structure in the water column, is also provided.

4. References

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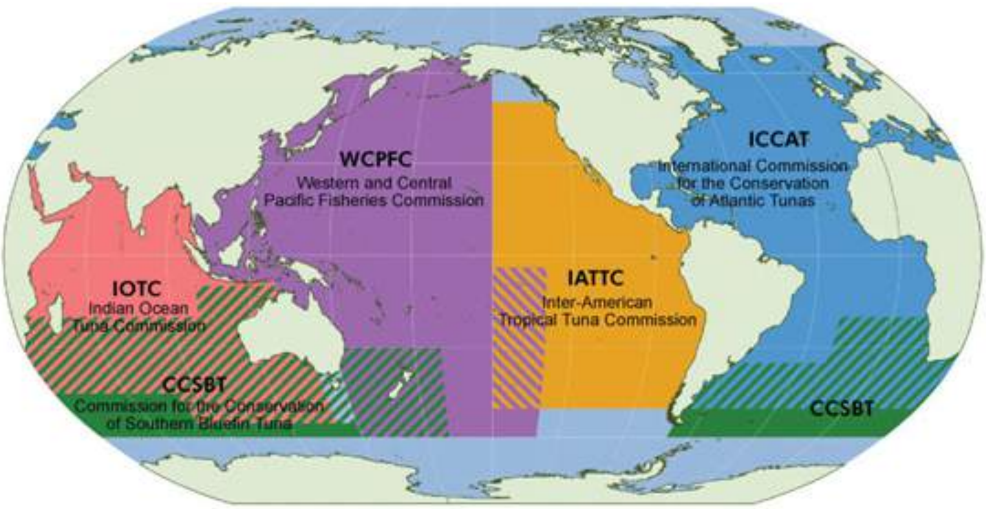
Chapter 2

Banning is not enough: The complexities of oceanic shark management by tuna regional fisheries management organizations



Source: FAO

Abstract

Recently, declining populations of several pelagic shark species have led to global conservation concerns surrounding this group. As a result, a series of species-specific banning measures have been implemented by Regional Fishery Management Organizations (RFMOs) in charge of tuna fisheries, which include retention bans, finning bans and trading bans. There are both positive and negative aspects to most management measures, but generally, the positive aspects outweigh the negatives, ensuring the measure is beneficial to the resource and its users in the long term. Banning measures are a good first step towards the conservation of pelagic shark species, especially since they improve conservation awareness among fishers, managers and the public. Measures that impose total bans, however, can lead to negative impacts that may jeopardize the populations they were intended to protect. The majority of pelagic shark catches are incidental and most sharks die before they reach the vessel or after they are released. The legislation set out by RFMOs only prevents retention but not the actual capture or the mortality that may occur as a result. Managers should be fully aware that the development and implementation of mitigation measures are critical for a more effective conservation strategy.

1. Introduction

As populations of highly migratory species decline due to over-exploitation or other human induced causes, management measures are often implemented to aid their conservation and restore populations to pre-existing levels (Hoffmann et al., 2010). Such measures have a variety of forms, typically linked to the level of concern surrounding the population in question. Generally, as concerns become increasingly severe, management measures follow suit and often conclude with total bans on harvesting and global trade of a species. While these measures are generally believed to aid in species conservation, they can, at times, lead to increased pressure on the population at risk (Rivalan et al., 2007).

Recently, declining populations of several pelagic shark species have led to global conservation concerns surrounding this group (Fowler et al., 2005; Dulvy et al., 2008; Aires-da-Silva and Gallucci, 2008; Cortés et al., 2010). These sharks are both targeted and taken incidentally as bycatch by a range of fleets from coastal artisanal to industrial vessels operating in distant waters (Bonfil, 1994; Wormet al., 2013). An inherent issue with exploitation of elasmobranch species, as compared to their teleost counterparts, is their low rebound capacity resulting directly from their characteristic life history traits of slow growth, late maturation and low fecundity (Cortés, 2000). As such, this group is generally far more vulnerable to overfishing than teleost fish species (Musick et al., 2002; Compagno et al., 2005).

With the increasing conservation concern over this sensitive group, a series of species-specific banning measures have recently been established by Regional Fishery Management Organizations (RFMOs) responsible for the management of tuna fisheries. These measures include retention bans, finning bans and trading bans. There are both positive and negative aspects to most management measures, but generally, the positive aspects outweigh the negatives ensuring the measure is beneficial to the resource and its users in the long term. Management measures based on retention, finning or trading bans are no different. Here we highlight both the benefits and drawbacks of such measures, in order to assess their overall efficacy and long-term benefit to populations.

2. Banning measures

Fisheries that target widely distributed and highly migratory species are managed by international commissions, of which cooperating countries/parties are members. There are five such commissions (RFMOs) that regulate the world's tuna fisheries, each with jurisdiction over an ocean/ocean region or target species: the International Commission for the Conservation of Atlantic tuna (ICCAT), the Indian Ocean Tuna Commission (IOTC), the Western and Central Pacific Fisheries Commission (WCPFC), the Inter-American Tropical Tuna Commission (IATTC), overseeing fishery activity in the eastern Pacific Ocean, and the Commission for the Conservation of Southern Bluefin Tuna (CCSBT), overseeing all fisheries targeting southern bluefin tuna (*Thunnus macoyii*). Aside from tuna species, these RFMOs are also usually responsible for the management of any other species caught in association with tuna fisheries. Management measures generally stem from the results of annual stock assessments and the advice from scientific committees linked to RFMOs. These measures are set out in the form of recommendations or resolutions, which contracting parties are then required to implement and report upon.

To date, several species-specific management measures have been developed under the tuna RFMOs that pertain to the incidental capture of pelagic sharks. These measures are hereafter referred to as banning measures. Generally, they stipulate that all contracting parties shall prohibit retention, transshipment, landing or storing any part, or whole carcass, of the species in question. Additionally, some of these measures require captured sharks to be promptly released unharmed and/or further state that trading, selling or offering for sale is also prohibited (Table 1). As a result, oceanic whitetip (*Carcharhinus longimanus*), silky (*C. falciformis*), thresher (*Alopias* spp.) and hammerhead (*Sphyrna* spp.) sharks fall under such resolutions in at least one ocean (Table 1). These measures were all developed fairly recently by tuna RFMOs (2010–2013). The oceanic whitetip shark is the only species covered by such measures across all oceans.

In addition to RFMO management measures, international treaties also regulate the trade of certain marine species. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) is one such treaty and plays an important role in managing wildlife. CITES represents an international agreement among governments that aims to ensure that international trade of wild fauna and flora does not threaten their survival. In accordance with this convention, the international trade of specified species can either be closely controlled (species listed on appendix II) or completely banned (appendix I), depending on its population status or vulnerability. During the most recent meeting of CITES (March 2013), the oceanic whitetip and hammerhead sharks were included in appendix II (CoP16 Prop. 42 and 43), requiring their international trade to be closely controlled.

Table 1. Pelagic shark species currently under banning measures on tuna RFMOs.

		SHARK SPECIES				
		oceanic whitetip	silky	bigeye thresher	thresher spp.	hammerhead spp.*
ICCAT	Retain	X	X	X		X
	Fin	X	X	X		X
	Trade	X		X		X
	Release		X	X		X
	REF	Rec.10-07	Rec.11-08	Rec.09-07		Rec.10-08
IOTC	Retain	X			X	
	Fin	X			X	
	Trade				X	
	Release	X			X	
	REF	Res.13-06			Res.12-09	
WCPFC	Retain	X	X			
	Fin	X	X			
	Trade					
	Release	X	X			
	REF	CMM 11-04	CMM 13-08			
IATTC	Retain	X				
	Fin	X				
	Trade	X				
	Release	X				
	REF	Res.11-10				

* The hammerhead shark species *Sphyrna tiburo* is excluded from this measure.

3. In what scenario can banning measures be effective?

Banning the retention and trade of pelagic sharks can drastically decrease their fishing mortality in fisheries where they are directly targeted. Essentially, the aim of these measures is to give the stocks the opportunity to recover to pre-exploitation levels. It is well known, however, that the great majority of pelagic shark mortality results from their incidental capture in high-seas pelagic longlines, gillnets and purse seine fisheries that primarily target tuna and tuna-like species

(Gilman et al., 2008; Bonfil, 1994). Nevertheless, sharks are undeniably considered a valuable bycatch in many fleets and are increasingly becoming a target as well (Hareide et al., 2007). The implementation of banning measures in these fisheries not only encourages fishers to modify their current practices, but also prevents these species from shifting from an incidental catch to a specific target.

An increasing number of marine populations are showing signs of recovery after an advance on conservation efforts, especially through measures that ban trade or any exploitation activity (Lotze et al., 2011). Marine mammals represent the group with the greatest results in terms of conservation success for this ecosystem. A recent study has shown that 42% of 92 spatially non-overlapping marine mammal populations are significantly increasing as a result of measures that ban their exploitation and trade (Magera et al., 2013). Whales are, perhaps, the best example of this success. The banning regulations set by the International Whaling Commission (IWC) have reduced whale hunting dramatically and brought most exploited species out of extinction risk (Magera et al., 2013). Some humpback whale populations from the Southern Hemisphere are even expected to reach their estimated pre-whaling abundance levels over the next decade (Gales et al., 2011).

Such banning measures, however, can also bring unintended negative effects. By prohibiting their trade, the products from these species may develop into rare and luxurious commodities. This perceived rarity could lead to increased consumer demand, making their illegal trade highly profitable. In extreme cases, when demand is sufficiently high, the protected species could eventually be driven to extinction (Courchamp et al., 2006; Hall et al., 2008). There is strong evidence that demonstrates how moving a species to a more restrictive CITES appendix can lead to a drastic increase in its illegal trade (Rivalan et al., 2007). During the transition period, between initial announcement of such a measure and its final implementation into the legislation, trade volumes have been observed to increase up to 135% (Rivalan et al., 2007). Furthermore, the black market price of rhinoceros horn increased by more than 400% within 2 years of their listing under Appendix I (Rivalan et al., 2007).

Shark fins are highly valued and their trade is currently very profitable. The global value of this market ranges between approximately US$ 400 and 550 million per year (Clarke et al., 2007). Being a luxury commodity in Asian cuisine, these species could become highly vulnerable should their availability decrease. Fin traders generally distinguish the fins of different shark species (Clarke et al., 2006) and the rarity of a particular species could be capitalized upon, although consumers do not currently make that distinction. Owing to their large rounded shape and characteristic white marking (Compagno, 1984), the fins of the oceanic whitetip shark are among the easiest to identify (Clarke et al., 2006), meaning its vulnerability could increase to dangerous levels should their rarity become an attractive quality. Additionally, in light of the multitude of conservation regulations set forth for this species of late, awareness regarding its threatened status has clearly increased. Once considered amongst the most abundant oceanic sharks, the oceanic whitetip is now commonly perceived as rare and there is a wide consensus that populations are decreasing (Baum and Blanchard, 2010; Clarke et al., 2012; Rice and Harley, 2012). Although future scenarios are difficult to predict, it seems that many of the rarity-associated black market factors described above are possible for this shark species, especially in light of the global ban on its retention in pelagic fisheries under tuna RFMO management.

4. In what scenario are banning measures not enough?

As stated above, pelagic shark mortality is primarily due to their incidental capture in high seas fisheries as a result of the shared habitat of pelagic sharks and tunas. Since retention and trade are banned but not the actual capture, banning measures in their current form will have little impact on Fisher-behavior. As such, capture rates are unlikely to change. While mortality rates are both gear and species specific (Skomal, 2007; Campana et al., 2009; Clarke et al., 2013), they are often high as a large portion of incidentally caught sharks are already dead/dying by the time they reach the vessel or after release (Rogan and Mackey, 2007; Poisson et al., 2014a; Hutchinson et al., 2015).

In the case of the tropical tuna purse seine fishery, the conditions in the sack of the net creates a highly stressful environment, with low oxygen levels and increased temperatures, which directly affect the mortality of the catch (Hall and Roman, 2013). Subsequently, the brailing process further reduces the chances of survival as sharks are compressed between the 2 and 8 tons of tuna in the brail (scoop net used to load the catch onboard the seiner). Brailed silky sharks were found to have an overall mortality rate of 85%, including the ones that appeared to be in relatively good condition upon release (Poisson et al., 2014a; Hutchinson et al., 2015). Scalloped hammerhead sharks exhibited one of the lowest survival rates compared to other pelagic sharks when caught on pelagic longlines (Gallagher et al., 2014). The authors considered that the incidental capture of this species in tuna longline fisheries played an important role in the substantial population decline reported for the Northwest Atlantic (Baum et al., 2003).

While it is true that species with high rates of live caught individuals as well as post release survival could benefit from banning measures, in cases similar to the silky and scalloped hammerhead sharks the outcome of these measures alone would be rendered biologically ineffective for the recovery of the stocks. Furthermore, should illegal trade prices be sufficiently high, fishers may be willing to take the risk of prosecution and retain the sharks (or their fins) for commercialization.

The complication associated with the mixed capture of target and bycatch species preclude banning measures from being the final solution for curbing mortality and aiding the recovery of pelagic shark stocks. However, this does not mean that these measures provide no benefits. Whenever a banning measure is established, it directly implies that the population concerned is under severe threat. As such, the establishment of a ban indirectly results in improved public awareness regarding the species' conservation risk and that extreme action is required for its protection. Essentially, such bans can act as an awareness campaign to alert fishers and consumers who play a crucial role in conservation. In 1990, following strong media pressure regarding the mortality of dolphins in the eastern Pacific Ocean by tuna purse seine fisheries, the US Congress approved the Dolphin Protection Consumer Information Act establishing the use of a ''dolphin safe'' label on tuna cans which contained tuna not caught in association with dolphins (Joseph, 1994). A market analysis showed that media pressure and subsequent implementation of dolphin-safe labeling affected consumer behavior (Teisl et al., 2002), providing an insight in how public awareness can be a useful tool for wildlife conservation. This public pressure led to the development of a mitigation technique, the backdown process, where the seiner is put into reverse elongating the net and causing the cork line to sink at one extremity. This maneuver allows dolphins to safely swim away over the sunken corks. Thanks to the backdown process, fishers can still target tuna schools associated with dolphins. The technique is mandatory for tuna purse seiners fishing in the eastern Pacific Ocean (IATTC) and its compliance is controlled thanks to the presence of onboard observers.

Pelagic shark populations could benefit significantly from an increase in public awareness. In the not too distant past, sharks were seen as little more than a threat to humans. Although this perception is slowly changing (Simpfendorfer et al., 2011), the need for continued efforts to raise public awareness regarding conservation requirements is essential and the establishment of species specific bans will aid in this effort.

5. Potential solutions

The incidental nature of shark catches in tuna fisheries worldwide suggest that mitigation measures are an essential tool for an effective conservation strategy. A set of integrated measures will more effectively aid in the conservation and recovery of threatened pelagic sharks than banning measures alone. These measures should mainly include: (1) the development of alternative fishing techniques; and (2) the reduction of fishing effort, e.g. developing spatial or temporal management measures such as closed areas/seasons.

Developing techniques that prevent the capture of pelagic sharks is critical. Gear modifications have been proved effective in reducing capture and mortality of some bycatch species, such as dolphins, seabirds and marine turtles (Coe et al., 1984; Gilman et al., 2006; Løkkeborg, 2011; Andraka et al., 2013). Gear modifications to mitigate pelagic sharks capture represent a real challenge as their distributions and behavior have strong similarities to that of targeted species. However, some techniques that have been proposed could be investigated further. Fishing gears with the highest incidence of incidentally caught sharks are gillnets, pelagic longlines and purse seiners. Gillnets together with longlines are responsible for the greatest impacts, but very little research has been done to develop mitigation methods to reduce shark bycatch in this fishing gear (Oliver et al., 2015). More research has been conducted on longline and purse seine gear.

In pelagic longline fisheries, epipelagic species, such as the oceanic whitetip shark, could benefit from the removal of shallow hooks (Tolotti et al., 2013). This simple measure has been shown to reduce the capture of several bycatch species, while also increasing the number of hooks available for the target species (Kitchell et al., 2004; Beverly et al., 2009; Watson and Bigelow, 2014). Rare earth metals are a potential tool to mitigate shark bycatch, as they can work as a repellent due to the strong electric field they produce the in water (Stroud, 2007). Much research is still required, however, as this method seems highly complex and results can be conflicting as well as species specific (Stoner and Kaimmer, 2008; Robbins et al., 2011; Hutchinson et al., 2012; Godin et al., 2013). To

To reduce the fishery induced mortality of pelagic sharks caught by tropical tuna purse seiners, it is imperative to direct research efforts at finding ways to release them before the retrieval of the net or to attract them away from the tuna aggregation before the net is set. A natural segregation between sharks and tuna inside the net has been repeatedly observed, which could allow for the establishment of a release system (Itano et al., 2012). Preliminary tests were conducted in the Western Pacific ocean and scientists believe this mitigation measure has potential (Itano et al., 2012).

Another relevant issue with purse seine fisheries that has recently been brought to light is the exceptionally high rate of silky sharks becoming entangled on the nets hanging below fish aggregating devices (Filmalter et al., 2013). The construction of such devices should be controlled and the use of nets needs to be banned. In fact, several RFMOs have recently adopted recommendations in this regard, which stipulate that the use of netting in the construction of fish aggregating devices should be avoided (ex.: IATTC Res.13-04, IOTC Res.13-08).

The handling of sharks after capture plays an important role in the survival rate of released individuals. To increase their chances of survival, best handling practices guides need to be developed for each fishery (see Poisson et al., 2014b as an example). Naturally, the development of such guides has to be paired with post release survival studies. Investigating post-release mortality is also an essential part when assessing the efficacy of banning measures and, although costly, require significant research attention. Once best practices guides are developed, incentives or disincentives should be promoted in order to facilitate the adoption of good practices by fishers. Market related incentives, such as eco-labels, could be an encouraging tool (ex. MSC certification and ISSF PVR).

Time area closures have helped the recovery of stocks of a variety of species, from marine invertebrates, such as mollusks, to teleost fishes (Lester et al., 2009; Roberts, 2012; Kerwath et al., 2013). Although most of the successful experiences come from coastal fisheries, positive results encourage the investigation of implementing such measures for pelagic sharks. The great challenge with pelagic time area closures resides on the high mobility of pelagic species and on the lack of data concerning this complex ecosystem (Game et al., 2009). This means that the protected area would have to have exaggerated proportions or target smaller areas where fishing activities would provoke higher impacts, such as nurseries and/or spawning zones (Kaplan et al., 2010). Considering the high cost of enforcement, a targeted time area closure seems more feasible. Watson et al. (2008) found some promising results regarding silky shark bycatch in the Eastern Pacific Ocean tuna fishery. The authors found that juveniles silky sharks are mostly concentrated north of the equator and estimated that area closures could have reduced up to 33% of the species bycatch while compromising only 12% of the tuna catch. A similar hotspot of juvenile silky sharks has also been identified in the Indian Ocean and authors noted that this area does not overlap with the highest catch per unit of effort area of the purse seine fisheries (Amandè et al., 2011).

Finally, monitoring is key for any successful management system. There is a history of poor reporting of shark catches, largely due to their incidental nature (Bonfil, 1994; Camhi et al., 2008; Clarke, 2013; Oliver et al., 2015). Despite improvements in recent years (FAO, 2014), notably due to RFMO requirements to report shark bycatch (ex. ICCAT Rec.04- 10), a banning measure may jeopardize this trend. Under these regulations captains may be inclined not to report the capture of a banned species at all as to avoid repercussions, especially if they have the intention of illegal commercialization. The current low coverage level of independent observers in most high seas fisheries makes this scenario particularly concerning (Worm et al., 2013).

Data deficiency is a paramount issue for fisheries management, as stock assessment methods rely largely on catch and effort time series data (Barker and Schleussel, 2005). To date, only a handful of stock assessments have been conducted for pelagic sharks (ICCAT, 2009; Rice and Harley, 2012, 2013). Additionally, the results of these assessments are usually interpreted with considerable caution due to the data deficiencies and the resulting high level of uncertainty of the assessments (Cortés et al., 2010). Until every vessel exploiting the high seas has some form of independent observer or observation system onboard, the reliability of such data will remain questionable. Standardized fisheries independent surveys could be a simple solution to overcoming this issue. Electronic observation systems still have limitations, especially regarding bycatch identification, but promising results indicate this system could also be a useful tool to improve both monitoring and data collection (Ames et al., 2007; Ruiz et al., 2014)

6. Final remarks

The problem faced in pelagic shark management is a direct result of the way fishermen catch their fish in an environment shared by target and bycatch species. The current fishing methods are not selective enough to avoid catching sharks. Banning measures in their present form do little to discourage the incidental capture of sharks and are unlikely to be effective enough, even with an increase in release numbers, to rebuild stocks. Banning measures are one form of management, but cannot be the only one applied. They are a positive initial step towards the conservation of endangered shark species. They act on a precautionary approach basis and also improve conservation awareness among fishers, managers and the general public.

Banning measures can provide positive outcomes to the conservation of pelagic sharks, but their effectiveness is directly linked to whether the species at issue is the target of the fisheries or a bycatch component (Fig. 1). For fisheries where sharks are bycatch, the banning measure would imperatively need to be accompanied by (i) high observer coverage and (ii) mitigation measures. Viewing banning measures as a final solution could result in lowered research incentives and hamper the further development of appropriate mitigation measures. Furthermore, without high observer coverage, such a measure could lead to less catch data, therefore less monitoring of the impacts of fisheries on these species, and less opportunities to improve our knowledge on the biology of these species at risk. We consider that the implementation of high observer coverage is urgent, especially on longline fisheries, as well as the adoption of measures that can reduce the fishing mortality of sharks by avoiding their catch and increasing their survival after release.

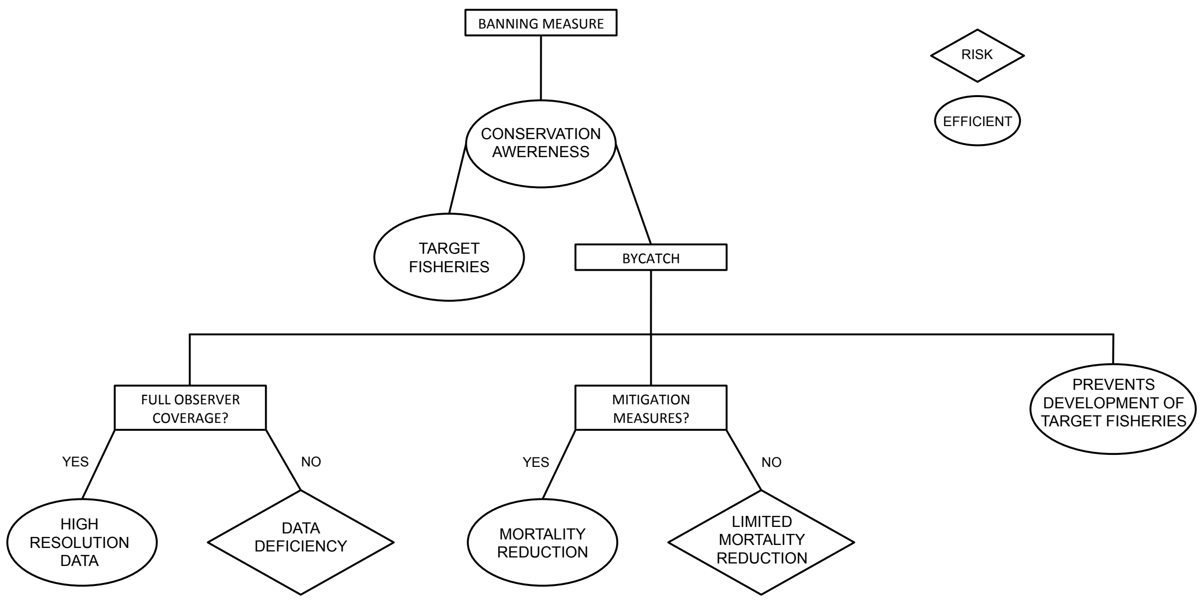


Figure 1. Flow chart depicting the different scenarios where the banning measures can be effective or generate risks.

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Chapter 3

Size, distribution and catch rates of the oceanic whitetip shark caught by the Brazilian tuna longline fleet

Abstract

Catch and effort data from 14,835 longline sets conducted by foreign tuna longline vessels chartered by Brazil, from 2004 to 2010, were analyzed aiming at assessing the size, distribution and the relative abundance of the oceanic whitetip shark (*Carcharhinus longimanus*) in the southwestern and equatorial Atlantic Ocean. The nominal catch per unit of effort (CPUE) exhibited a gradual increase, from 0.04 sharks/1000 hooks, in 2004, the first year of the time series, up to 0.13, in 2007. In 2008, however, the CPUE increased sharply, reaching 0.43, dropping, then, back to 0.15, in 2010. A CPUE standardization was performed using a delta-GLM approach, but the standardized index of abundance did not differ significantly from the nominal CPUE. The models indicated that the catches of oceanic whitetip sharks are higher for the Spanish fishing strategy, which is characterized by the deployment of hooks at shallower depths. These results indicate that the use of deep longline hooks (>100 m) may help to mitigate the bycatch of this species.

1. Introduction

The oceanic whitetip shark (*Carcharhinus longimanus*) is a circumtropical species known as one of the main pelagic sharks worldwide (Bonfil et al., 2008; Compagno, 1984), being caught as a bycatch by a variety of pelagic fishing gears, such as tuna and swordfish pelagic longlines, pelagic gillnets, and, to a lesser extent, tuna purse seines (Amande et al., 2011; Bonfil, 1994). It is easily distinguishable from the other species of the Carcharhinidae family by the round shape of its long pectoral and dorsal fins, as well as by the white stains in their margins (Compagno, 1984). Their large fins are highly valued in international trade and make them a target of this market.

Inadequate monitoring makes the estimates of their populations very difficult but there is a general consensus that populations are decreasing (Baum et al., 2006). This species is listed vulnerable by IUCN worldwide and even critically endangered in the northwest and western central Atlantic Ocean. Consequently, conservation and management actions are urgently required for this species. The

International Commission for the Conservation of Atlantic Tunas (ICCAT) has recently decided to ban the landing, storing, and selling of this species in the Atlantic Ocean (Rec. 10-07). Similar measures were adopted in the Pacific Ocean by the Inter American Tropical Tuna Commission (IATTC Rec. C-11-10) and the Western and Central Pacific Fisheries Commission (WCPFC CMM 11-04).

Despite its worldwide distribution and frequent catches in most pelagic fisheries (Bonfil, 1994) little has been published on the species biology and ecology. Some general studies, including diet, reproduction and behavior of the oceanic whitetip shark were conducted in the western North Atlantic and in the eastern Pacific Ocean, more than fifty years ago (Backus et al., 1956; Strasburg, 1958). Since then, however, very little was added to the knowledge on the species until the past decade when new data from the South Atlantic was published by Lessa et al. (1999a,b), Domingo et al. (2007) and Coelho et al. (2009).

Most of the information available for the South Atlantic, however, is related to biological aspects (morphometry, reproduction, age and growth), with very little known in relation to its spatial distribution and relative abundance. The present study analyses data from foreign tuna longline fleets chartered by Brazil, with the goal to assess distribution, catch rates and size composition of the oceanic whitetip shark in the southwestern and equatorial Atlantic Ocean in order to fill gaps on species knowledge and to help define appropriate measures for their conservation.

2. Material and methods

Catch and effort data from 14,835 longline sets conducted by foreign tuna longline vessels chartered by Brazil, from 2004 to 2010 were analyzed. Longline sets were distributed in a wide area of the equatorial and southwestern Atlantic Ocean, ranging from 10°N to 35°S and from 007°E to 045°W. Data were obtained from logbooks filled out by on-board observers of the Brazilian National Observer Program. Logbooks contained information on the number of hooks, the number of fish caught, by species, and the geographic position at the beginning of each set.

The Brazilian National Observer Program aims to collect precise information on fishing strategy, catch composition and biological samples from catches taken by foreign vessels chartered by Brazil. In this study, logbook information was obtained from the chartered fleet operating off northeast Brazil for which there is 100% observer coverage. These chartered vessels make up for approximately 30% of the whole foreign and Brazilian longline fleet and almost 60% of the fleet based in the northeast.

During the period analyzed, six different flags were active: Spain, Panama, Morocco, United Kingdom, Honduras, and Portugal. However, they can be divided into two distinct fishing strategies, Spanish and Japanese. The first (Spain, Morocco, Honduras and United Kingdom) aims for swordfish and operates during the night with surface longlines (down to 100 m) using light attraction and squid as bait. The latter (Panama and Portugal) aims for tuna species and operates early in the morning with deep longlines (down to more than 200 m) using small pelagic fish as bait (mainly mackerel).

Nominal catch per unit of effort (CPUE) was calculated as the number of sharks/1000 hooks by year and by quarters (years combined). For the spatial distribution of the CPUE the catch and effort data were grouped into 5°×5° squares of latitude and longitude. In this case, the CPUE was calculated by the sum of all catch and all effort in each square. Information regarding discards of this species were not available, thus CPUE was calculated based only in the retained catches.

In order to account for the possible influences of seasonality, area and fishing strategy on CPUE annual variability, a standardization was performed assuming negative binomial and delta-lognormal distributions. The evaluation of residual plots indicated that the delta-lognormal outperformed the negative binomial model and therefore the delta-lognormal was chosen as the preferred model. In the delta-GLM approach the presence–absence (PA) of fish in the data set was modeled assuming a binomial distribution, while the proportion of positive catches (POS) was modeled assuming a lognormal distribution. Year, fishing flag and quarter, expressed as categorical variables, and the interaction between latitude and longitude, expressed as continuous variables, were used as explanatory variables for both presence–absence and positive catch models. Fishing flag was represented by two categories: Japanese (JAP) and Spanish (ESP). These were defined based on the two configurations of fishing gear employed by the fleet analyzed in this study. The indices per year for these two models were multiplied in order to obtain the overall index of abundance. Confidence intervals for the overall index of abundance were calculated using the delta method (Lo et al., 1992).

From 2005, additional data on sex, total length (TL), fork length (FL) and inter-dorsal (ID) length were also collected. All lengths were obtained by laying the fish on the deck and measuring it in a straight line. Whenever the TL was not available, the FL and the ID were converted to TL by linear regressions estimated with the available data from the present research (Table 1). A total of 1612 individuals were measured, representing 64% of the oceanic whitetip sharks caught (2491) and 1218 were sexed. For the spatial analysis, the mean length was calculated for each 5°× 5° square. Squares were excluded from the spatial analysis if the number of fish measured was less than five. To test the possibility of spatial segregation by sex a chi-squared test of independence was performed through a contingence table with the counts of males and females divided into three areas (north, central and south). A chi-squared goodness-of-fit test was also performed to test the 1:1

sex ratio hypothesis. Both statistical tests were performed at 0.05 significance level.

Table 1. Length conversion equations for the oceanic whitetip shark estimated by linear regressions with data collected in the scope of the Brazilian National Observer Program.

Equations	R^2	n	Standard deviation (0.95)	
			a	b
TL=3.42207*ID+27.39642	0.8064	898	0.05602	1.78851
TL=1.13477*FL+12.53738	0.9067	374	0.01887	2.37455

TL = total length; ID = inter-dorsal length; FL = fork length

3. Results and discussion

Fishing effort peaked in 2005, when about 8 million hooks were deployed, almost double from the previous year. Since 2005, the number of hooks exhibited a declining trend, until 2010 the last year included in the series when about only 1 million hooks were deployed (Figure 1). The Japanese fishing strategy was the most common whereas the Spanish strategy was dominant in 2006 and 2007. During the last three years of the time series the Japanese strategy was completely absent.

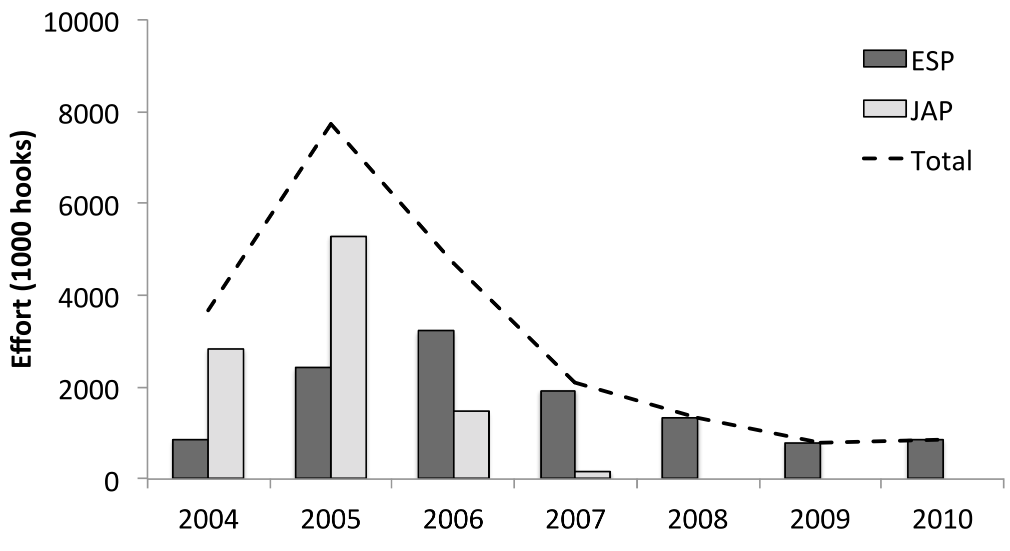

Figure 1. Annual effort, total and by fishing strategy, of foreign tuna longline vessels chartered by Brazil operating in the equatorial and southwestern Atlantic Ocean.

The spatial distribution of the fishing effort also varied throughout the period, with 2005 showing the greatest spatial coverage, naturally due to the higher number of hooks deployed that year. All active flags operated in similar areas, although vessels fishing with the Spanish strategy represented a broader range and also operated more southward (Figure 2).

The area with the highest concentration of effort was located between the latitudes of 5°N and 5°S (Figure 2). Oceanic islands, such as the archipelago of Saint Peter and Saint Paul, Fernando de Noronha Island and Rocas Atoll, as well as several seamounts, pertaining to the North Brazil Chain and to the Fernando de Noronha Chain, present in that area, are considered to be important fishing grounds for tuna and tuna-like species off northeast Brazil (Hazin, 1993). Important fishing grounds are located at a rather short distance from the ports where the longliners were based (Natal-RN, Recife-PE and Cabedelo-PB). Another important fishing area is located further south, near the seamounts and islands of the Vitoria–Trindade Chain.

The nominal catch per unit of effort (CPUE) for the oceanic whitetip shark exhibited a gradual increase, from 0.04 sharks/1000 hooks, in 2004, the first year of the time series, up to 0.13, in 2007. In 2008, however, the CPUE increased sharply, reaching 0.43, dropping, then, back to 0.15, in 2010. The standardized index of abundance did not differ markedly from the nominal CPUE index (Figure 3). This fact could indicate that the nominal CPUE is a good proxy for the overall index of abundance for this species or that the standardization was not efficient in accounting for the factors that affected CPUE but were not related to abundance. It is possible that the CPUE standardization was compromised due to the low number of years in the data series and the lack of a homogeneous distribution of fishing effort and fishing strategy across the areas, years and quarters.

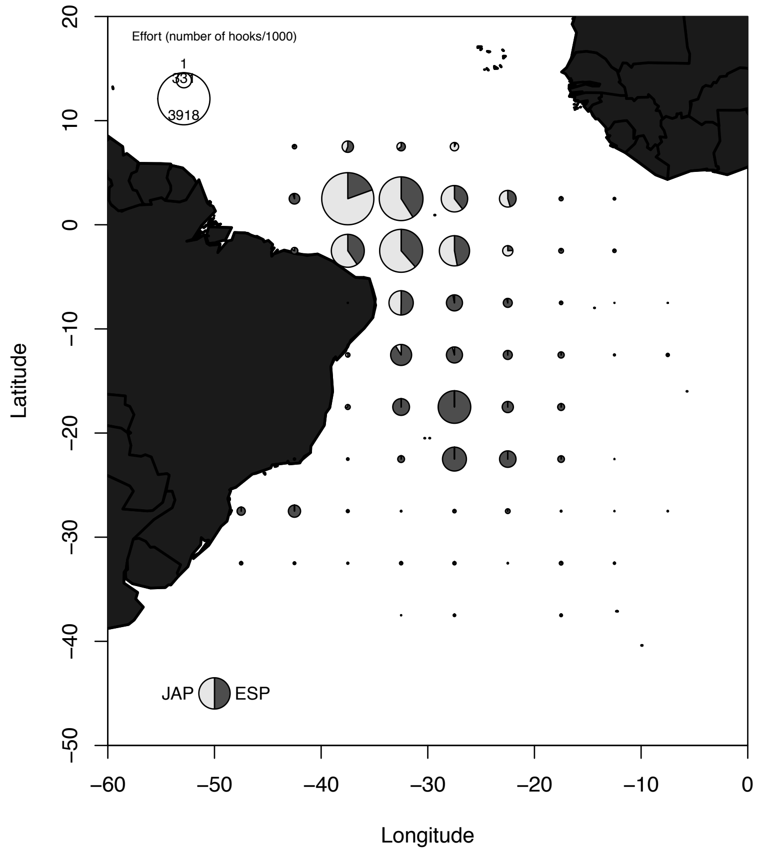

Figure 2. Distribution of the effort by fishing strategy of foreign tuna longline vessels chartered by Brazil from 2004 to 2010.

For the presence–absence portion of the delta-GLM, years, quarters and strategy were the most significant factors, whereas for the positive catches portion of the model the order of relative importance of those variables changed to strategy, years and quarters. The parameter estimates associated with the presence–absence and positive catch models show which variables were significant for each model and in which direction the factors affect the index. For the presence–absence model, all years had positive estimates in relation to 2004, meaning that those years had a positive effect in the presence of oceanic whitetip shark. However, all years had negative estimates for the positive catch model, meaning that years had a negative effect on CPUE values. In summary, it appears that the fish was more frequently encountered but at lower numbers with time. The fishing strategy was the only factor found to be significant for both presence–absence and positive catch models, with the Japanese fishing strategy showing a negative effect for both, indicating that the catches of oceanic whitetip are higher for the

Spanish fishing strategy which is characterized by the deployment of hooks at shallower depth (Tables 2 and 3). This relationship is in agreement with the described preference of this shark for near-surface waters (Musyl et al., 2011) and with the results obtained by Bromhead et al. (2012) showing that the oceanic whitetip is caught in higher numbers when hooks are set at a shallower depths.

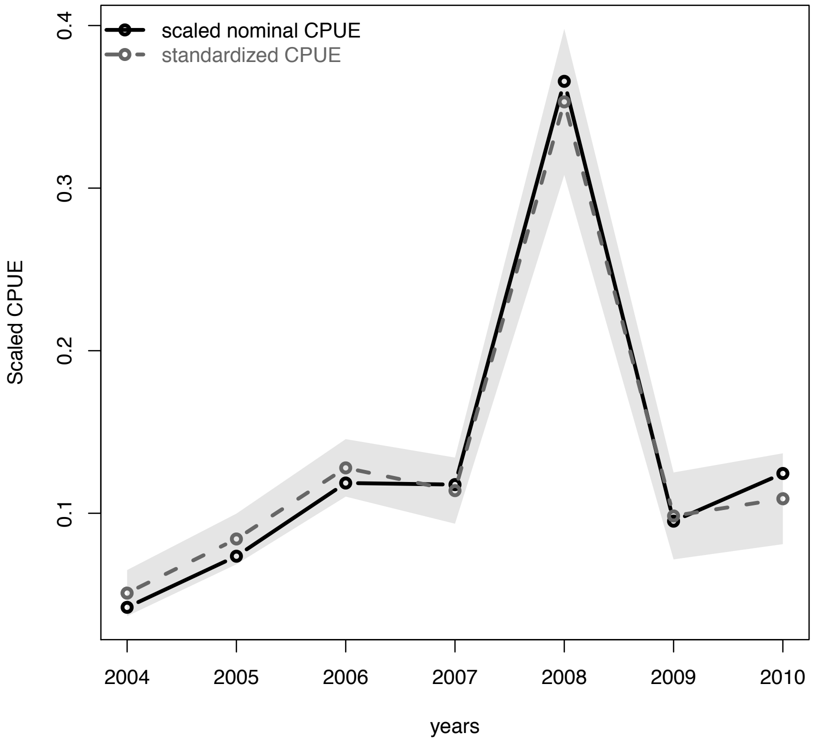

Figure 3. Nominal and standardized CPUE (per 1000 hooks) for oceanic whitetip sharks caught by foreign tuna longline vessels chartered by Brazil operating in the equatorial and southwestern Atlantic Ocean. The shaded gray area represents the confidence intervals.

The spatial distribution of the CPUE by year (Figure 4) shows that, in 2004, the number of zero catches was very high, with positive catches being only recorded between the latitudes of 10°N and 5°S, and CPUE values ranging from 0.01 to 0.07 sharks/1000 hooks. From 2005, positive catches were recorded more southward (up to 30°S) and eastward (up to 10°W), than in 2004. High CPUE values (>0.50), from 2005 to 2007, were recorded in the square from 10°S to 20°S and from 30°W to 40°W, with the only exception of a high value also recorded in 2006, close to the African coast (0–5°N; 10–15°W). In 2008, the year with the highest mean CPUE (0.43), the area with the highest catch rates expanded northwestward, extending from 5°S to 20°S and from 25°W to 40°W. During 2008, catches of oceanic whitetip shark were recorded in almost all 5° squares where there was effort. In 2009, the 5° square mean CPUE values became generally low again, with only one being above 0.50 located off north Brazil and close to the equator. During 2010, a high CPUE value reappeared in the square from 10°S to 20°S and from 30°W to 40°W.

Table 2. Coefficients estimates for presence–absence model for oceanic whitetip sharks.

Factor	Estimate	Std. Error	Pr(>|z|)	
Intercept	-3.16E+00	1.39E-01	2.00E-16	***
2005	5.78E-01	1.18E-01	1.07E-06	***
2006	1.13E+00	1.25E-01	2.00E-16	***
2007	9.85E-01	1.38E-01	9.15E-13	***
2008	2.33E+00	1.38E-01	2.00E-16	***
2009	8.95E-01	1.79E-01	5.60E-07	***
2010	1.01E+00	1.68E-01	1.97E-09	***
Apr-Jun	-1.85E-01	8.08E-02	0.02235	*
Jul-Sep	3.58E-01	7.90E-02	5.70E-06	***
Oct-Dec	2.07E-01	8.15E-02	0.01101	*
Strategy JAP	-2.65E-01	8.31E-02	0.00143	**
Latitude: Longitude	7.32E-05	1.04E-04	0.48144	

*** p-value = 0; ** p-value = 0.001; * p-value = 0.01

Table 3. Coefficients estimates for positive CPUE model for oceanic whitetip sharks.

Factor	Estimate	Std. Error	Pr(>|t|)	
Intercept	9.13E-02	6.80E-02	0.1793	
2005	-4.40E-02	5.91E-02	0.4568	
2006	-1.31E-01	6.16E-02	0.0331	*
2007	-1.14E-01	6.78E-02	0.0927	.
2008	-7.50E-02	6.51E-02	0.2493	
2009	-1.79E-01	8.52E-02	0.036	*
2010	-1.77E-01	8.20E-02	0.0307	*
Apr-Jun	6.35E-02	3.81E-02	0.0954	.
Jul-Sep	1.54E-01	3.65E-02	2.71E-05	***
Oct-Dec	3.70E-02	3.87E-02	0.3395	
Strategy JAP	-3.48E-01	4.17E-02	2.00E-16	***
Latitude: Longitude	3.03E-04	5.97E-05	4.44E-07	***

*** p-value = 0; ** p-value = 0.001; * p-value = 0.01

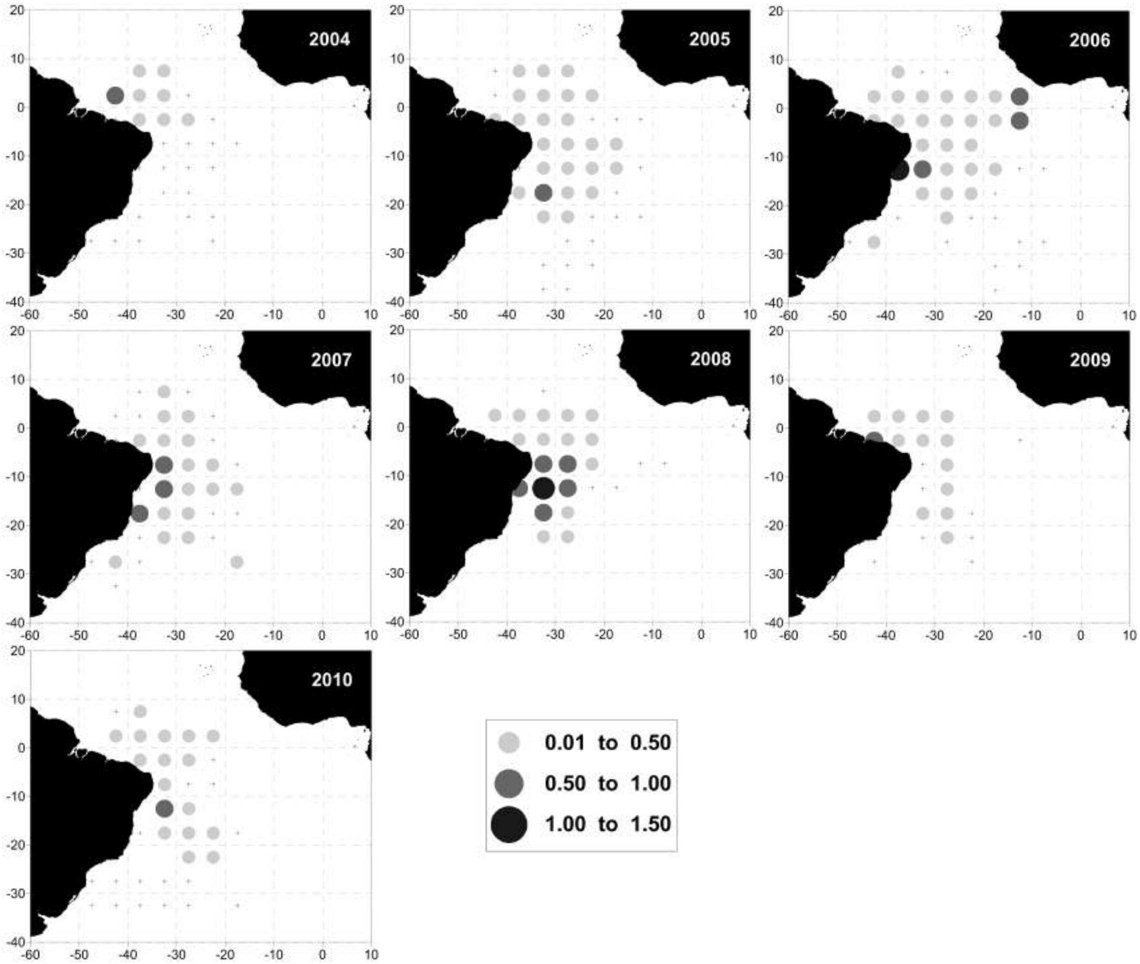

Figure 4. Annual distribution of CPUE (per 1000 hooks) of oceanic whitetip sharks caught by foreign tuna longline vessels chartered by Brazil from 2004 to 2010. Crosses represent squares with effort and zero catch

Domingo et al. (2007), analyzing data from the Uruguayan longline fleet, found the highest CPUE (0.49 sharks/1000 hooks) for the species in an area close to the one that showed the highest CPUE in the present study (around 20°S/35°W). Except from an apparent trend for the oceanic whitetip shark to move away from the Brazilian southeast coast in the fourth quarter of the year, the CPUE distribution by quarters (Figure 5) showed no clear pattern of seasonal change.

The proportion of the oceanic whitetip shark in relation to the total catch and in relation to the catches of elasmobranches were very low (Figure 6), 0.3% and 2.7%, respectively. The oceanic whitetip shark yearly proportion of the total catch did not exceed 0.4%, except for 2008, when it reached 1.4%. Its proportion in relation to the elasmobranch catches also showed a peak of 8.2% in 2008. In the remaining years this proportion ranged from 0.8% to 3.4%. These values are much lower than those observed by Lessa et al. (1999a), in an experimental survey of pelagic fishes conducted between 1992 and 1997 in the southwestern equatorial Atlantic, where the whitetip catches represented almost 30% of all elasmobranchs, being the second most abundant shark, outnumbered only by the blue shark (*Prionace glauca*).

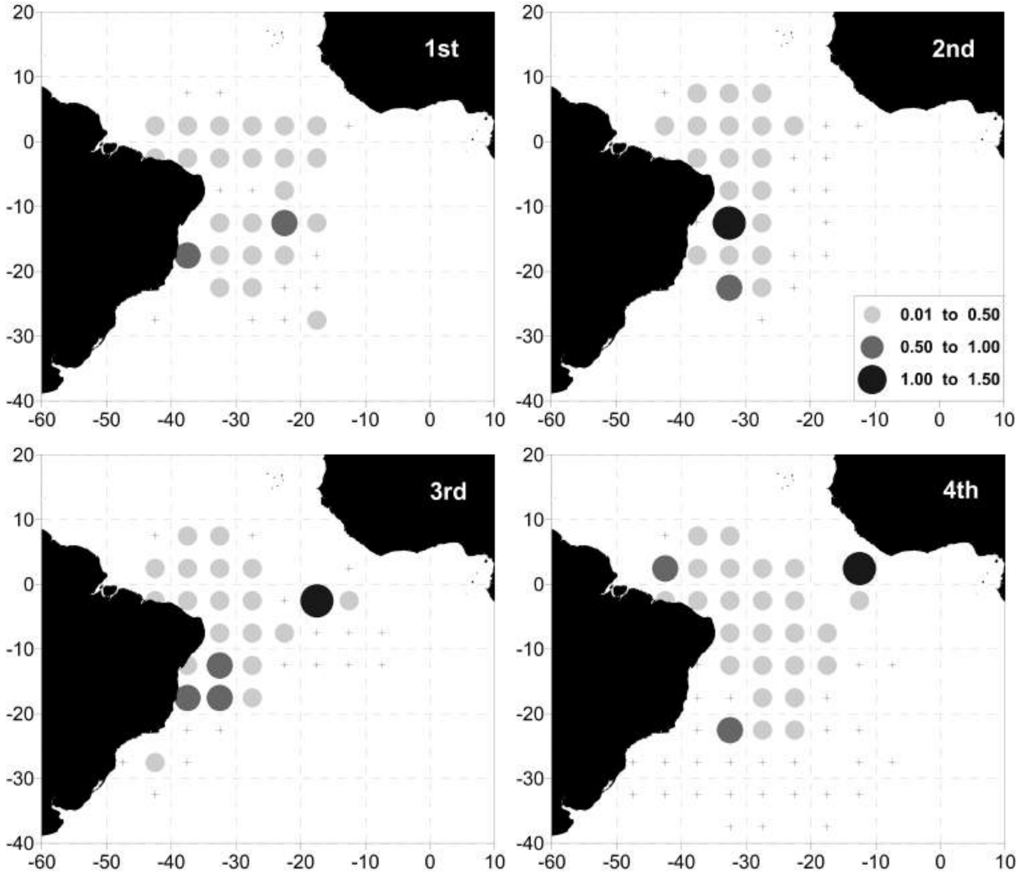

Figure 5. Quarterly distribution of CPUE (per 1000 hooks) of oceanic whitetip sharks caught by foreign tuna longline vessels chartered by Brazil from 2004 to 2010. Crosses represent squares with effort and zero catch.

The results, however, are not comparable, due to the operational differences in the fishing gear and methods used by the experimental and the commercial operations, the first ones having operated in much shallower layers, where the species is known to be much more frequently caught (Bromhead et al., 2012; Nakano et al., 1997). More recent results, obtained with the use of PSAT tags

(Pop-up satellite archival tags), have confirmed that this species is largely confined to the uniform temperature surface layer (Musyl et al., 2011). Off northwest Brazil the thermocline is as shallow as 50 m deep (Travassos et al., 1999).

Besides the depth of fishing, there are several other factors that may directly influence the catchability of a fish species in the longline fishery, thus altering the relationship between its catch rate (CPUE) and its actual abundance. Hazin et al. (1998), for instance, described marked fluctuations in the CPUE of several species, including the oceanic whitetip shark, over a period of many years, due to modifications in fishing strategy, such as changes on target species, discovery of new fishing grounds and introduction of new fishing technologies. Burgess et al. (2005), in turn, reported that the material of the branch line (nylon or steel), as well as the size, type and depth of the hook can greatly influence the catchability of shark species. They also indicated that market changes might modify the target species of the fishery, directly interfering, therefore, in the catchability of the species caught. In the present case, as well, the changes of CPUE over the years can probably be explained, at least in part, by changes in fishing strategies, especially related to longline configuration of the different flags that were active during the study period, as the models indicated.

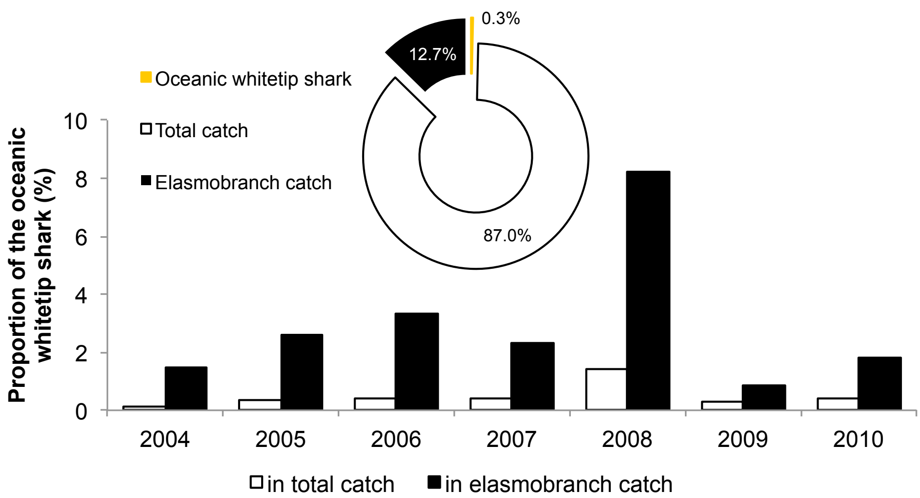

Figure 6. Proportion of oceanic whitetip shark in total and elasmobranch catches, from foreign tuna longline vessels chartered by Brazil operating in the equatorial and southwestern Atlantic Ocean from 2004 to 2010

The total length of the 1612 individuals measured ranged from 50 to 320 cm, in males, and from 50 to 311 cm, in females. The majority of males and females were between 100 and 180 cm TL (Figure 7), with 78% having less than 180 cm and were probably juvenile, according to Lessa et al. (1999b). Of the 1218 specimens sexed, 653 were female and 565 were male, resulting in a sex ratio of 1:0.86 (female: male) significantly different from 1:1 ($p = 0.0117$). These values were very close to those found by other studies carried out in the same area, although in most cases the sex ratio was not significantly different from 1:1 (Lessa et al., 1999a,b; Asano-Filho et al., 2004; García-Cortéz and Mejuto, 2002; Coelho et al., 2009). This could be explained by the much lower sample sizes of these studies.

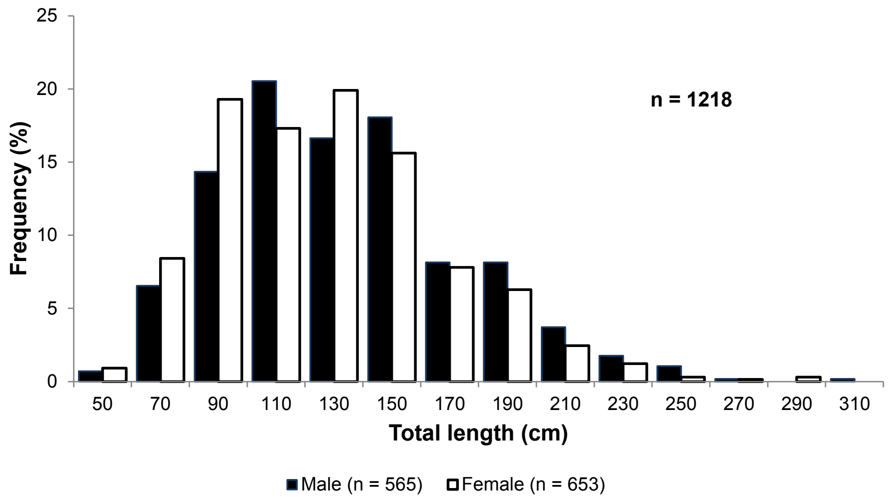

Figure 7. Length–frequency distribution of oceanic whitetip sharks caught in the southwestern equatorial Atlantic Ocean between 2005 and 2009.

Lessa et al. (1999b) suggested, based on a small individual caught with fresh umbilical scars, that the size at birth is around 70 cm TL. Coelho et al. (2009) found near-term embryos measuring 52 cm, and therefore hypothesized that the size at birth should be around 55 and 65 cm, as proposed by Compagno (1984). The three individuals measuring 50 cm TL found in the present work, however, indicate that the size at birth might be even smaller than previously reported.

Previous studies indicated that a geographical segregation by sex might occur for oceanic whitetip shark (Backus et al., 1956; Strasburg, 1958). In the present study the hypothesis of sex and area being independent was rejected ($p = 0.0409$), which could also indicate that a geographical segregation by sex might occur in the study area (Figure 8). The evidence for such segregation, however, is not very strong as the hypothesis of independence was only marginally rejected.

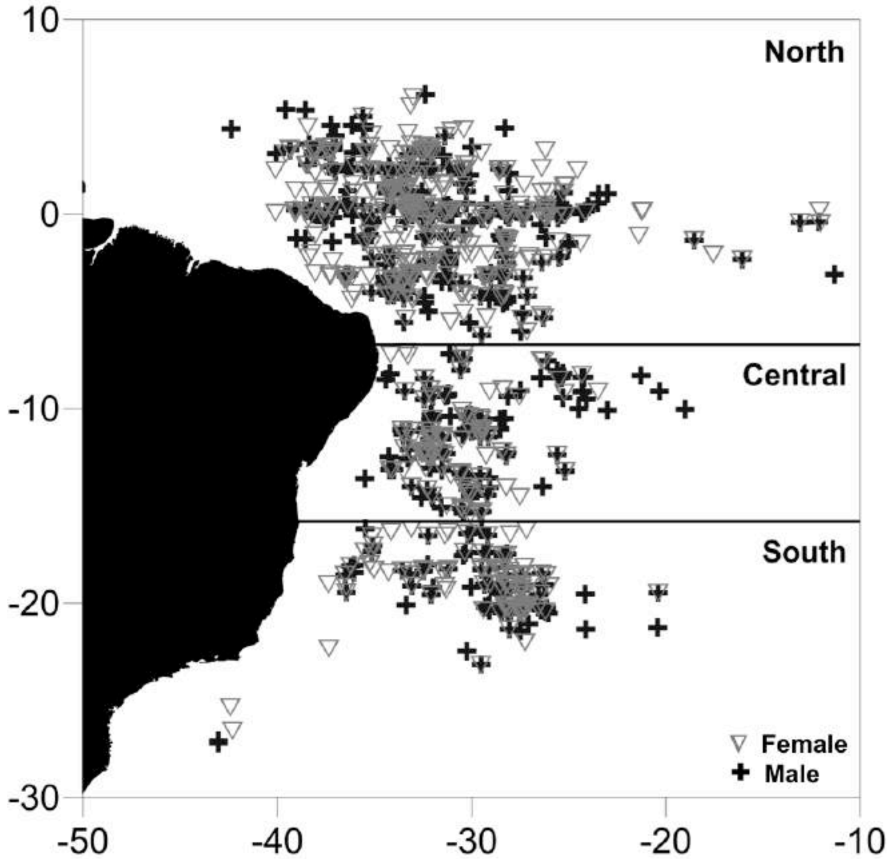

Figure 8. Spatial distribution of males and females oceanic whitetip sharks caught between 2005 and 2009.

Coelho et al. (2009) suggested that the high percentage of small individuals in the southwestern equatorial Atlantic, also found in the present work, might indicate segregation by size in the Atlantic Ocean. Alternatively, Lessa et al. (1999a and b) hypothesized that the large proportion of juveniles might be a result of continuous fishing pressure on the entire population. Nonetheless, in order to clarify this matter data from a much longer time series and a much broader geographical coverage of the Atlantic Ocean are necessary.

The spatial distribution of the 5° square mean lengths (Figure 9) shows a concentration of larger specimens from about 020°W to 035°W and from 5°S to 15°S. Another area of concentration of larger specimens seems to be present to the north of the equator and just off north of Brazil.

This study has shown the catch rates of the oceanic whitetip shark are very sensitive to changes in fishing strategy and gear, especially to those related with hook depth. It is also clear that the great majority of catches from this species in the southwestern equatorial Atlantic are composed of juveniles. These results indicate that efficient conservation measures need to be adopted and that mitigation methods, such as promoting deep hooks by longliners, should be particularly investigated.

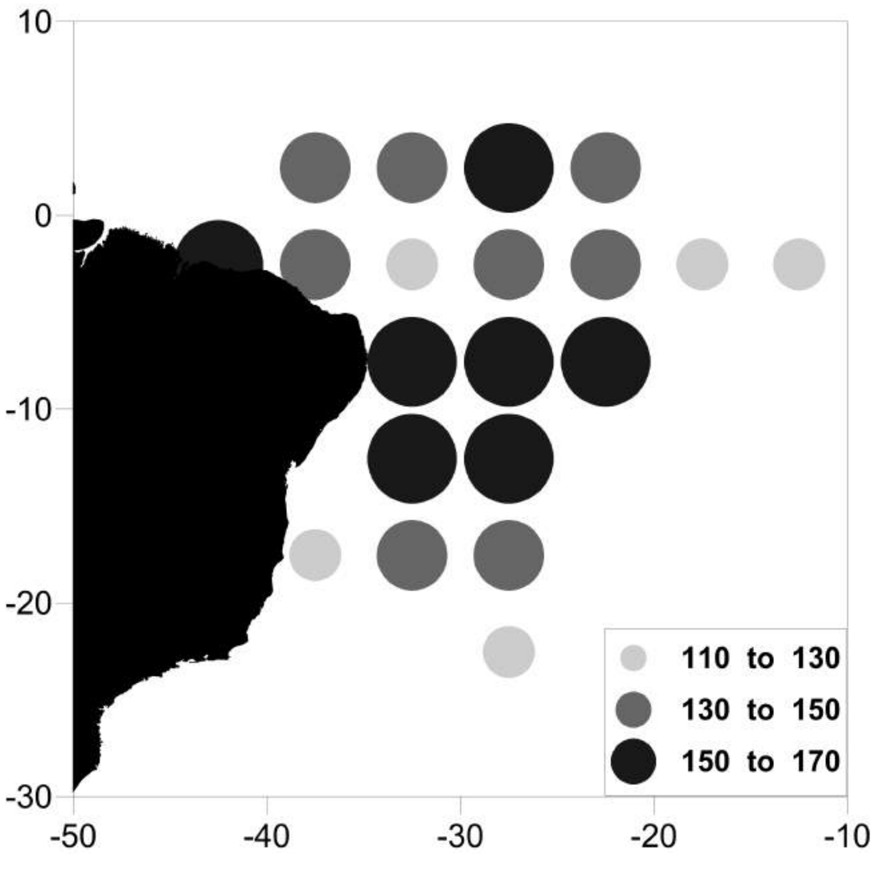

Figure 9. Mean lengths, by 5-degree squares, of oceanic whitetip sharks caught between 2005 and 2009.

4. Acknowledgments

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Chapter 4

Interactions of oceanic whitetip sharks with the tuna purse seine fishery in the Atlantic and Indian oceans

Abstract

The interaction between oceanic whitetip sharks (OCS) and the purse seine fishery in the eastern Atlantic and western Indian oceans was analyzed, in order to investigate the potential of using this fishery's database to derive abundance indices and determine population trends for the species. Observer data from the French purse seine fleet combined with a historic Indian Ocean database from the Soviet Union were used in the analyses. In the Atlantic the time series ranged from 1995 to 2014, while in the Indian Ocean the combined time series spanned from 1986 to 2014. A well-marked change on the proportion of Fishing Aggregating Devices (FADs) with the presence of oceanic whitetip sharks in the Indian Ocean was observed, fluctuating around 20% from mid 80's to mid 90's and dropping to less than 10% as from 2005. The changes on the OCS/FAD proportion along the years show a clear link between the two distinct databases from this ocean. The results indicate that the proportion of FADs with OCS could be relevant when deriving abundance trends for the species from multiple data sources. Occurrence rates were lower in the Atlantic when compared to the Indian Ocean. No marked temporal trends were observed for this ocean. Results might indicate that the oceanic whitetip population is more severely impacted in the eastern Atlantic Ocean, since this area has been industrially exploited for longer.

1. Introduction

The oceanic whitetip shark, *Carcharhinus longimanus*, is a pelagic predator widely distributed in tropical and subtropical areas of all oceans (Compagno, 1984). It is easily distinguishable from the other species of the Carcharhinidae family by the round shape of its long pectoral and dorsal fins, as well as by the white stains in their margins. The species is commonly caught as bycatch by a variety of pelagic fishing gears, such as tuna longlines, gillnets, and purse seines (Bonfil et al., 2008).

Concerns regarding the conservation of oceanic whitetips started to rise substantially in the past decade due to increasing fishing pressure throughout the species range, associated with an acute lack of both knowledge and adequate monitoring of their catches (Baum et al., 2006). As a result, Tuna Regional Fisheries Management Organizations (RFMOs) from all oceans decided to ban landings, storing, and selling of the oceanic whitetip shark (International Commission for the Conservation of Atlantic Tuna Rec. 10-07; Inter-American Tropical Tuna Commission Rec. C-11-10; Western and Central Pacific Fisheries Commission CMM 11-04; Indian Ocean Tuna Commission Res. 13-06). The OCS has also been recently included in CITES appendix II (March 2013, CoP16 Prop. 42).

All of these measures, including the recent listing on CITES appendix II, were taken under the precautionary approach concept and represent a first step towards the conservation of OCS worldwide. Knowledge gaps concerning the species ecology and biology are still wide, imposing a barrier on the development of mitigation measures for fisheries and accurate stock assessment.

The oceanic whitetip shark is believed to have been more severely impacted by pelagic longlines, as its catch rates are usually higher in fisheries using this fishing gear (Rice and Harley, 2012). As a result, the interactions of the species with pelagic longlines have been more often investigated (Cortés et al., 2010; Semba and Yokawa, 2011; Tolotti et al., 2013; Walsh et al., 2009). In the purse seine fishery, on the other hand, these interactions received much less attention. The work presented here is a first look on how this species interacts with the purse seine fishery in the eastern Atlantic and western Indian oceans. The goal is also to investigate the potential of using this fishery's database to derive abundance indices and determine population trends for the oceanic whitetip shark in the global pelagic realm.

2. Material and methods

2.1. French database

Data from 10,441 purse seine sets conducted by the French tuna fleet in the eastern Atlantic and western Indian oceans were analyzed. The time series includes data from the mid 90's, starting in 1995, up until 2014. In the Indian, however, no data was collected between the years of 1997 and 2005. Sets cover a large area of both oceans (Figures 1 and 2). In the Atlantic Ocean, the fishing area is roughly limited by the latitudes of 20°N and 05°S and by the African coast and the longitude of 025°W. In the Indian Ocean, the fishing is roughly limited by the latitudes of 05°N to 20°S and by the longitudes of 070°E to 040°E. All French data comes from scientific observer programs, either conducted within the framework of specific European Union (EU) research projects in the 1990s and early 2000s, or since 2005, within continuous data collection programs under the European Data Collection Regulations (Council Regulation no. 1543/2000, Commission Regulation no. 1581/2004, Council Regulation no. 199/2008, and Commission Decision 2008/949/EC). All observer programs were developed under the same main objectives (Amandè et al., 2012; Bourjea et al., 2014).

On-board observers were evenly distributed to cover the four quarters of the year. They collected information regarding all fishing activities, including bycatch estimations and size frequencies by species. Each set was recorded on an exact geographic position basis and divided into two distinct fishing strategies, sets on Free Swimming Schools (FSC) and sets on Fish Aggregating Devices (FAD). Sets on both natural and man-made devices were recorded under the same FAD category. Whale-associated sets were treated as free-school sets and sets on whale sharks were pooled with FAD sets. All collected information is gathered in a common database managed by the Observatoire Thonier, from where the data presented here was extracted. These observer programs were estimated to cover 10% of the French purse seine sets in the Atlantic and around 9% in the Indian Ocean (Amandè et al., 2012; Bourjea et al., 2014).

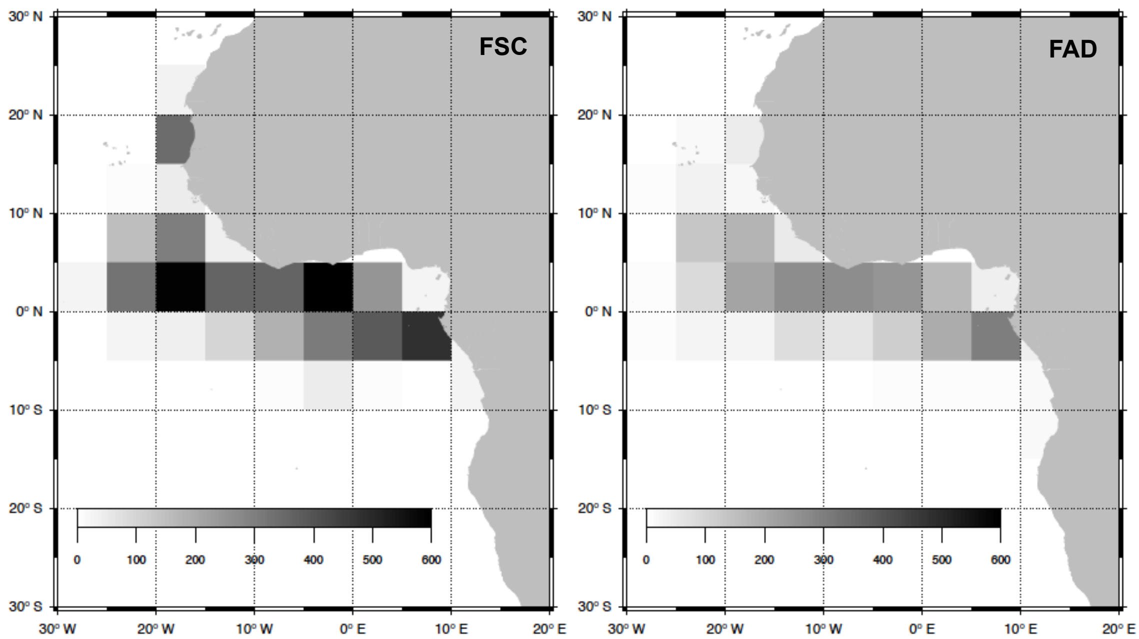

Figure 1. Distribution of the observed fishing sets from the French tuna purse seine fleet operating in the eastern Atlantic Ocean between 1995 and 2014. Right panel represents sets on Free Swimming Schools (FSC) and left panel sets on Fish Aggregating Devices (FAD).

2.2. Historic Indian Ocean database

Additional historic data were incorporated into the analyses in order to investigate possible changes on population trends. A total of 497 purse seine sets conducted by the Soviet Union (USSR) were analyzed. These fishing operations were carried out between 1986 and 1992 and data was collected by scientific on-board observers in the scope of various programs developed by regional fisheries research institutes and affiliated organizations. Database was developed within the framework of YugNIRO[1] research activities in the Indian Ocean. The USSR sets fall inside the area covered by the French database in the Indian Ocean, roughly ranging from 05°N to 10°S and form 070°E to 050°E (Figure 3). Some fishing sets were also made in the northeastern portion of the Mozambique Channel. Each set was also recorded on an exact position basis. For comparison purposes with the

[1] Southern Scientific Research Institute of Marine Fisheries and Oceanography, Kerch, Crimea.

French database, sets were grouped into two distinct fishing strategies as well, free swimming school (FSC) and object associated (here referred as FAD).

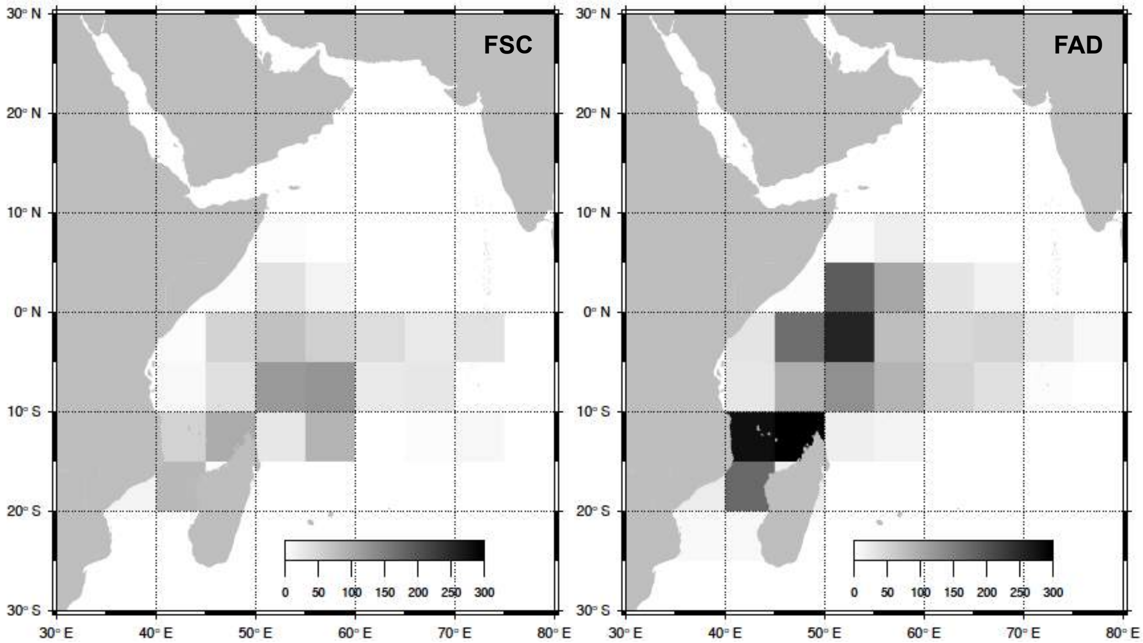

Figure 2. Distribution of the observed fishing sets from the French tuna purse seine fleet operating in the western Indian Ocean between 1995 and 2014. Right panel represents sets on Free Swimming Schools (FSC) and left panel sets on Fish Aggregating Devices (FAD).

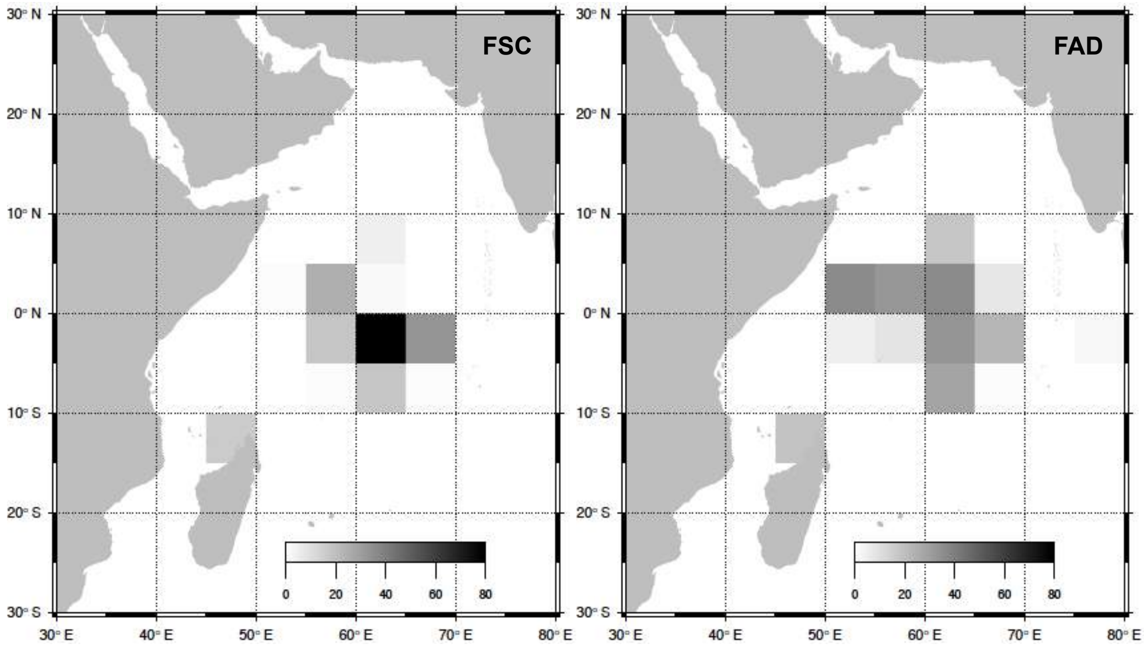

Figure 3. Distribution of tuna purse seine sets from the Soviet Union historic surveys (USSR) conducted in the western Indian Ocean between 1986 and 1992. Right panel represents sets on Free Swimming Schools (FSC) and left panel sets on Fish Aggregating Devices (FAD).

2.3. Data analysis

The interaction between oceanic whitetip sharks (OCS) and the tropical purse seine fisheries was analyzed in terms of occurrence per set, not taking into account the number of OCS caught per set but only the presence of the species in a set. For the spatial analysis, sets were grouped into 5°x°5 squares of latitude and longitude. The two datasets were analyzed separately and then compared. To facilitate the comparison, some figures combine the two but their origin is always indicated. A general summary that includes total catches is also provided.

3. Results

3.1. Fishing sets

3.1.1. French database – Atlantic Ocean

Of the 7,102 sets analyzed from the French fleet in the Atlantic Ocean, 65% were done on FSC and 35% were done on FADs (Table 1). On the first two years of the time series (1995 and 96), sets on FSC were unanimity and on the following years a gradual increase of sets on FAD was observed (Figure 4). Even with an increase on FAD sets, the overall pattern was the predominance of FSC sets. FAD sets only predominated over FSC sets in 2005 and 2006. These years, however, up until 2009, were characterized by very low sampling efforts (Figure 4). The effort was considerably higher in 1998, exceeding 1400 sets, and in 2014, when it reached four digits again. The high number of fishing sets in 2014 is due to the implementation of 100% observer coverage in this ocean.

Both fishing strategies share the same geographical area, with sets concentrating in the equatorial zone between the parallels of 05°N and 05°S (Figure 1). Regarding FSC sets, three hotspots are observed: one between the coast of Ghana and the equator, one just above the equator and between the meridians of 020°W and 015°W, and one just off the coast of Gabon. An important concentration of FSC sets is also observed up north, just off the coast of Mauritania and delimited by the latitude of 20°N. FAD sets were mostly concentrated in the five degree square just off Gabon, especially during the 2nd and 3rd quarters of the year. The areas off Liberia, Ivory Coast and Ghana also concentrated a considerable amount of FAD sets, especially on the 1st quarter.

Table 1. Summary results of the interactions between oceanic whitetip sharks and the tuna purse seine fisheries in the Atlantic and Indian oceans.

	French - AO		French - IO		USSR - IO	
	FSC	FAD	FSC	FAD	FSC	FAD
Number of sets	4637	2465	1055	2284	238	259
Number of sets with OCS	47	43	30	135	12	45
Number of OCS caught	63	106	48	249	20	175
Proportion (OCS occurrence/set)	0.01	0.02	0.03	0.06	0.05	0.17
Proportion (OCS total/set)	0.01	0.04	0.05	0.11	0.08	0.68
Sets ratio (%)	0.65	0.35	0.32	0.68	0.48	0.52
Total OCS caught ratio (%)	0.37	0.63	0.16	0.84	0.10	0.90

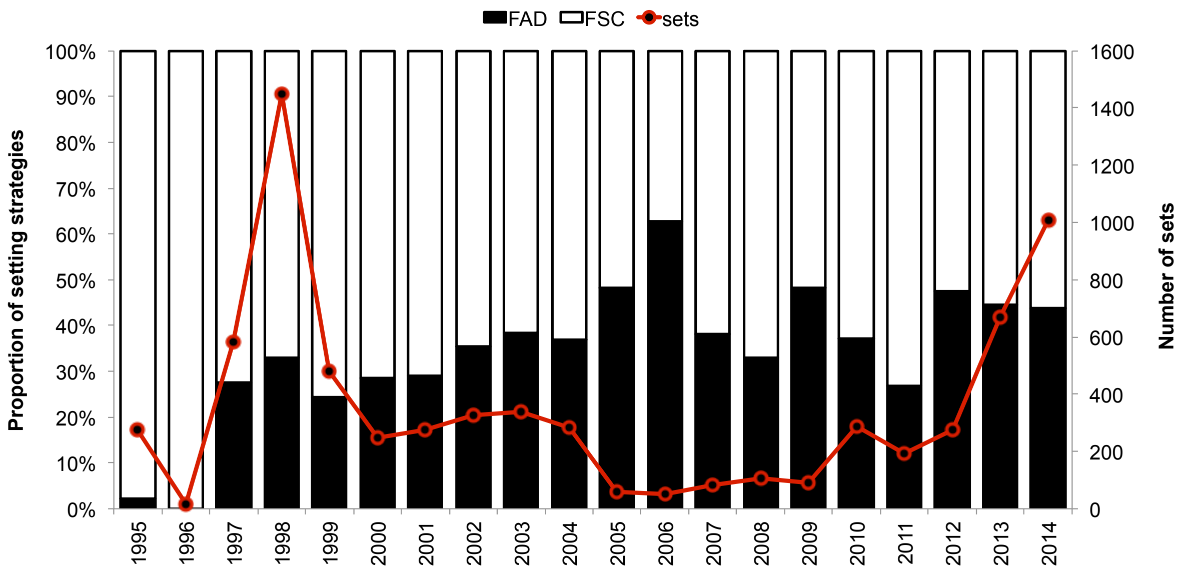

Figure 4. Observed tuna purse seine sets in the eastern Atlantic Ocean highlighting the proportion between sets on Free Swimming Schools (FSC) and on Fish Aggregating Devices (FAD).

3.1.2. French database – Indian Ocean

Of the 3,339 sets analyzed from the French fleet in the Indian Ocean, 32% were done on FSC and 68% were done on FADs (Table 1). The proportion of the two fishing strategies varied considerably along the years, but, with the exception of 2005 and 2007, sets on FADs were always predominant (Figure 5). The number of observed sets also showed a great deal of variation throughout the time series and very low effort was recorded for the years 1996 and 2005 (Figure 5). These low numbers of observed sets are due to transition periods between observer programs in this ocean. Sampling effort was considerably high on 1995, 2009, 2010 and 2014.

Regarding the spatial distribution of sets, both fishing strategies shared the same area (Figure 2). Two effort hot spots are observed for sets on FADs, one inside the Mozambique Channel and another one right around the Equator (from 05° north to south) and between the meridians of 045° and 055° east. The sets on the Mozambique Channel are seasonal, occurring mildly on the 1st quarter of the year and also on the 2nd, when it reaches its peak. There are no sets in the Mozambique Channel during the 3rd and 4th quarters. Still concerning the Channel, the number of sets was remarkably high in 2009 and 2010 when compared with the other years of the time series. Sets on FSC were more frequent in the area bonded by the 05°S and the 10°S parallels and by the 050°E and 060°E meridians.

3.1.3. USSR database

In the Soviet Union database the number of sets per fishing strategy was more proportionately balanced, with 259 out of 497 sets done on FADs and 238 on FSC (52% and 48%, respectively – Table 1). This proportion also varied along the years, but remained relatively balanced for most part of the time series (Figure 5). The exceptions were the years 1989, when almost 100% of observed sets were on FSC, and 1991, when no FSC sets were observed. Some variation is seen on the number of observed sets throughout the time series, but not as pronounced as seen on the French database (Figure 5). Sampling effort below average is seen on 1988 and 1992.

Sets of both fishing strategies were done on the same area, with FAD sets being more widely spread (Figure 3). The latter strategy was more frequently observed along a "corridor" between 050°E and 065°E, ranging from the Equator up to 05°N and down to 10°S in the squares bounded by 060°E and 065°E. Sets on FSC were mostly concentrated in the square between the Equator and the 05°S parallel and between the 060°E and 065°E meridians. Fishing sets in the Mozambique Channel were only observed during its peak season on the 2nd quarter of the year. Both FSC and FAD sets were observed inside the channel, with a great predominance of sets on FADs.

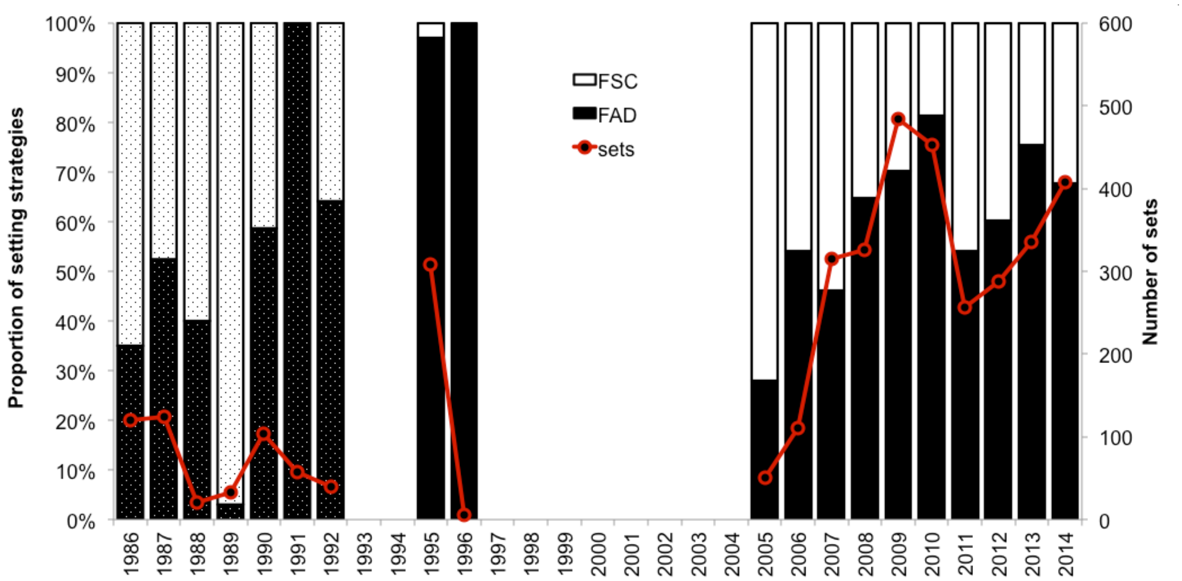

Figure 5. Observed tuna purse seine sets in the western Indian Ocean highlighting the proportion between sets on Free Swimming Schools (FSC) and on Fish Aggregating Devices (FAD). The shaded bars represent the historic database from USSR.

3.2. OCS and the purse seine fishery

3.2.1 Atlantic Ocean

From the 7,102 sets observed in the Atlantic Ocean only 90 had the presence of OCS (Table 1). Most sharks were caught on FAD sets, totaling 106 OCS or 63%, while the remaining 37% (63 sharks) were caught on FSC sets. The number of OCS caught on FSC sets seems high, but it is important to note that sets on FSCs in this ocean were almost twice more observed then sets on FADs (65% against 35%). Proportionally, the total OCS catch represented only 1% of FSC sets against 4% of FAD sets (Table 1).

For every set on a free swimming school only 0.01 oceanic whitetip sharks were present. For FAD sets the proportion of OCS occurrence was slightly higher, representing 2% of these sets. Looking at each year individually a marked trend was not evident for neither of the fishing strategies (Figure 6). However, values tended to decrease slightly over the observed years. On FAD sets the highest proportion value occurred in 1997 (5%) and the lowest value occurred in 2014 (0.2%). This declining trend was not constant either and some zero values also occurred in between. A declining trend is clearer for the OCS proportion on FSC sets (Figure 6). The highest value occurred in 1995 (6%) and the lowest occurred (0.3%). Despite the great number of observed FSC sets, the presence of OCS was rarely recorded and zero values occurred more frequently than on FAD sets.

On FAD sets, the presence of OCS was most frequently recorded in the area just above and just below the 10°N parallel (Figure 7). Occurrence hotspots were observed in this area in the 2nd and 4th quarters, a seasonal pattern, however, is not clear. OCS occurrences along the equator were mainly observed during the 1st quarter. Overall, catches were highly dispersed over the fishing area and 5 degrees squares with zero occurrences were abundant during the four quarters of the year. Occurrences on FSC sets were even more dispersed than on FAD sets

(Figure 8). The main difference between the two strategies was the lack of OCS occurrences on FSC sets in the area around the 10°N parallel. For this strategy, catches along the equator were more frequent in the 4th quarter.

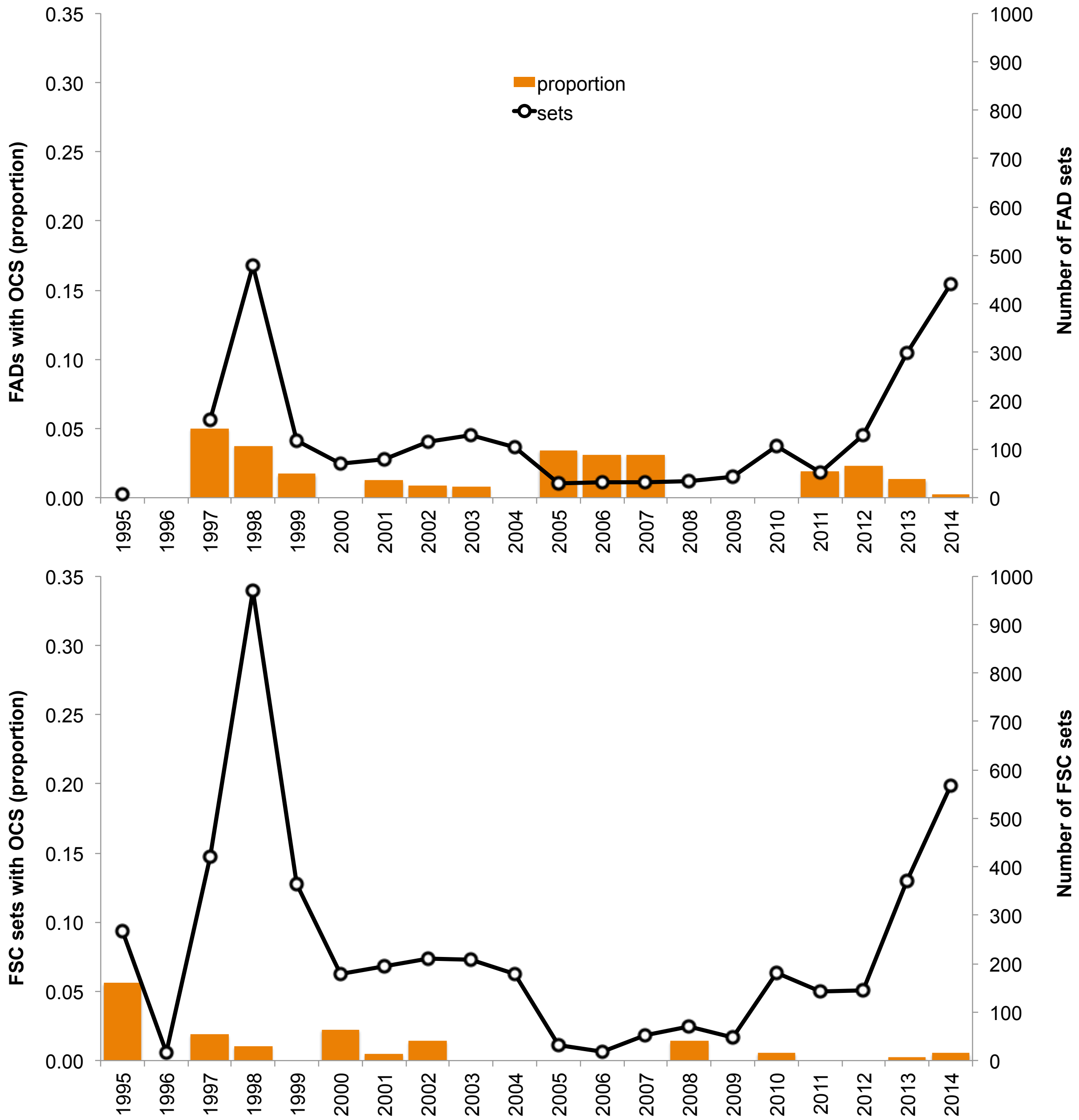

Figure 6. Proportion between observed sets in the Atlantic Ocean with the presence of oceanic whitetip sharks (bars) and the total number of sets (points). Top panel shows the proportion on FAD sets and bottom panel on FSC.

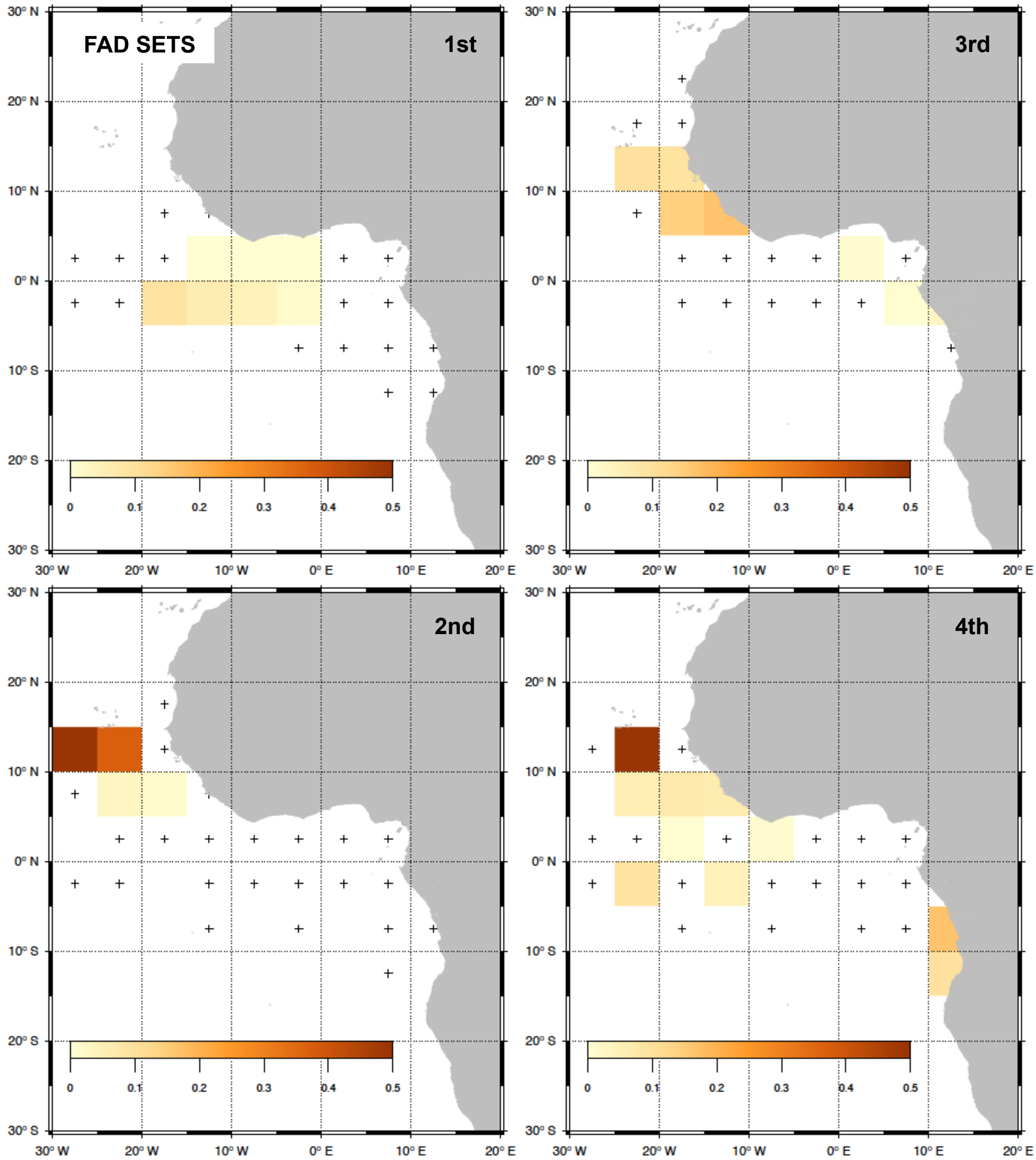

Figure 7. Quarterly distribution of the proportion of oceanic whitetip sharks on FAD sets from the French tuna purse seine fleet operating between 1995 and 2014. The crosses represent squares where sets were observed but no OCS capture was reported.

3.2.2. Indian Ocean – French database

Compared with the Atlantic, oceanic whitetip sharks were more frequently caught in the Indian Ocean. A total of 165 sets were recorded with the presence of OCS, and a total of 297 oceanic whitetip sharks were caught on both fishing strategies (Table 1). Most of OCS catches came from FAD sets, but the species catches on FSC sets were not negligible as 16% of sharks were caught with this fishing strategy. Balanced by the number of sets, OCS total catches represented 5% of FSC sets and 11% of FAD sets.

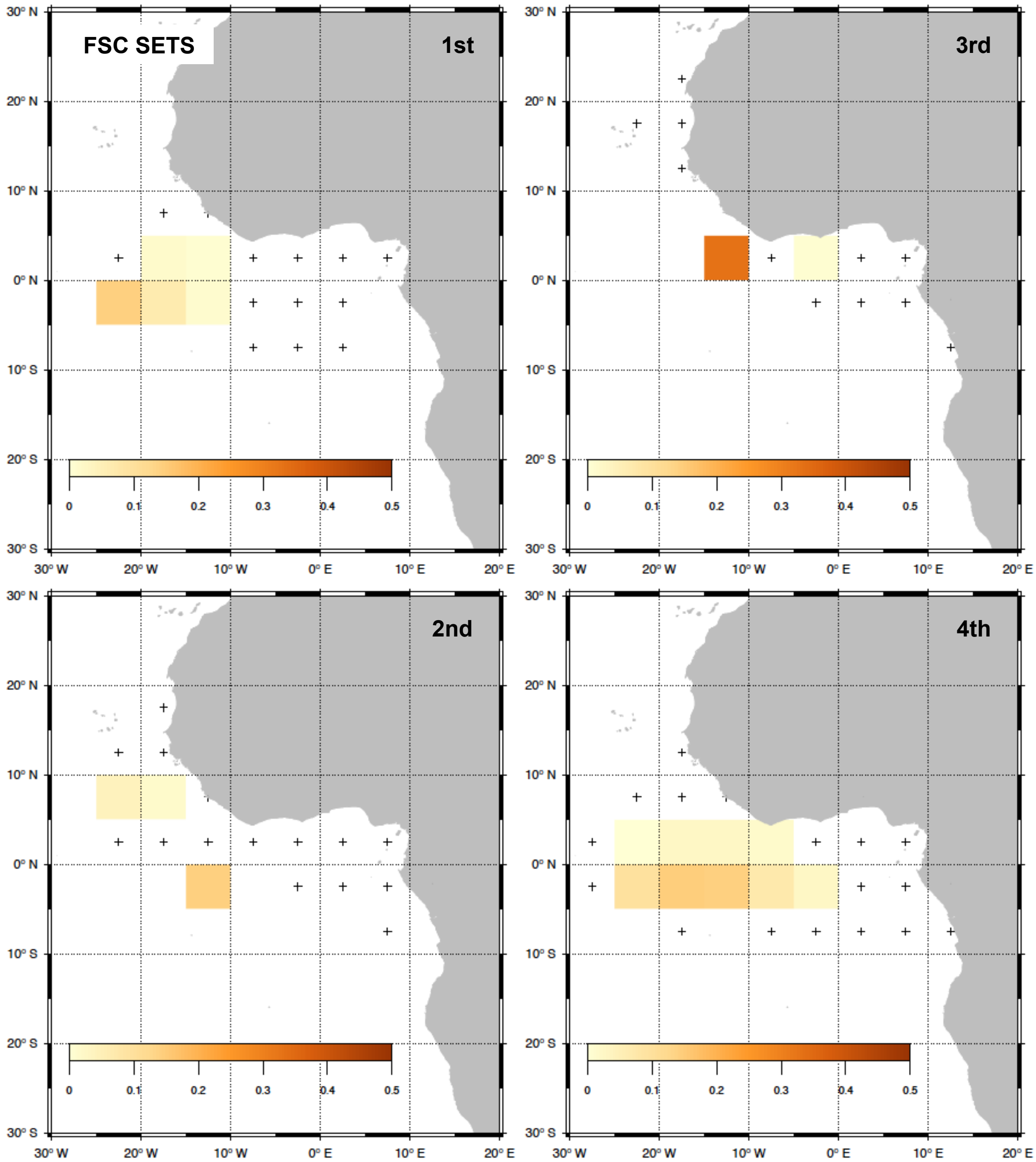

Figure 8. Quarterly distribution of the proportion of oceanic whitetip sharks on FSC sets from the French tuna purse seine fleet between 1995 and 2014. The crosses represent squares where sets were observed but no OCS capture was reported.

Overall, OCS was present in 3% of FSC sets and in 6% of FAD sets. Along the years, the proportion on FAD sets varied and a marked change was observed between mid 90's and the rest of the time series (Figure 9). The proportion of FADs with the presence of OCS went somewhere from 20 to less then 10%

between these two periods. The exception is a peak in 2011 and minor one in 2014. Another remark is the extremely low values, way below 5%, seen in 2009 and 2010. The presence of OCS on FSC sets did not vary as much, remaining below 5% for most of the time series (Figure 9). A very high value is seen in 1995, but this must be regarded with caution since it is derived from a low sample size, only 9 sets. Interestingly, high proportion peaks are also seen in 2011 and 2014.

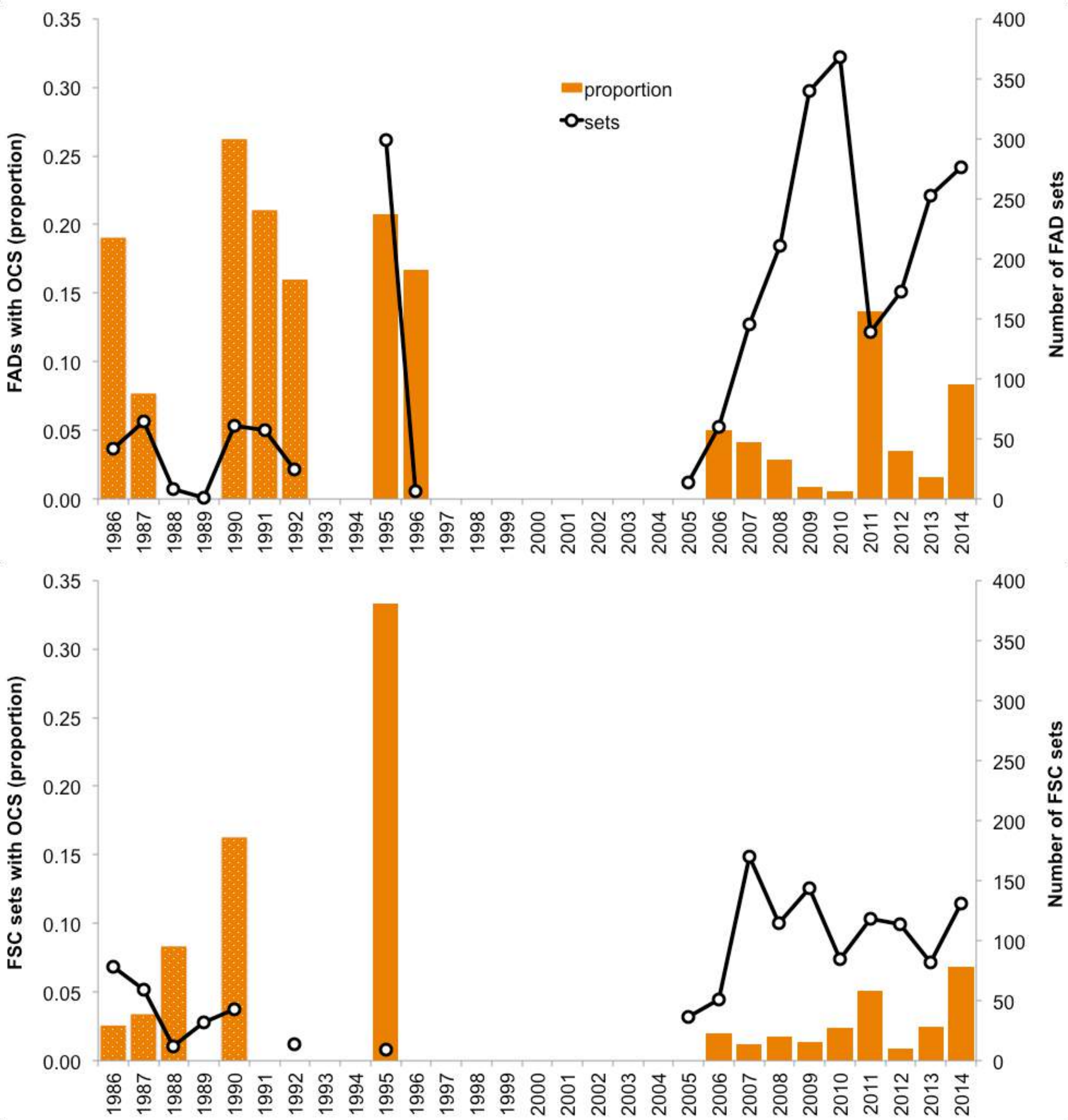

Figure 9. Proportion between observed sets in the Indian Ocean with the presence of oceanic whitetip sharks (bars) and the total number of sets (points). Top panel shows the proportion on FAD sets and bottom panel on FSC. The shaded bars represent the historic database from USSR.

Contrary to what was observed in the Atlantic Ocean, the catches of OCS on FADs was highly associated with the equatorial zone and there were no catch records of the species above 10°N and very few below 10°S (Figure 10). Even with the considerably high effort on the Mozambique Channel during the 2nd quarter, the presence of OCS in this area was very weak. A seasonal pattern is not evident. Overall, occurrences were more frequently recorded on the 1st and 3rd quarters. The big 10 degrees square off Tanzania and Kenya and up to 050°E is an area with frequent occurrences all year round, with the exception of the 4th quarter. Catches on FSC were also more frequent on the equatorial zone, although more occurrences were recorded below the 10°S parallel (Figure 11). The species was more present on FSC sets during the 2nd and 4th quarters, but the highest occurrence level was observed on the 3rd. This "hotspot" also needs to be looked at with caution as observed fishing effort in this square is very low, only 2 sets.

3.2.2. Indian Ocean – USSR database

From the historic data, 57 sets were recorded with the presence of OCS, totaling 195 oceanic whitetip sharks caught on both fishing strategies (Table 1). The presence of OCS was also more frequent on FAD sets, representing 90% of the total number of sharks caught. Combining the years, OCS was present in 5% of FSC sets and in 17% of FAD sets. The proportion of FADs with OCS did not vary a great deal throughout the time series, remaining at around 20% (Figure 7). The year of 1987 was the exception showing a value below 10%. No sharks were caught on FADs in 1988 and 1989, which could be explained by the low sample size of these years. The presence of OCS on FSC sets exhibited a crescent trend, varying from 3% in 1986 to 16% in 1990 (Figure 7). Despite the reasonable sample size in 1989, no OCS catch was reported for this year. A zero catch scenario is also seen in 1992.

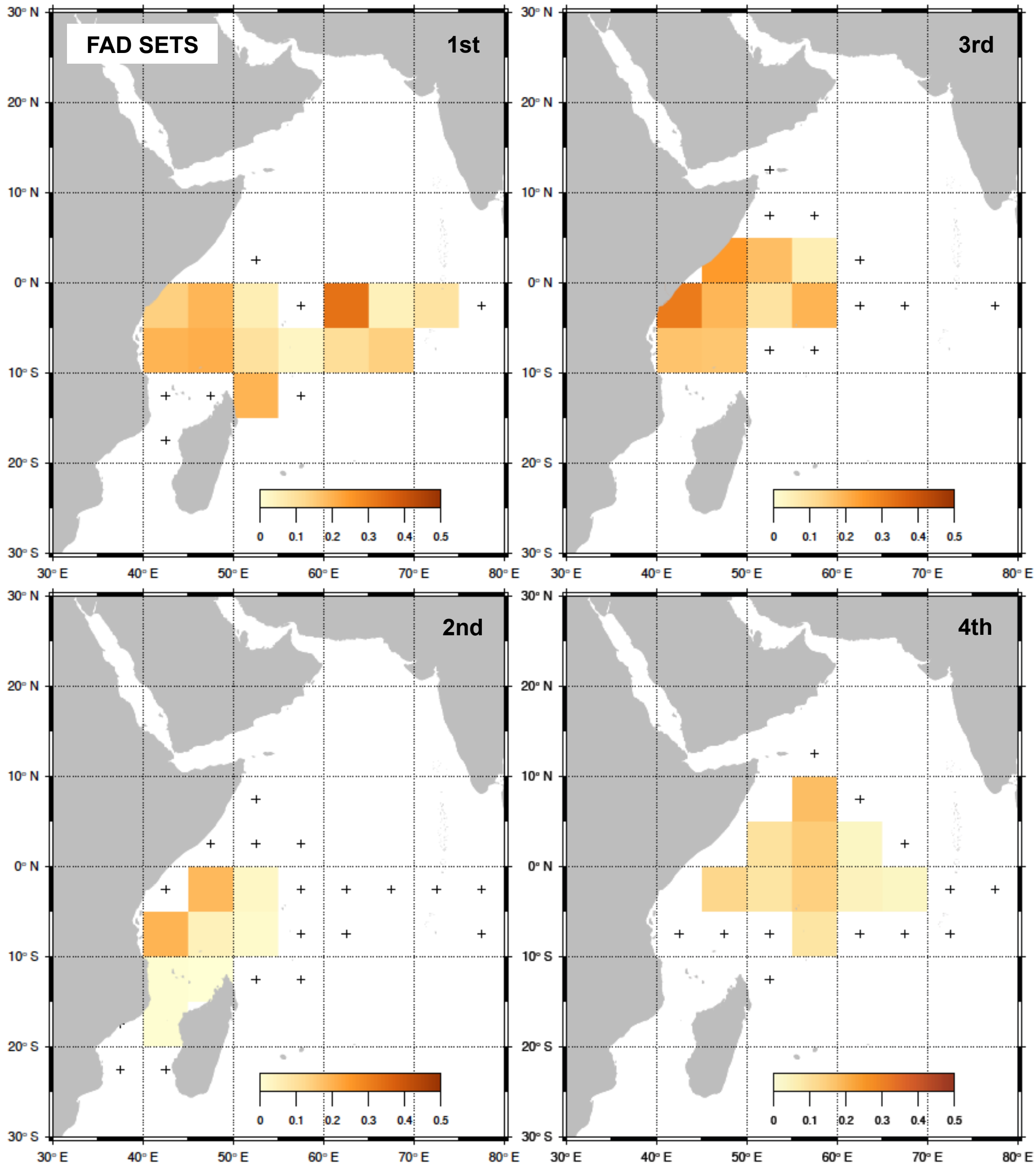

Figure 10. Quarterly distribution of the proportion of oceanic whitetip sharks on FAD sets from the French tuna purse seine fleet operating between 1995 and 2014. The crosses represent squares where sets were observed but no OCS capture was reported.

Spatially, the presence of OCS on FAD sets varied between the quarters of the year, which might suggest a seasonal effect (Figure 12). The species was much more frequent on FAD sets from the second half of the year (3rd and 4th quarters). A similar spatial pattern is seen in these two quarters as their higher proportion squares occur in the same area. These squares are located along the Equator, up to 05°N, from the 050°E to the 065°E meridians. The Mozambique Channel was not heavily sampled as on the French database, but the few sets conducted on the 2nd quarter resulted on a few OCS catches. The occurrence of OCS on FSC sets is very low and dispersed across the fishing area, which prevents the identification of spatial patterns (Figure 13). On most of the 5 degrees squares where FSC sets were observed no OCS catch was recorded.

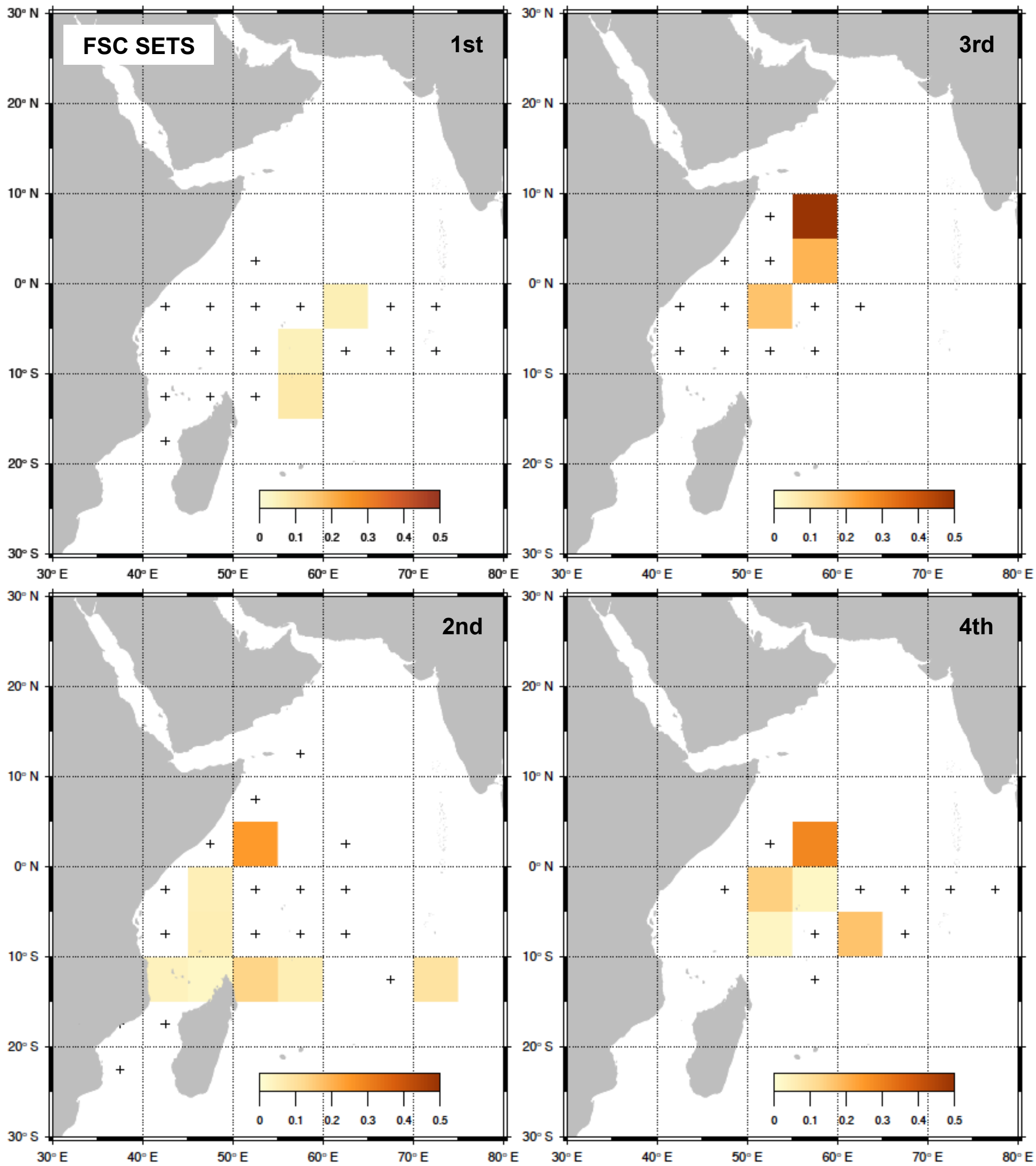

Figure 11. Quarterly distribution of the proportion of oceanic whitetip sharks on FSC sets from the French tuna purse seine fleet operating between 1995 and 2014. The crosses represent squares where sets were observed but no OCS capture was reported.

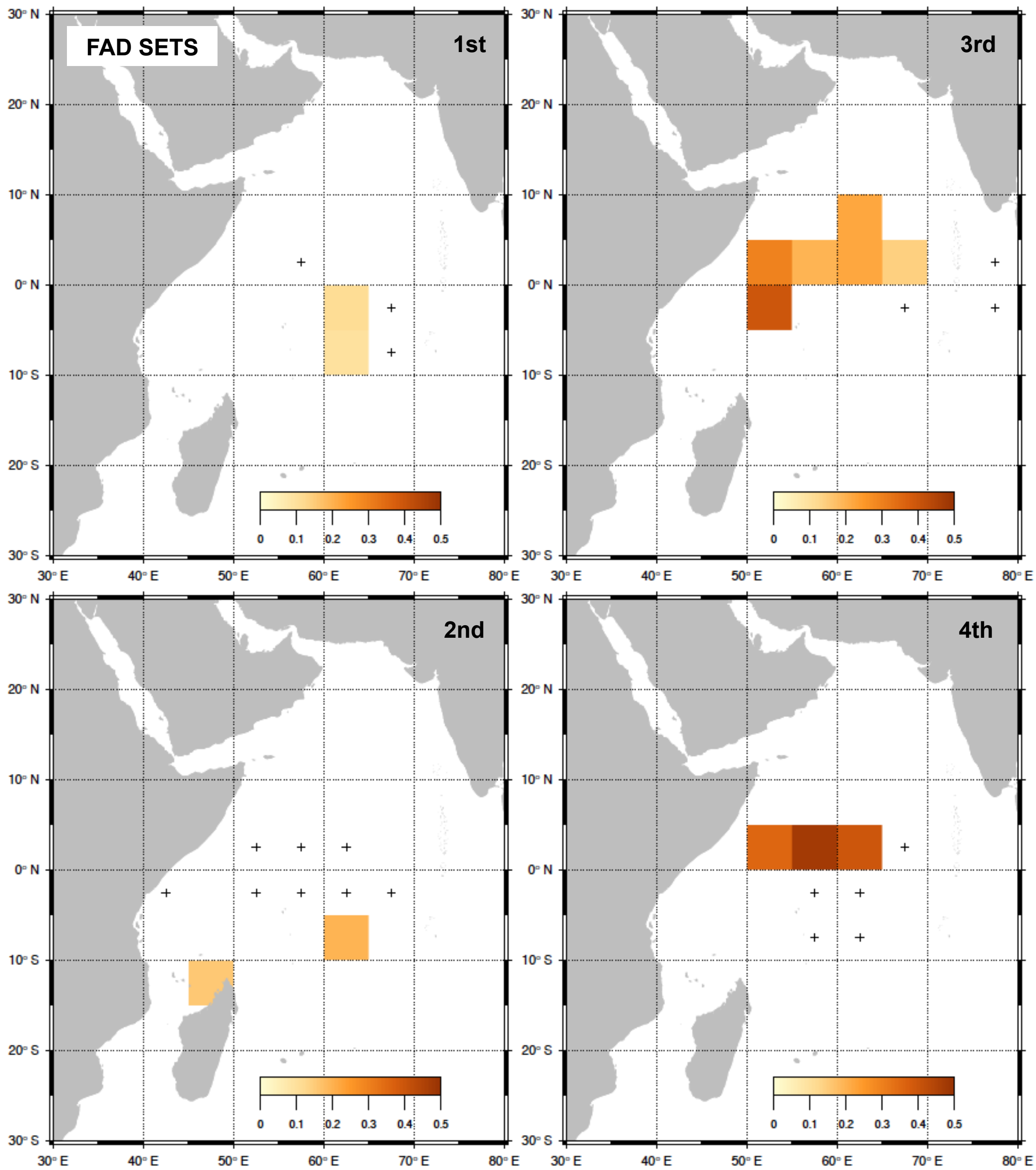

Figure 12. Quarterly distribution of the proportion of oceanic whitetip sharks on FAD sets from the Soviet Union historic surveys (USSR) conducted between 1986 and 1992. The crosses represent squares where sets were observed but no OCS capture was reported.

4. Discussion

The oceanic whitetip shark is believed to associate with floating objects. This statement is supported by catch data from tuna purse seine fisheries setting on floating objects, either natural or man-made (Clarke et al., 2013; Torres-Irineo et al., 2014). The species is the second mostly caught shark by the tropical tuna purse seine fishery and its catch rates are considerably higher on FAD sets (Amandè et al., 2012; Santana et al., 1998; Stretta et al., 1998). This pattern, revealing an associative behavior around drifting objects, was observed on both French and USSR databases. Still, the number of OCS caught with free-swimming tuna schools was meaningful, constituting at least 10% of total OCS catch in the Indian Ocean and reaching 37% in the Atlantic. This result indicates that the association of oceanic whitetip sharks with free-swimming tuna schools does not seem to be a random event, as, although not often, it occurs systematically.

When looking at the Indian Ocean database as a whole, historic and recent, a well-marked change on the proportion of FADs with the presence of oceanic whitetip sharks is seen on the time series chart (Figure 9). From mid 80's to mid 90's this proportion fluctuated around 20% and dropped to less than 10% as from 2005. There are a few odd high and lows, but, as the general pattern is quite evident, this could be a result of noise due to variations on sample size and area. Taking into account that the number of FADs has greatly increased since the 90's (Dagorn et al., 2013b; Maufroy et al., 2015), the decrease in the proportion of FADs with OCS by more than 10% could indicate an important population decline. Following the simple line of thought that a greater number of FADs would increase the chances of an OCS finding and associating with one, we would expect to see an increase on the proportion of FADs with the species (assuming, of course, the population size remained stable) (Sempo et al., 2013). The data, however, shows that this is not the case. The populations of oceanic whitetip sharks are believed to have suffered substantial declines in the Atlantic and Pacific Oceans (Baum and Blanchard, 2010; Rice and Harley, 2012). Similar studies have not been conducted in the Indian Ocean, but the results presented here might indicate a similar scenario. Additionally, a preliminary analysis conducted on catch and effort data from the Japanese longline fishery also suggested that OCS population is showing signs of decline in the western Indian Ocean (Semba and Yokawa, 2011).

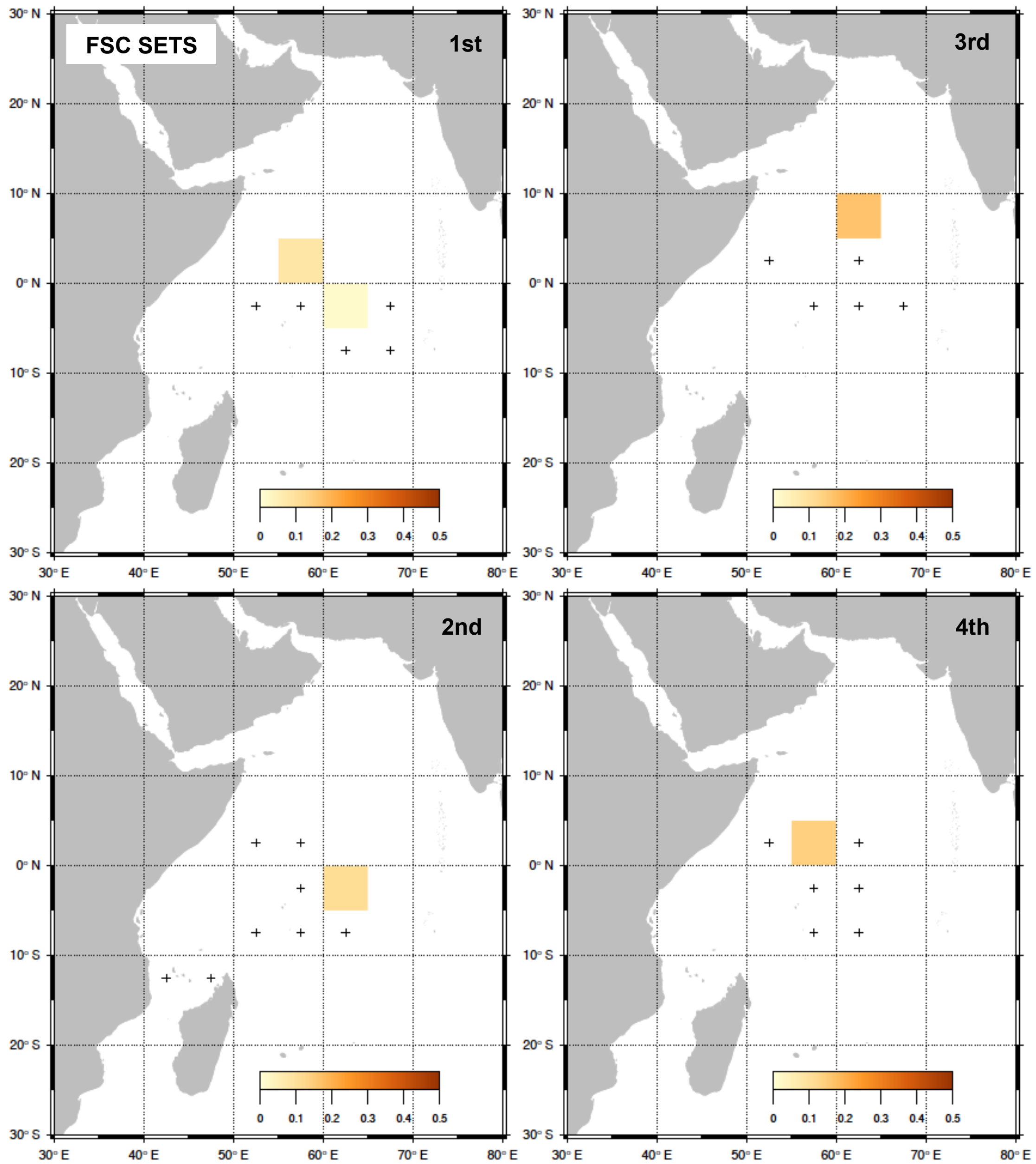

Figure 13. Quarterly distribution of the proportion of oceanic whitetip sharks on FSC sets from the Soviet Union historic surveys (USSR) conducted between 1986 and 1992. The crosses represent squares where sets were observed but no OCS capture was reported.

Another possible interpretation for the decline of OCS occurrence per FAD in the Indian Ocean could be a sharp increase on FAD densities combined with a small and stable population size. In this scenario, the proportion OCS/FAD would simply decrease because there are not enough sharks to aggregate around that many FADs. The analyzed data does not provide a straightforward interpretation, as both hypotheses seem plausible. However, when considering the population declines caused by the increased fishing pressure in other oceans and that the fishing pressure also increased greatly in the Indian Ocean, this second scenario seems less likely. In any case, a thorough analysis taking other factors into account, especially FAD density trends, is necessary to draw more definite conclusions. Studies on the associative behavior of oceanic whitetip sharks around floating objects, like what has been done with silky sharks (Filmalter et al., 2015), are also crucial.

The data shown on Figure 9 comes from two distinct databases (USSR and French), yet the changes on the OCS/FAD proportion along the years show a clear link between them. Proportions derived from the early years of the French database are at the same magnitude order of the proportions derived from the historic database (USSR). This indicates that this index (proportion of FADs with OCS) could be relevant when deriving trends from multiple data sources. The proportion of sets on FSC with the presence of oceanic whitetip seems to have decreased between historic and recent data, however this change was minor and a well-defined trend is not evident. As discussed above, the capture of OCS on free swimming schools in not negligible, but still is very sparse. Being an index derived from a less frequent event, the proportion of OCS on FSC sets is more subject to noise than the proportion on FAD sets, making it more difficult to pick up trends and requiring a much bigger sample size. This issue becomes more evident when looking at the spatial distributions of the occurrence of OCS/FSC sets on Figures 11 and 13. Surely that when deriving population estimates from catch and effort data all sources of catch must be taken into account. However, when it comes to deriving indices and examining trends the focus should be on FAD sets.

Seasonal patterns could not be distinguished when looking at the distributions of oceanic whitetip occurrences per set. The data, however, indicates that there is a spatial component to be considered in the Indian Ocean. The Mozambique Channel was heavily sampled on the French database, but both total catch and occurrence rate were very low in this area (Figures 10 and 11). The extremely low values of FADs with OCS seen in Figure 9 seem to be influenced by this spatial component. In the years in question, 2009 and 2010, the number of sets inside the Channel was around 6 times higher than the other years. Since the species is less observed in purse seiners catches in this area, these high effort values pulled the OCS/FAD proportion down. This is an interesting result to be investigated further, specially considering that the Mozambique Channel is an area with great density of floating objects (Dagorn et al., 2013a).

Oceanic whitetip sharks were less frequently caught in the Atlantic than in the Indian Ocean (Table 1). Only 2% of the FAD sets in this ocean had the presence of an OCS, as opposed to 6% for the same period in the Indian Ocean. This low proportion ranged from the beginning to the end of the time series and, although a slight decrease seems to have occurred, no marked trend was observed. The low rate of occurrence and the lack of a marked trend hamper a discussion concerning the time evolution of the abundance of the species in the eastern Atlantic and leaves unanswered questions. Has the OSC population in the western Indian Ocean always been bigger or are the lower proportion values in the Atlantic a result of a high fishing pressure over a longer period? Large-scale longline vessels started exploring the Atlantic in the late 1950's and purse seine vessels have been fishing for tuna off topical West Africa since the 1960's, while in the Indian Ocean large-scale fisheries developed slower, only reaching big proportions in the 1980's (Miyake et al., 2004). The eastern Atlantic has been under big fishing pressure for longer, thus the OCS population might have been bigger before the 90's and at comparable levels with the western Indian Ocean. The analysis of historic data is crucial to elucidate this matter. Another question that can be asked is if the associative behavior of OCS is the same between the two oceans. Maybe, the proportion of OCS on FAD sets in the Atlantic are lower simply because they associate less on floating objects than in the Indian Ocean. This highlights the importance of understanding the species behavior around FADs.

Using longline data to derive bycatch population trends is typically problematic, as small variations on gear type and fishing strategy can greatly impact the catchability of a species and interfere on the relationship between its catch rate and its actual abundance (Ward, 2008). Abundance trends for the oceanic whitetip have been heavily questioned due to standardization problems (Baum et al., 2003; Burgess et al., 2005) and question marks still remain regarding the species population status. The proportion of FADs with the presence of oceanic whitetip sharks could potentially provide a simple abundance trend index, with the advantage of a probably lower catchability bias when compared to pelagic longline catches. To further investigate population size trends for the endangered OCS derived from the purse seine fishery, however, key information on the evolution of FAD densities is required. Knowledge on the associative behavior of this species, in particular the time they spend at floating objects and the time between two associations, is also essential.

5. Acknowledgments

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Chapter 5

Vulnerability of the oceanic whitetip shark to pelagic longline fisheries

Abstract

A combination of fisheries dependent and independent data was used to assess the vulnerability of the oceanic whitetip shark to pelagic longline fisheries. The Brazilian tuna longline fleet, operating in the equatorial and southwestern Atlantic, is used as a case study. Fisheries dependent data include information from logbooks (from 1999 to 2011) and on-board observers (2004 to 2010), totaling 65,277 pelagic longline sets. Fisheries independent data were obtained from 8 oceanic whitetip sharks tagged with pop-up satellite archival tags in the area where longline fleet operated. Deployment periods varied from 60 to 178 days between 2010 and 2012. Tagging and pop-up sites were relatively close to each other, although individuals tended to travel long distances before returning to the tagging area. Some degree of site fidelity was observed. High utilization hotspots of tagged sharks fell inside the area under strongest fishing pressure. Despite the small sample size, a positive correlation between tag recorded information and catch data was detected. All sharks exhibited a strong preference for the warm and shallow waters of the mixed layer, spending on average more than 70% of the time above the thermocline and 95% above 120 m. Results indicate that the removal of shallow hooks on longline gear might be an efficient mitigation measure to reduce the bycatch of this pelagic shark species. The work also highlights the potential of tagging experiments to provide essential information for the development of spatio-temporal management measures.

1. Introduction

The oceanic whitetip shark (*Carcharhinus longimanus*, OCS) is a tropical predator [1,2] commonly taken as bycatch in pelagic fisheries using longlines, gillnets, and purse seines [3]. Inadequate monitoring hampers the assessment of stock status for this species, but there is a broad consensus that populations are decreasing [4,5]. Concerns regarding the conservation of oceanic whitetips have risen substantially during the past decade due to increasing fishing pressure throughout the species range and inadequate catch monitoring, associated with an acute lack of knowledge on the behavior and ecology of the species. In response to an evident, and in some cases drastic, decline of abundance trends, Tuna Regional Fisheries Management Organizations (RFMOs), responsible for the management of tuna fisheries and associated species, adopted a series of strong measures to bolster conservation efforts for the oceanic whitetip shark (International Commission for the Conservation of Atlantic Tuna Rec. 10–07; Inter-American Tropical Tuna Commission Rec. C-11-10; Western and Central Pacific Fisheries CommissionCMM11–04; Indian Ocean Tuna Commission Res. 13–06). These measures essentially banned the take of oceanic whitetip sharks by prohibiting the retention, landing or storing of the whole carcass or any part thereof. The oceanic whitetip is the only pelagic shark species covered by such measures across all oceans. The species was also recently included in CITES appendix II (March 2013, CoP16 Prop. 42).

Under current fishing practices, however, the incidental capture of this species is difficult to be avoided. Furthermore, many individuals are dead or dying by the time the fishing gear is retrieved. As such, the measures currently in place do little to alleviate fishing mortality, which continues to impact oceanic whitetip populations across all oceans. The development of mitigation measures capable of not only reducing their catch rates but also increasing their post-release survival are therefore crucial for improving population levels [6]. In ecological terms, the vulnerability of a species depends upon two factors: the sensitivity of the species to an external factor and how extensive the exposure to this hazard is [7,8]. Shark species are known to have low rebound capacities resulting directly from their life history traits of slow growth, late maturation and low fecundity. These biological characteristics make this group much more sensitive to overexploitation than teleost fishes [9–11].

The present study assesses the vulnerability of the oceanic whitetip shark by analyzing the extent of its fishing exposure (accessibility) to pelagic longline fisheries. The Brazilian tuna longline fleet, operating in the equatorial and southwestern Atlantic, is used as a case study. The overall goal is to provide information needed to aid in the design of management measures and improve conservation efforts for this species. Both fisheries dependent (fisheries logbooks, observers) and independent (electronic tags) datasets were used as complementary sources of information. This integrating approach provided a better understanding of the interactions between oceanic sharks and this fishery. Vulnerability was assessed with regard to both spatial dynamics (horizontal) and depth distribution (vertical) of both sharks and longline gear, taking into consideration seasonality and strategies in the fishery.

2. Material and methods

2.1. Tagging

A total of 11 oceanic whitetip sharks were tagged with pop-up satellite archival tags (PAT), manufactured by Wildlife Computers (Redmond, USA), in the South Atlantic Ocean. From these, 7 reported data to the satellites as scheduled, 1 reported prematurely and 3 never reported (Table 1). Two models of PAT were used: 7 MK10s and 4 miniPATs, with all of the non-reporting tags being Mk10s. Both models were set to collect data on depth, water temperature and ambient light level (for estimation of geolocation) every 10 seconds. The Mk10, however, only transmitted a summary of that data in the form of depth and temperature histograms, while the MiniPATs transmitted time series data at a resolution of 5 minutes.

The first two Mk10 tags (AOCS1 and AOCS2) were programmed to summarize the collected data into one-hour histograms while all others were set to generate six-hour histograms. One MK10 was recovered (AOCS3) allowing the complete time series, with 10-second resolution, to be accessed. The miniPATs were programmed to transmit only depth time series data and not temperature.

Table 1. Meta data of the oceanic whitetip sharks tagged in the western Atlantic Ocean

					TAGGING			POP-UP			
ID	TL (cm)	SEX	TAG	PROGRAMMED	DATE	LAT	LON	DATE	LAT	LON	DURATION
AOCS1	135	F	MK10	60 days	29/01/2010	-0.995	-30.88	30/03/2010	-1.914	-34.637	60
AOCS2	152	M	MK10	90 days	05/02/2010	0.158	-29.777	06/05/2010	-0.218	-38.255	90
AOCS3	167	M	MK10**	180 days	16/01/2011	-0.139	-34.218	10/07/2011	-3.802	-32.466	178
AOCS4	197*	F	miniPAT	140 days	06/12/2011	-3.589	-34.918	25/04/2012	-18.754	-35.771	141
AOCS5	180*	F	miniPAT	140 days	01/03/2012	-0.501	-37.354	20/07/2012	3.215	-41.015	141
AOCS6	134	F	miniPAT	100 days	02/03/2012	-0.736	-37.534	11/06/2012	-0.598	-36.235	101
AOCS7	161	F	miniPAT	100 days	02/03/2012	-0.435	-37.629	14/06/2012	1.306	-35.345	104
AOCS8	100	F	MK10	90 days	05/03/2012	-2.403	-37.983	21/05/2012	4.492	-32.624	77
-	140	F	MK10	180 days	20/01/2011	-1.3889	-34.533				
-	168	M	MK10	90 days	06/03/2012	1.763	-42.977	NEVER REPORTED			
-	100	M	MK10	180 days	13/03/2012	-0.0565	-38.140				

*Individuals larger than the size at first maturity (180 cm).

**Recovered tag.

Temperature data were received as a daily histogram (24 hours). Both tag models transmitted light data in the form of two daily light curves (representing dawn and dusk) that were used to reconstruct geographic positions. The MiniPATs and the recovered MK10 also provided a daily analysis of the surface mixed layer depth and the amount of time the tagged shark spent therein.

All OCS were caught off the Northeast coast of Brazil by a commercial tuna longliner and tagging was conducted by an on-board observer with the help of the crew. Sharks were brought onboard to be measured and tagged and were out of the water for no longer than five minutes prior to release. Tags were attached at the base of the first dorsal fin using a loop of polyamide monofilament (2.0 mm) passed through a silicon tube, to minimize friction related injuries. Tagging locations were recorded using the vessel's global positioning system (GPS).

2.2. Vertical distribution

Depth data were analyzed in relation to the different periods of the day to account for diel movement patterns. Day, night, dawn and dusk data were grouped according to local times, which were estimated using the calculation procedure available from NOAA (http://www.srrb. noaa.gov/highlights/sunrise/sunrise.html). Data from the Mk10 tag that were summarized into six-hour histograms could not be grouped. Day was defined as the period between sunrise and sunset, and night as the period between astronomical dusk and astronomical dawn. Dusk comprised the hours between sunset and astronomical dusk, while dawn comprised the hours between astronomical dawn and sunrise. To compare daytime and nighttime depth distributions, Pearson's chi-squared test was performed at 95% confidence level. Crepuscular periods (dawn and dusk) were omitted from this analysis.

2.3. Horizontal movements

The horizontal movements of tagged sharks were estimated by processing the data received from the Argos satellite system using the manufacturer light-based geolocation software (WC-GPE: Global Position Estimator Program suite, available at: www.wildlifecomputers. com). Longitude is estimated from the time of local noon and latitude from the length of the day through the dawn and dusk symmetry method. In order to minimize the errors usually associated to this geolocation estimation [12,13], the tracks were post-processed using the IKNOS Walk model [14]. In this approach, tracks are corrected and interpolated at fixed intervals by bootstrapping random walk particles. The locations are estimated from a cloud of weighted particles and corrections can be applied based on known constraints or available data.

In the present study, the tracks were interpolated to obtain one position a day and were prevented from crossing land. A maximum speed threshold was also implemented into the model. Starting from 3 km/h, several speeds were tested up to 10 km/h (by 1 km/h increments). The maximum speed of 9 km/h was selected based on the end point criteria, meaning this maximum speed was the slowest speed that allowed all tracks to end at the known pop-up point. The error around estimated positions is displayed by 50 alternative positions for each point, representing minimum and maximum latitudes and longitudes.

To estimate the areas of high utilization, a Two-Dimensional Kernel Density Estimation was applied to the cloud of alternative points (error). Data from all individuals were combined in this analysis, conducted using the MASS package [15] in the R environment [16]. The bandwidth was chosen via Normal Reference Distribution. In order to expose areas of high utilization, density values smaller than 0.01 were excluded from the plot.

2.4. Fisheries data

Fishing effort data from the Brazilian tuna longline fleet between 1999 and 2011, totaling 65,277 sets, were used to assess the vulnerability of oceanic whitetip sharks to this fishery. The Brazilian fleet operates in a wide area of the equatorial and southwestern Atlantic Ocean and uses two distinct fishing strategies commonly referred to as "Japanese" (JAP) and "Spanish" (SPA). In general, vessels fishing with the Spanish strategy target swordfish (*Xiphias gladius*) and set surface longlines (down to 100 m) at night, using light sticks and squid as bait. Alternatively, vessels fishing with the Japanese strategy target various tuna species and set deep longlines (down to more than 200 m) early in the morning, using small pelagic fish as bait (mainly mackerel) [17]. Fishing effort was represented by the number of hooks deployed, grouped into 5° squares for spatial analyses.

Nominal catch per unit of effort (CPUE) data were analyzed to account for possible seasonal variations. A subsample of the dataset previously analyzed by Tolotti et al. [17] was considered for this purpose. This dataset was collected by the Brazilian Observer Program from foreign-chartered tuna longline vessels between 2004 and 2010. Spatial bounds for this data were selected based on the shark high utilization areas (from tag data), as well as on the area where the fishing effort was concentrated. The CPUE represented the number of OCS/1,000 hooks per quarter. Mean values were calculated using the sum of all catch and all effort in each quarter. Data were also grouped according to the fishing strategy. Two-sample Kolmogorov-Smirnov tests were used for inter-quarter comparisons at a 95% confidence level.

To evaluate the spatial overlap between fisheries and tagging data precisely, it would be necessary to use a CPUE index that accounts for the depth distribution of the hooks. In the absence of such data, an occurrence index was adopted. For this analysis, data were also grouped into 5° squares and by quarter. For each square, the number of sets with the presence of OCS were summed and then divided by the total number of observed sets. The occurrence values were then paired with the Kernel densities (also grouped by quarters and 5°×5° squares). For each square, density values were summed. A Spearman's Rank test was conducted to verify possible correlation between fisheries and tagging data (occurrence and Kernel density). The non-parametric Spearman's Rank was chosen after verifying that the two datasets did not conform to a bivariate normal distribution (Royston's Multivariate Normality Test, p = 9.217239e-06).

Table 2. Data reception of pop-up satellite archival tags and distances traveled by oceanic whitetip sharks tagged in the western Atlantic Ocean between 2010 and 2012.

ID	Tag	General data (%)	Geolocation (%)	Total track length (km)	Straight line distance (km)	Movement rate (km.day^{-1})
AOCS 1	MK10	07.63	10.00	1701	439	28
AOCS 2	MK10	31.39	63.33	6217	949	69
AOCS 3*	MK10	100.00	100.00	19043	493	107
AOCS 4	miniPAT	79.51	98.58	14273	1733	101
AOCS 5**	miniPAT	63.56	73.05	11355	580	81
AOCS 6	miniPAT	82.57	98.02	12117	145	120
AOCS 7	miniPAT	80.56	97.12	11250	305	108
AOCS 8	MK10	53.57	46.75	7118	966	92

*Recovered.

**Tag stopped recording data after 104 days of deployment and reception rates for the period were 86.17 and 99.04%.

3. Results

3.1. Tag performance

In total, 719 geolocation days, 1,643,249 depth records and 1,537,920 temperature readings from the 8 reporting tags were analyzed. Time at depth histograms totaled 951 and time at temperature 1,340. Overall, the miniPATs had higher reception rates than the MK10s for both general and geolocation data (Table 2). Except for one miniPAT (OCS5), reception rates were approximately 80% for general data and over 97% for geolocation. The OCS5 miniPAT stopped collecting data after 104 days of deployment, but popped to the surface and transmitted the data after 140 days as scheduled. Nonetheless, these data sets were almost entirely received (86.2% and 99.0% of general and geolocation data, respectively). The MK10 tags varied considerably in their reporting rates, and ranged from as low as 7% to up to 53% of the general data and from 10% to 63% for geolocation data (Table 2).

3.2. Temperature preferences and vertical distribution

Oceanic whitetip sharks exhibited a strong preference for warm and shallow waters. Tagged sharks remained at temperatures between 24 and 30°C for approximately 96% of the monitoring period (Figure 1). The time spent inside the mixed layer was very similar for all sharks, regardless of their size, and it varied between 70 and 83% (Table 3). AOCS4 and 7 entered the coldest waters of all tagged sharks. The minimum recorded temperatures were 8.2°C, with a corresponding depth of 368 m, for AOCS4, and 8.8°C at 448 m, for AOCS7. The latter also represented the deepest recorded dive of this study.

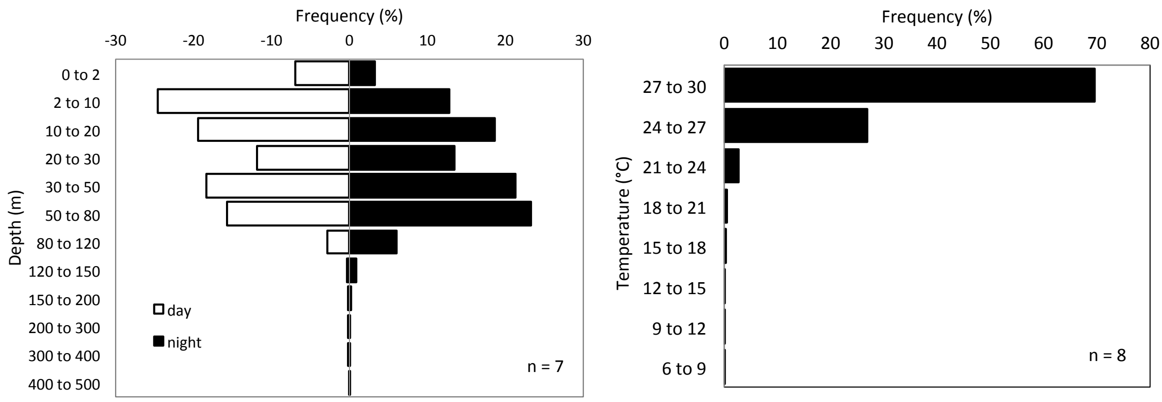

Figure 1. Depth and temperature preferences of oceanic whitetip sharks tagged in the western Atlantic Ocean between 2010 and 2012. Depth frequencies includes sharks OCS1 to 7 and temperature frequency includes data on all sharks.

For more than 95% of the monitoring period tagged sharks remained above 120 m, during both day and night periods (Figure 1). The aggregated data showed similar frequency distributions between day and night, although during the day shallower depth intervals were slightly more frequent, whilst the night distribution showed higher frequencies in deeper intervals. These differences, however, were not statistically significant (χ^2 test, p = 0.6727).

Table 3. Average time spent within the mixed surface layer by oceanic whitetip sharks tagged in the western Atlantic Ocean.

%MixL	AOCS 3	AOCS 4	AOCS 5	AOCS 6	AOCS 7
mean	76.97	70.43	73.87	73.47	83.56
SD	18.11	13.45	16.52	18.04	10.86
SE	0.68	1.71	1.71	1.87	1.14
1st quart.	67.00	61.00	64.00	61.00	79.50
median	80.00	72.00	79.00	77.00	85.00
3rd quart.	92.00	79.00	86.00	88.00	91.50

3.3. Horizontal movements

All sharks were tagged close to the equator and although individuals tended to travel long distances the pop-up positions were relatively close to the tagging locations (Figures 2A and 2B). The individual AOCS6, for example, moved as far as 12,117 km during the tag deployment, but the distance between tagging and pop-up locations was only 145 km (Table 2). A similar pattern was observed on AOCS1, 3, 5 and 7. AOCS5 and 7 stayed within 500 km of the tagging position during most of their track, while AOCS1 remained in this range for the entirety of its monitoring period (Figure 3). AOCS3 made more extensive movements but returned to de 500 km range after 127 days at liberty (Figure 3). Only one shark made extended movements to the south (AOCS4), reaching latitudes below 10°S. This shark moved south shortly after tagging and did not return to the tagging area within the 141 days of monitoring. The last part of its track, however, shows a northward movement (Figure 2A).

Total track lengths varied from 1,701 km, represented by the shortest deployment period (60 days), to 19,043 km, represented by the longest (178 days). Daily displacements varied considerably among sharks and ranged from 28 to

120 km.day^{-1} (Table 2). Overall, the horizontal movements were more pronounced in terms of latitude, whereas longitudinal movements were more restricted, not surpassing the 25° meridian.

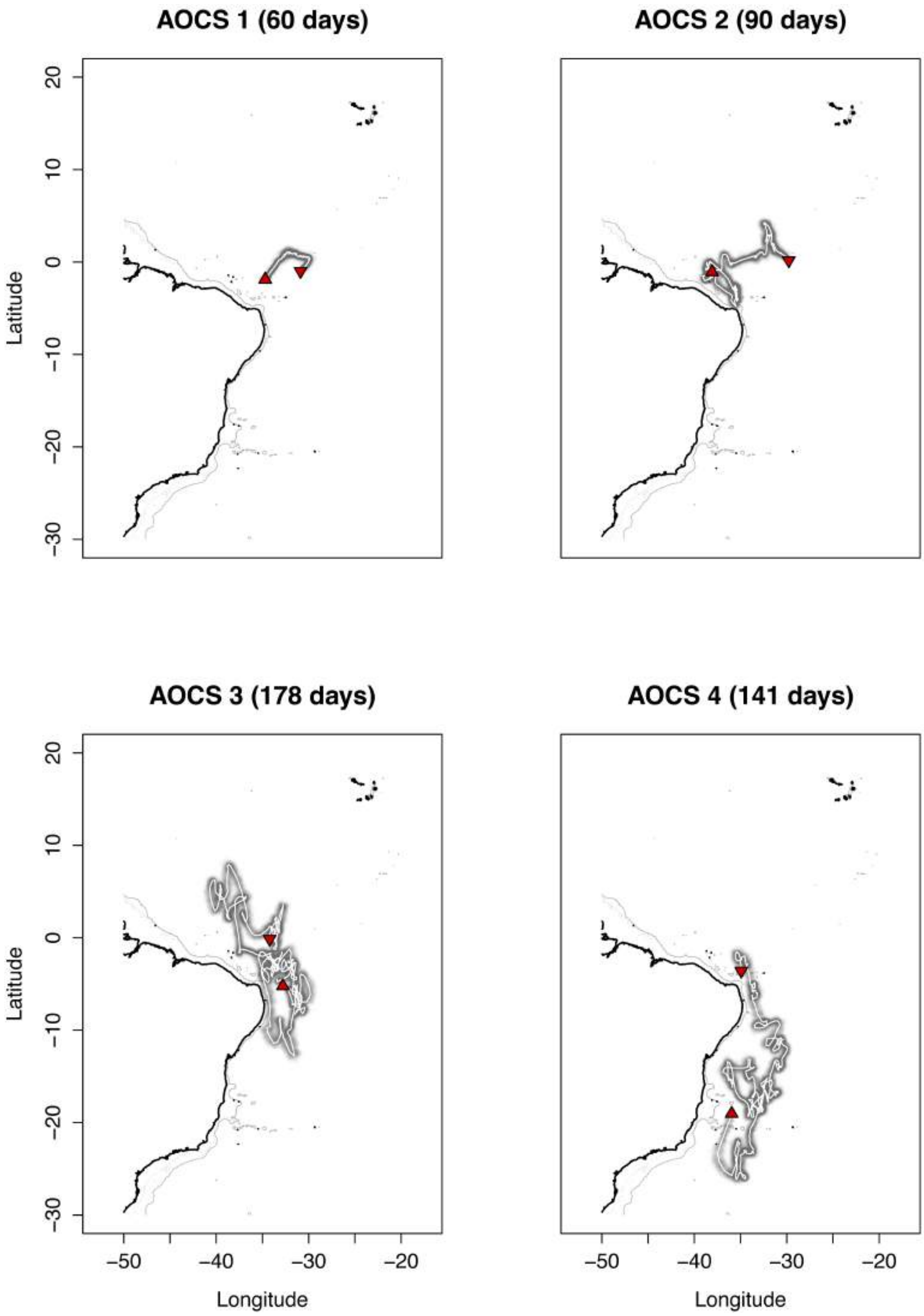

Figure 2A. Post-processed tracks of oceanic whitetip sharks tagged in the western Atlantic Ocean in 2010 and 2011. The downward triangles represent the tagging position and the upward triangles the end of the track. The grey-shaded area represents the error around estimated positions.

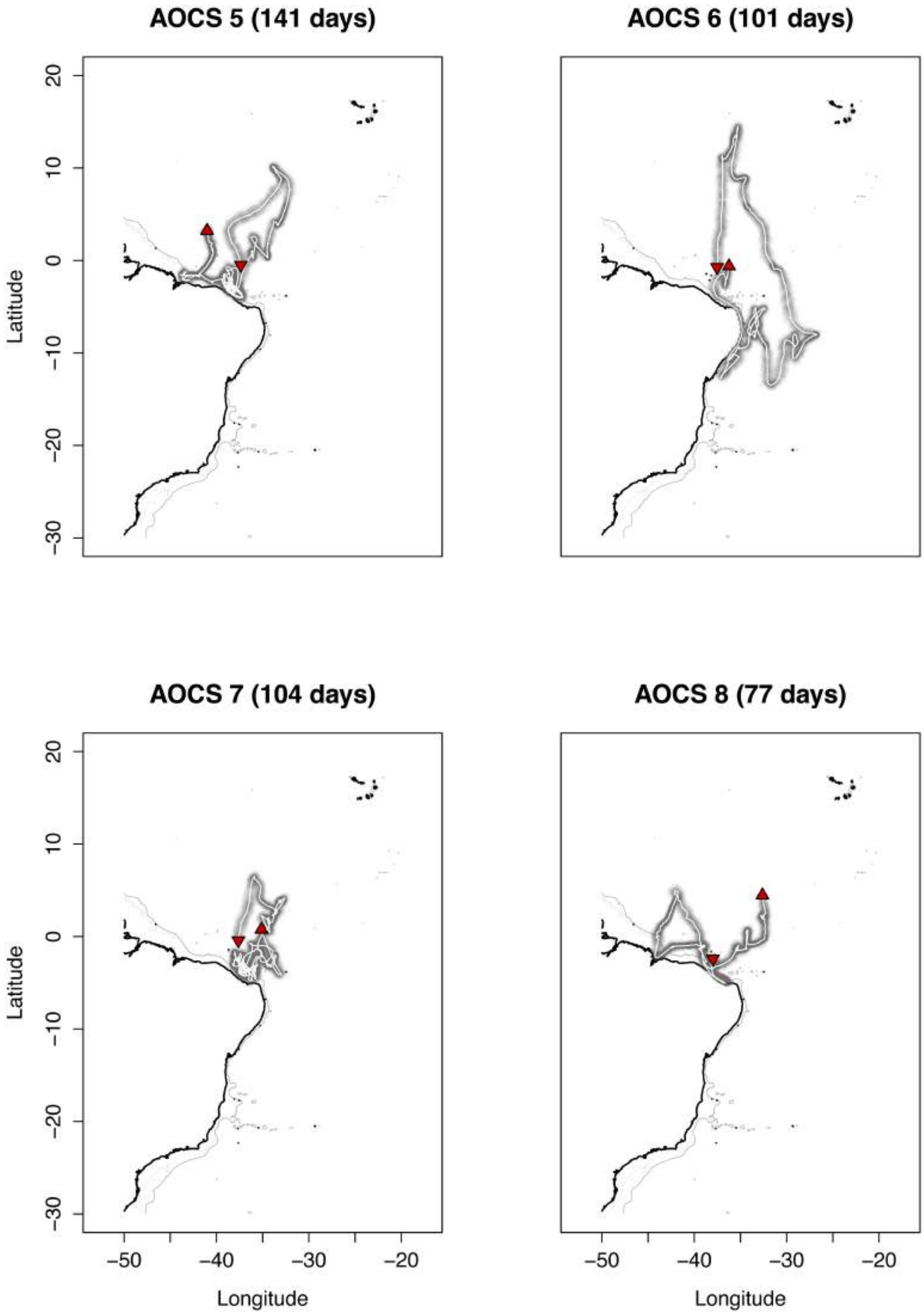

Figure 2B. Post-processed tracks of oceanic whitetip sharks tagged in the western Atlantic Ocean in March 2012. The downward triangles represent the tagging position and the upward triangles the end of the track. The grey-shaded area represents the error around estimated positions.

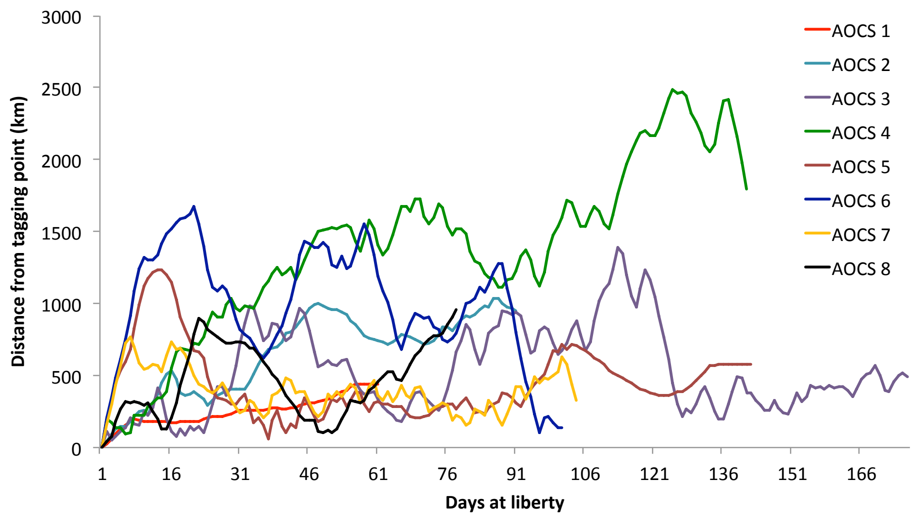

Figure 3. Distance from the tagging position as a function of days at liberty for oceanic whitetip sharks tagged in the western Atlantic Ocean between 2010 and 2012.

3.4. Fishing effort and CPUE

Between 1999 and 2011 the Brazilian tuna longline fleet deployed a total of 102,201,242 hooks. The sets were widely distributed in the equatorial and southwestern Atlantic Ocean, ranging from 10°N to 65°S in latitude and from 007°E to 055°W in longitude. The area with the highest effort concentration was bound by the 5°N and the 15°S parallels and by the 040°W and 035°W meridians (Figure 4). Despite the wide distribution of fishing sets, this area of highly concentrated effort is clearly evident. For both fishing strategies, SPA and JAP, most hooks were deployed within this area of concentrated effort. In contrast, the proportion of hooks deployed by fishing strategy varied considerably over time (Figure 5). From 1999 to 2002 the Japanese strategy accounted for the majority of hooks deployed, starting at 70% and gradually decreasing to 60%. From 2003 onwards, the Spanish strategy was consistently dominant, although some fluctuations were observed. During the years of 2008, 2009 and 2010 the Brazilian fleet consisted entirely of vessels fishing with Spanish strategy.

Mean CPUE values were similar throughout the year with slight differences in the second quarter. Overall CPUE values ranged between 0.08 and 0.17 sharks/1000 hooks for SPA and from 0.03 to 0.06 for JAP (Figure 6). The same trend was observed in both fishing strategies, although Spanish CPUE values were always considerably higher. For this fishing strategy the mean CPUE value of the second quarter was significantly lower compared to the other quarters (Table 4).

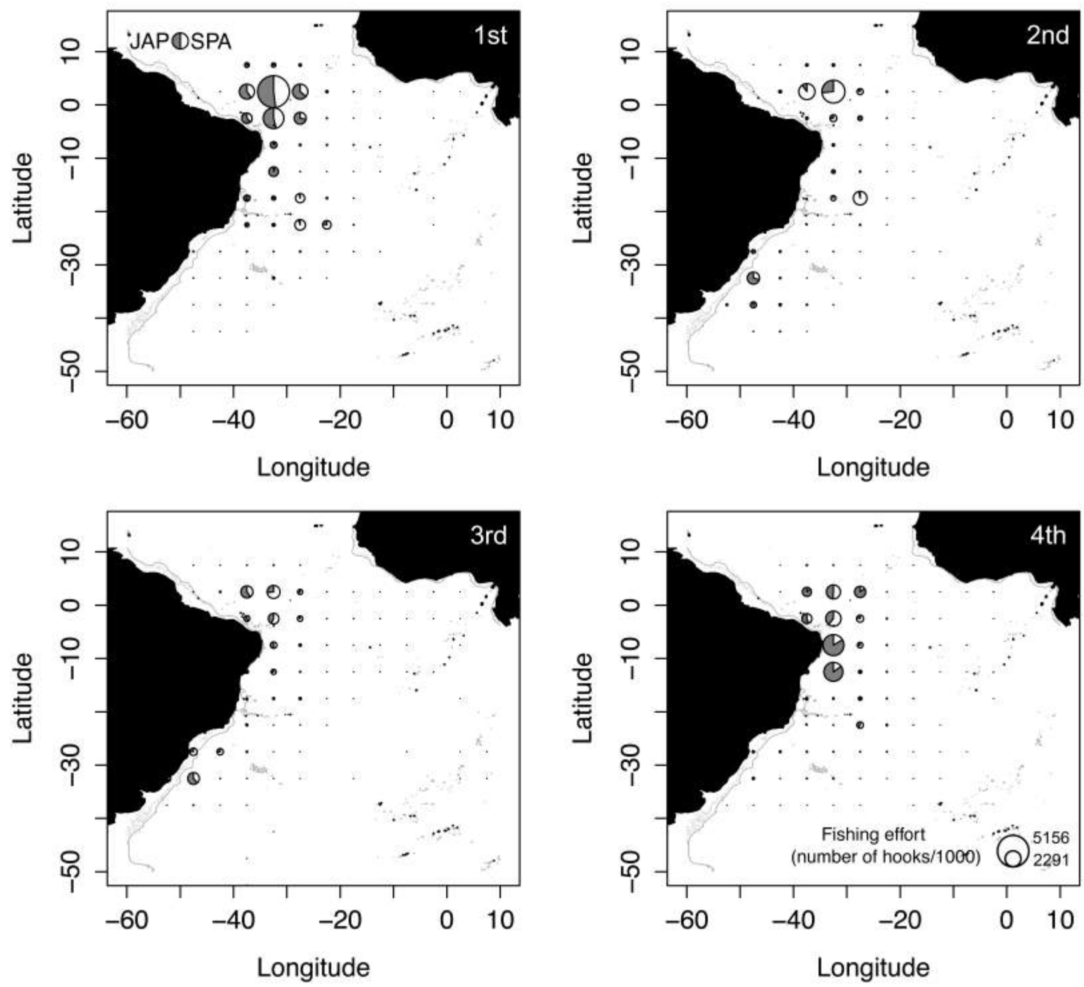

Figure 4. Fishing effort of the Brazilian longline fleet represented by the number of hooks deployed from 1999 to 2011.

Table 4. P-values of Two-sample Kolmogorov-Smirnov tests comparing CPUE values for all quarters of the year.

Quaters	*p* (combined)	*p* (SPA)	*p* (JAP)
1st x 2nd	0.0926	0.0195*	0.6940
1st x 3rd	0.5758	0.9505	0.9572
1st x 4th	0.9835	0.9921	0.8832
2nd x 3rd	0.0839	0.0584	0.5765
2nd x 4th	0.2976	0.0250*	0.9849
3rd x 4th	0.9957	1.0000	0.8950

*Statistically different, p = 0.05.

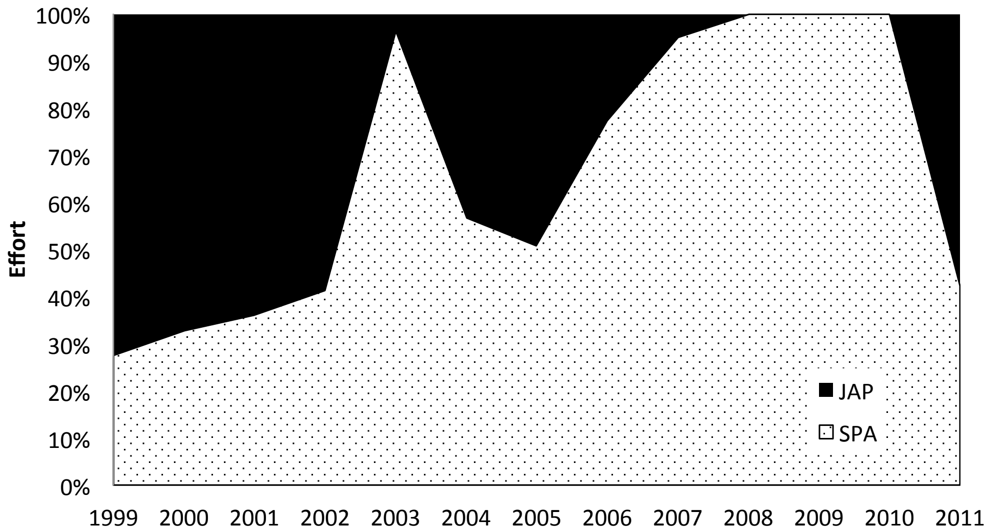

Figure 5. Proportion of the two different fishing strategies of the Brazilian longline fleet between 1999 to 2011.

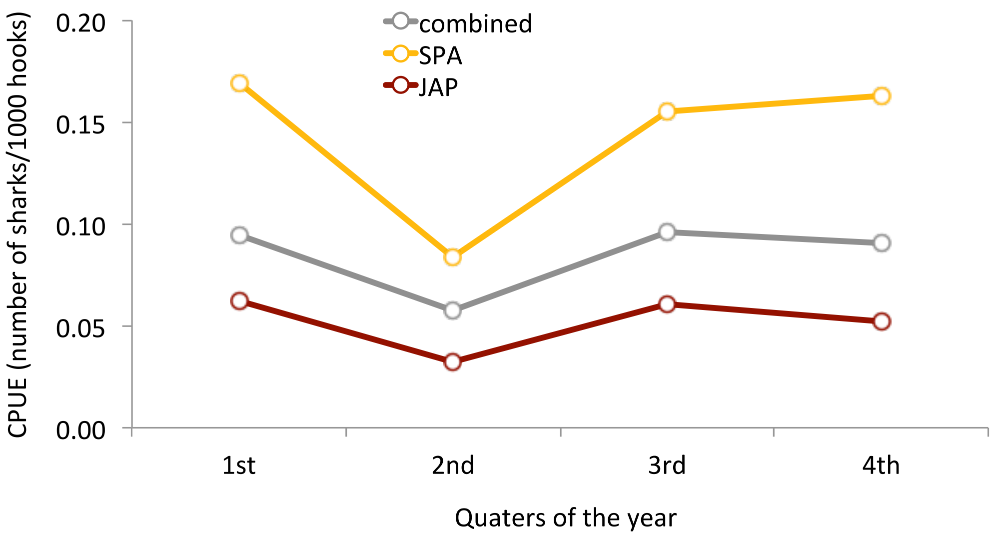

Figure 6. Mean CPUE values of oceanic whitetip sharks caught by foreign tuna longline vessels chartered by Brazil operating from 2004 to 2010.

3.5. Spatial dynamics of occurrence and Kernel density

Kernel densities were only estimated for the first two quarters of the year due to the concentration of tagging data during this period (Figure 7). The Kernel densities of combined tracks revealed two distinct areas of high utilization, one during each quarter of the year (Figure 8A). In the first quarter, high densities were concentrated very close to the Equator between the 035°W and the 030°W parallels. During the second quarter the highest density values were located closer to the coast just off northeast Brazil above the Cabo Calcanhar. Both high-utilization areas fall inside the high fishing effort zone, although second quarter sets were concentrated north of the OCS utilization hot spot (Figure 8B).

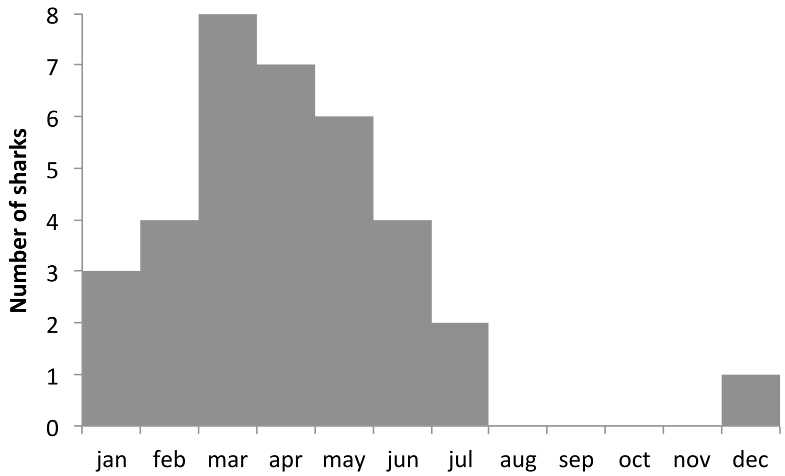

Figure 7. Number of oceanic whitetip sharks monitored per month.

The spatial distribution of OCS occurrence differed between the first two quarters of the year. Overall, high occurrence values appeared in the area towards the north of the study zone in the 1st quarter, while in the 2nd quarter high values were located towards the south (Figure 8A). The square located just off Cabo Calcanhar was the only area that showed similar values during both quarters. The greatest difference was seen in the southernmost square, with zero occurrences in the 1st quarter and 0.16 OCS presences per set in the 2nd.

A strong spatial correlation between occurrence and Kernel density estimation is not clearly evident in Figure 8A, although it is notable that high-density hotspots do fall inside squares with higher occurrence. Likewise, squares with very low occurrence (<0.05) have none or very little utilization according with the Kernel density estimation. This apparent positive correlation was confirmed by the Spearman's rank test, which rejected the null hypothesis that kernel density values and CPUE were not correlated (Spearman's Rank Test, p= 0.02009, rho= 0.5919304).

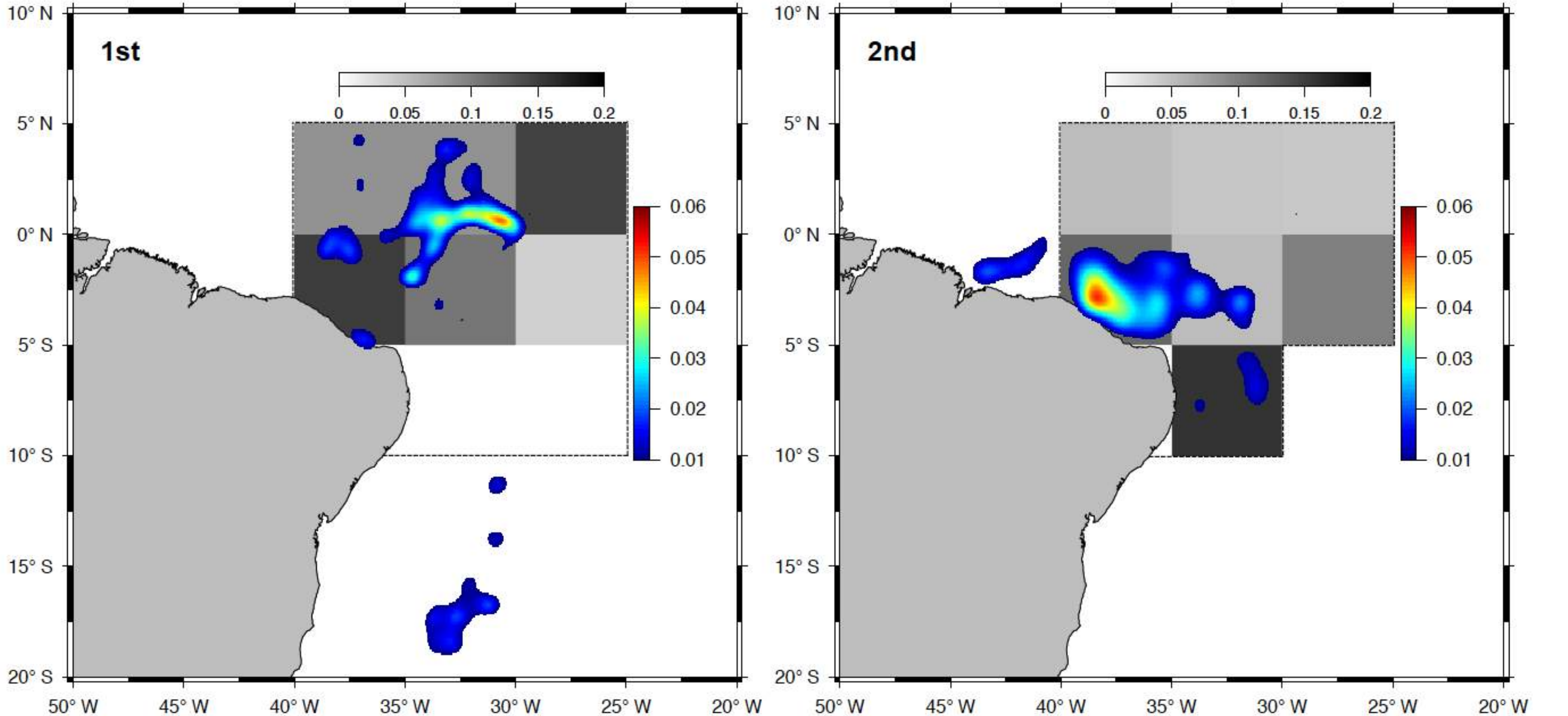

Figure 8A. Kernel density estimation of post-processed tracks showing the areas of high utilization by oceanic whitetip sharks tagged between 2010 and 2012 and values of occurrence per set (grey scale) for the species from foreign tuna longline vessels chartered by Brazil operating from 2004 to 2010. Doted lines mark the area where the occurrence data were analyzed. The left panel represents the 1st quarter of the year and the right represents the 2nd.

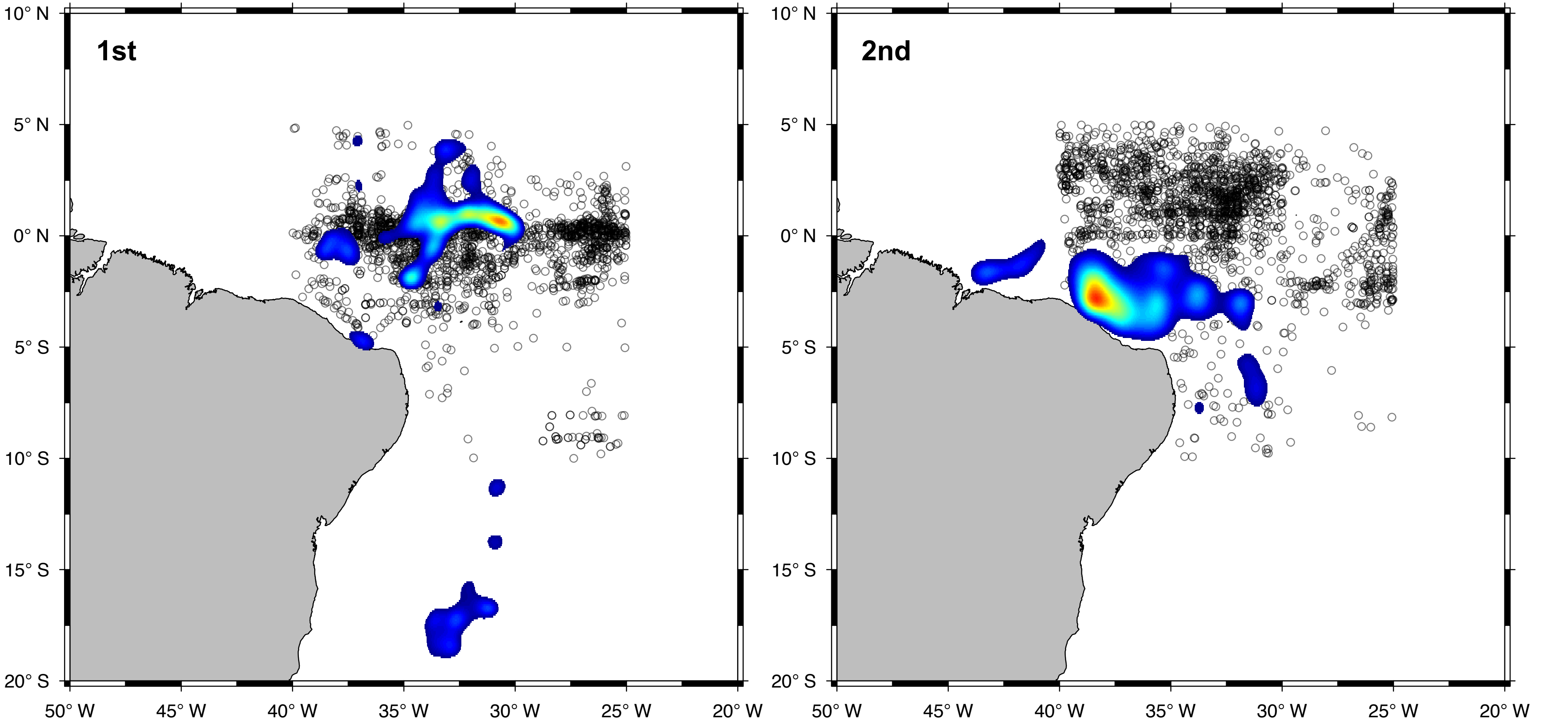

Figure 8B. Kernel density estimation of post-processed tracks showing the areas of high utilization by oceanic whitetip sharks tagged between 2010 and 2012 and fishing sets locations (circles) from foreign tuna longline vessels chartered by Brazil operating from 2004 to 2010. The left panel represents the 1st quarter of the year and the right represents the 2nd.

4. Discussion

4.1. Vertical vulnerability

The vertical movements observed in the present study are in agreement with the existing literature, which describes the oceanic whitetip shark as an epipelagic predator of warm tropical waters [2] and places the species in the group of pelagic fishes that spend the majority of their time in the upper uniform-temperature surface layer, rarely descending to waters below 20°C [18]. Through the use of electronic tags, two recent studies have also provided evidence to confirm these general statements. Musyl et al. [19], working near Hawaii, found that OCS were largely confined to the mixed layer (~120 m), spending>95% of their time at temperatures within 2°C of the sea surface temperature (SST). OCS from the North Atlantic (Bahamas) exhibited a similar vertical pattern, essentially occupying the upper 125 m of the epipelagic zone at temperatures close to the SST [20].

The oceanic whitetip shark's strong preference for shallow and warm waters is also reflected on the depths of the longline hooks where the species is most commonly caught. Nakano et al. [21], for instance, concluded that the catch rates of OCS increased significantly with the decrease of hook depth. In a more specific study, data from the Brazilian longline fleet showed that the CPUE for OCS tended to be lower for the vessels targeting tuna, which operate with deeper longlines (down to 200 m), than those targeting swordfish, which operate with shallower gear (>100 m) [17]. A sample of this data set, shown in Figure 7, further highlights the greater impact of the shallow Spanish fishing strategy on OCS CPUE values. This result comes with little surprise given that the depth range of the gear used in this fishing strategy corresponds exactly to the species vertical distribution.

This vertical overlap is particularly concerning when the majority of the Brazilian fleet operates with shallow longlines exactly in the area where the species can be most readily found. Although the proportion between the two fishing strategies (JAP-deep and SPA-shallow) in the Brazilian fleet varies considerably over the years, these fluctuations are mainly due to temporary fishing agreements between the Brazilian government and foreign companies [22]. The permanent Brazilian fleet, however, typically operates with shallow gear, primarily around the equator and close to seamounts [23], which means the vertical preferred habitat of the oceanic whitetip shark is extensively exploited.

The results from the present study, combined with other recently published works, show that the vertical distribution of the oceanic whitetip shark is well defined. Despite the clear need for further data to fill the extensive knowledge gaps on the ecology of the species, this information is already of great importance for defining mitigation measures. A ban on retaining, landing, storing or selling this species has been established by all tuna RFMOs. This measure, however, does not preclude fishers from catching oceanic whitetip sharks. Practical mitigation methods, such as eliminating shallow hooks (above 100 m) on longlines, require particular attention. The removal of shallower hooks has already shown promising results in reducing catch rates of several epipelagic bycatch species [24]. It is important to bear in mind, however, that mitigation measures can generate impacts on other species and so both their positive and negative impacts must be carefully evaluated [25].

4.2. Horizontal vulnerability

Oceanic whitetip sharks tagged in the southwestern Atlantic Ocean appear to have a certain degree of site fidelity to the area off northeast Brazil around the equator, where all of their tracks started. Five out of eight sharks have ended their tracks relatively close to their starting points, even after traveling several thousand kilometers. Three of these sharks also remained within 500 km of the tagging locations during most of the tracking period. Although time limitations prevent definitive conclusions from being drawn, a recent study conducted in the

Bahamas (northwestern Atlantic) also reported that OCS returned to the tagging area after long migrations [20]. The Bahamian study gathered data from 10 OCS with deployment periods up to 245 days. In the year following their study, scuba divers also spotted one of the tagged sharks near the tagging location [20]. The authors considered this returning behavior to fall under the definition of philopatry, which is the tendency of an organism to return or remain near a particular site [26]. The findings presented here further support this theory.

Another interesting observation is that oceanic whitetips from both studies (Northwestern and Southwestern Atlantic) did not mix. More data is certainly required before a conclusion can be reached, but this result could be an indication that northern and southern populations might well be separated. The recently developed “electronic spaghetti tag” could be a useful and cost-effective tool to investigate this matter. This new satellite tag does not record any data, but simply reports where it pops off, providing fisheries-independent measures of dispersal patterns and migration [27]. Fine scale genetic studies using microsatellite loci could also shed light on this matter [28]. If these hypotheses hold, well-defined populations and philopatric behavior can have substantial implications for the conservation of this species and suggest that the oceanic whitetip shark could benefit, not only from global management measures, but from local measures as well.

The distribution of the effort from the Brazilian longline fleet raises important concerns regarding the species’ vulnerability to fisheries, especially given its depleted population status [29–31]. The Kernel Density estimates indicate that the high utilization areas fall exactly within the area where the fishing pressure is considerably higher. The region off northeast Brazil, where OCS seems to have some degree of philopatry, is rich in oceanic features such as islands, banks and seamounts, mostly belonging to the North Brazil and Fernando de Noronha Chains, located between 2° and 4° South and 32° and 40° West [32]. The areas surrounding these features are considered important fishing grounds for tuna and tuna-like species, including sharks [23,33].

Interestingly, when looking at the study area at a finer scale the kernel hot spot for the second quarter appears to be slightly outside of the highest fishing pressure area (Figure 8B). In this quarter, the high-utilization hot spot of oceanic whitetip sharks is located just off northeast Brazil above the Cabo Calcanhar and below the equator, while most of the fishing sets at this time of the year were made just above the equator. This lack of overlap between the species high-utilization area and fisheries highest effort could explain the significantly lower CPUE during the second quarter as seen in Figure 6. A much stronger overlap is seen on the first quarter, which had a higher average CPUE. Considering the time limitation of the study (tagging data concentrated on the first semester) and the few individuals tagged, it is interesting to find a spatial correlation between fisheries and tagging data. The philopatric behavior combined with the fact that tagging was conducted through commercial fishing vessels, might have contributed for this result. Tagging oceanic whitetip sharks outside of the major fishing zone would provide essential information for validating these findings. In any case, the correlation found here highlights the potential that tagging experiments hold for providing knowledge for the design of spatio-temporal management measures.

More data are clearly needed to understand the spatial dynamics of oceanic whitetip sharks in the southwestern and equatorial Atlantic and more tagging experiments should be encouraged. Future studies should focus on covering the entire year cycle through both long deployment periods and tagging during different seasons. Improved fisheries monitoring is also of extreme importance and observer programs therefore require expansion. This study also highlights how fisheries dependent and independent data sources can complement one another.

5. Acknowledgements

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Chapter 6

Fine-scale vertical movements of oceanic whitetip sharks

Abstract

Time series of depth records from six oceanic whitetip sharks tagged with pop-up satellite archival tags (PAT) were analyzed in detail. The aim was to improve our knowledge on the vertical behavior of this specie. Sharks were tagged in the Atlantic (5) and Indian oceans (1) between 2011 and 2012. Deployment periods varied from 100 to 178 days. The sharks spent most of their time in the mixed layer, confirming the status of epipelagic species. However, the analyses revealed complex vertical movement patterns, including marked diel changes and behavior modes. Generalized Additive Models indicated that vertical movements were strongly correlated with variations of the depth of the mixed layer. A correlation between vertical movements and sea surface temperature (SST) was also observed. When SST was above average oceanic whitetips increased their vertical activity disregarding the shrink of the mixed layer. This pattern suggests that thermoregulation might occur for the species.

1. Introduction

The oceanic whitetip shark (*Carcharhinus longimanus*) is a threatened pelagic predator from tropical waters ocean wide (Bonfil et al., 2008). The species is a common bycatch of open water fisheries targeting tuna (*Thunnus* spp.), swordfish (*Xiphias gladius*) and other tuna-like species (Beerkircher et al., 2000; Frédou et al., 2015; Gallagher et al., 2014; Hall and Roman, 2013; Oliver et al., 2015). The oceanic whitetip acquired its threatened status due to the increasing fishing pressure throughout its range and due to a lack of knowledge regarding its biology and ecology (Baum et al., 2006). Under the precautionary approach, a series of management measures, which banned the landing, storing and selling of oceanic whitetip sharks, were recently implemented by all Tuna RFMOs (Tolotti et al., 2015a). The species is now the only pelagic shark protected in all three oceans. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) has also included the oceanic whitetip in appendix II, meaning its trade must now be closely controlled (CoP16 Prop. 42).

The lack of knowledge regarding the biology and ecology of the oceanic whitetip shark partly comes from its bycatch nature, which has historically resulted in fewer incentives for research and conservation (Barker and Schluessel, 2005). In light of the ocean wide declining scenario of the species' populations and of an increased interest for conservation of bycatch species, the scientific community has directed significant research efforts to fill these wide knowledge gaps. The recent research included reproductive biology (Tambourgi et al., 2013), feeding (Madigan et al., 2015), fisheries (Rice and Harley, 2012; Tolotti et al., 2013), movement patterns and behavior (Howey-Jordan et al., 2013; Musyl et al., 2011; Tolotti et al., 2015a). The latters used satellite archival tags to reveal valuable information concerning their horizontal movements, depth preferences and temperature ranges. Most of the published information, however, consisted on general summaries and vertical movements were not explored in detail.

The aim of this study is to provide information on the vertical movement patterns of the oceanic whitetip shark, in order to go beyond the existing knowledge that this is an epipelagic species. Do oceanic whitetip sharks exhibit diel vertical patterns? Do they display different vertical behavioral modes? Is their vertical behavior driven by the environment? Are they strictly restricted to the mixed layer? Improving our knowledge on bycatch species is an essential step towards an ecosystem-based fisheries management, which focus on the ecosystem as a whole rather then on maximizing individual target species (Garcia and Cochrane, 2005; Pikitch et al., 2004).

2. Material and methods

Time series of depth records from six oceanic whitetip sharks were analyzed in detail. All time series came from pop-up satellite archival tags (PAT) deployed in the Atlantic (5) and Indian (1) oceans on 2011 and 2012 (Table 1). Deployment periods varied from 100 to 178 days. Summarized results of the 5 tags deployed in the Atlantic were previously described in Tolotti et al. (2015), as well as the tagging protocol. The Atlantic sharks were tagged close to the equator on the western side of this ocean. All individuals made extensive movements, but remained mostly in the equatorial zone. Only one shark migrated south (Figure 1). The shark tagged in the Indian Ocean was caught with hand line during a research cruise on the Mozambique Channel. For the tagging procedure, this shark was brought on board and placed in a tagging cradle. The tag was attached intramuscularly under the first dorsal fin using a stainless steel tether and large Wilton anchors. This individual was tagged inside the Mozambique Channel and migrated north, following the African coast until Somali (Figure 1).

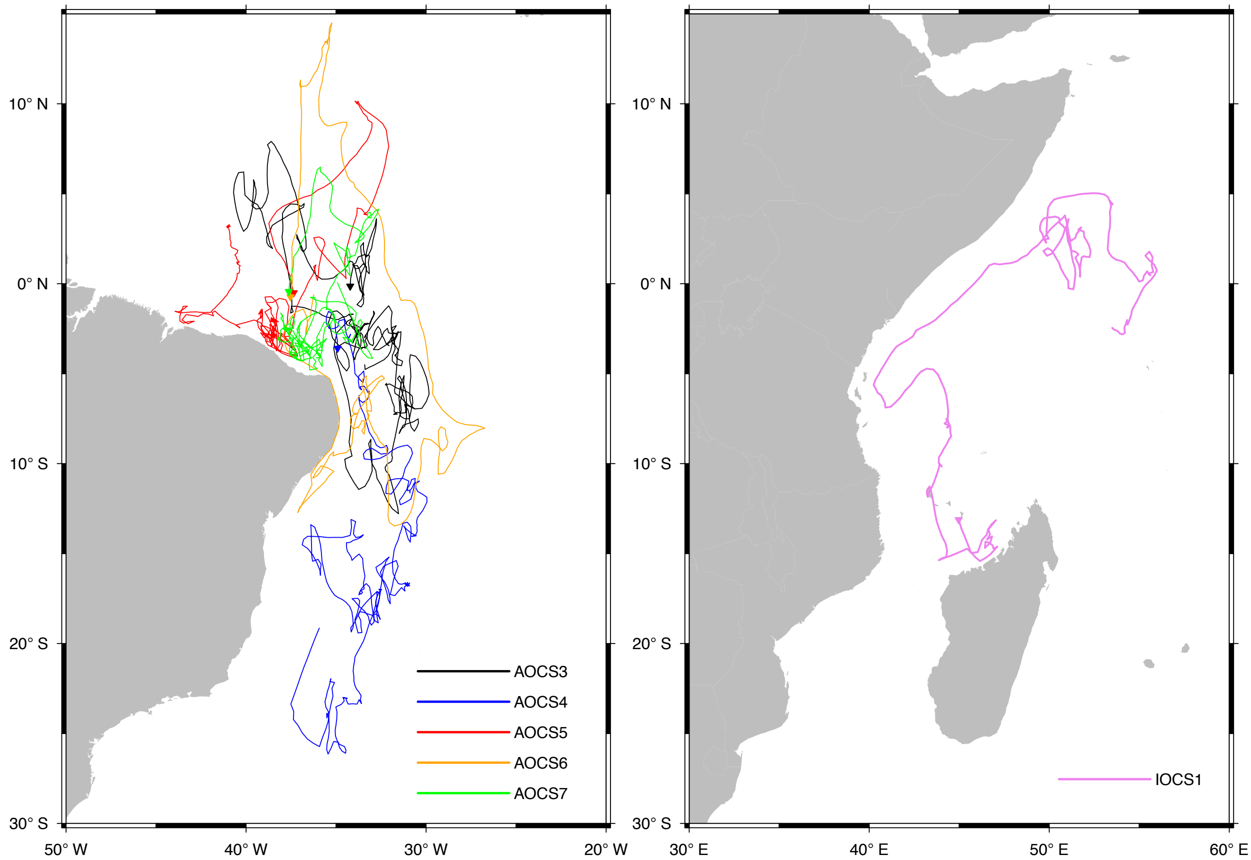

Figure 1. Tracks of oceanic whitetip sharks tagged with pop-up satellite archival tags in the Atlantic and Indian oceans during 2011 and 2012.

Table 1. General information regarding the electronic tagging of oceanic whitetip sharks in the Atlantic and Indian oceans.

						TAGGING			POP-UP			
ID	TL (cm)	SEX	OCEAN	TAG	PROGRAMED	DATE	LAT	LON	DATE	LAT	LON	DURATION
AOCS3	167	M	Atlantic	MK10**	180 days	16/01/2011	-0.139	-34.218	10/07/2011	-3.802	-32.466	178
AOCS4	197*	F	Atlantic	miniPAT	140 days	06/12/2011	-3.589	-34.918	25/04/2012	-18.754	-35.771	141
AOCS5	180*	F	Atlantic	miniPAT	140 days	01/03/2012	-0.501	-37.354	20/07/2012	3.215	-41.015	141***
AOCS6	134	F	Atlantic	miniPAT	100 days	02/03/2012	-0.736	-37.534	11/06/2012	-0.598	-36.235	101
AOCS7	161	F	Atlantic	miniPAT	100 days	02/03/2012	-0.435	-37.629	14/06/2012	1.306	-35.345	104
IOCS1	183*	F	Indian	miniPAT	100 days	15/04/2011	-13.119	44.967	24/07/2011	-2.522	53.554	100

*Individuals larger than the size at first maturity (180 cm);

**Recovered tag;

***Tag stopped recording data after 104 days of deployment

2.1. Data description

Pop-up satellite archival tags typically store depth (ambient pressure), water temperature and light level readings at 10 seconds intervals. This information is then used to produce different data products that are transmitted via satellite after the tag detaches from the animal. Transmitted data will depend on tag model and user-defined settings. Two models of PAT tags, manufactured by Wildlife Computers (Redmond, USA), were used in this study, 5 miniPATs and 1 MK10. The miniPATs were programmed to transmit depth time series with a resolution of 5 minutes. The MK10 do not transmit time series, only an aggregated summary of the recorded data, however this tag was physically recovered from Crystal Beach (Texas) after drifting at sea for about one year since its pop-up. This allowed the download of the complete depth and temperature time series with 10 seconds resolution. Although MiniPATs were not programmed to transmit temperature time series, other transmitted data products provided information on the surrounding environment. These products include a daily analysis of the surface mixed layer and sea surface temperature (SST), as well as a summary of temperature at depth profiles (PDTs). These data products were also available from the recovered MK10.

2.2. Data analysis

2.2.1. Vertical movement patterns

The periods of the day were classified according to local times of sunrise and sunset, following the procedure described in Tolotti et al. (2015) and according to the NOAA estimation (http://www.srrb.noaa.gov/highlights/sunrise/sunrise.html). Since sharks performed extensive horizontal movements during their monitoring periods, local sunrise and sunset times varied within and between individuals. These variations, however, were not superior to 50 minutes difference. To facilitate graphic representations where data is aggregated, day, night dawn and dusk were marked by their respective minimum and maximum estimated times. Daytime and nighttime depths were compared through the non-parametric Wilcoxon Test at 95% confidence level. For this analysis, depths corresponding to crepuscular hours were excluded. Depth data was also grouped into one-hour intervals of mean values to test for uniformity over the 24h cycle. The uniformity was tested using circular statistics (Rao's Spacing Test), also at 95% confidence level.

A spectral analysis was carried out with the time series of the recovered tag (AOCS3), since it does not have any transmission gaps. The aim was to look for periodicity in the vertical behavior and infer on possible temporal patterns. A fast Fourier transformation (FFT) algorithm was used through the build-in Stats package in R (R Core Team, 2013). The function calculates a smoothed periodogram using Daniell windows, which are modified moving average filters. The raw periodogram is a wildly fluctuating estimate of the spectrum with high variance and this smoothing methodology provides a stable estimate (Bloomfield, 2004). The spectral analysis is particularly well suited for long-term and high-resolution time series, including those from archival tagging studies (Shepard et al., 2006).

The time series were also visually assessed in order to examine any possible vertical patterns that could have been masked when grouping the data. They were conducted with the help of a visualization tool that enabled zooming and scrolling of the time series. The visualization window was adjusted to fit two days at a time. In this analysis, the times of sunrise and sunset did no need to be estimated. Instead, the depth readings were paired with the light readings transmitted by the tags. The light data is transmitted in the form of two daily light curves, representing sunrise and sunset. For the recovered tag the complete time series of light readings is available. The paring between light curves and depth readings was possible thanks to IGOR Pro, a graphing and analysis software developed by WaveMetrics, Inc. The tag's manufacturer data portal (WC-DAP:

Wildlife Data Analysis Program) exports a file that is formatted for use with IGOR Pro, which facilitated the visual assessment analysis. This paring also increased the precision when looking for diel patterns.

2.2.2. Vertical movements and the environment

To reconstruct the vertical environment occupied by the oceanic whitetip sharks during their monitoring periods the temperature at depth summary data (PDT) was used. This data product provides the minimum and maximum temperatures at fixed 8m depth intervals every 24h. The average temperatures of each depth interval were linearly interpolated to produce continuous daily temperature profiles with a 0.5m grid resolution, following the method described in Bauer et al. (2015). The interpolated temperature profiles were then plotted using a heat-color scheme. This method was chosen since it was proved to be a good alternative in the absence of temperature time series (Bauer et al., 2015).

Generalized Additive Models (GAMs) have been used to model habitat preferences on a variety of oceanic species, including sharks (Bustamante and Bennett, 2013; Damalas and Megalofonou, 2010; Lam et al., 2014; Zagaglia et al., 2004). In this study, a GAM was applied to model the vertical movement of oceanic whitetip sharks based on the environmental data transmitted by the tags. The daily standard deviation (SD) was considered to be a proxy of sharks' vertical variability (movement amplitude) and, therefore, chosen as response variable. The explanatory variables included geolocation estimates (longitude/latitude), sea surface temperature (SST), mixed layer depth (MLD) and shark size were introduced as smoothing terms (thin plate regression splines). To assess temporal effects, "month" was included as factorial variable. Since sharks were tagged in two ocean basins (Atlantic and Indian), "ocean" was also included as factorial variable. Modeling was conducted using the gam function of the mgcv R-package (Wood, 2006), using the Gaussian family. All possible combinations between variables and factors were tested, totaling 63 models. Models were also run separately for each individual shark in order to investigate individual variability. In this case, “ocean” and “size” were not considered, resulting on 15 possible combinations. Model selection was based on the Akaike’s information criterion (AIC) and further evaluated with residual analysis.

3. Results

3.1. Vertical movement patterns

3.1.1. Diel patterns

Diel changes in vertical behavior are visible across the time series of all individuals. However, different patterns were also observed within and between individuals. The strongest signal was observed during crepuscular hours, especially at dawn, when sharks swam at considerably shallower depths (Figure 2) and spent more time in the firsts 10 m. Circular statistics, applied to the average depth per hour of each individual, revealed a lack of uniformity over a 24h cycle for all oceanic whitetip sharks (Rao’s Spacing Test $p>0.001$). The tests result highlights the consistency of this crepuscular pattern, present even when day and night differences are not observed.

Regarding day and night differences, Figure 2 also shows a general pattern of shallower average depths during daytime as opposed to nighttime, when tagged sharks appear to move to deeper waters. This pattern is well marked for sharks AOCS4, 5, 7 and IOCS1, which exhibited statistically significant differences between occupied depths of light and dark hours (Table 2). For sharks AOCS3 and 6, the average depths did not evidence differences between day and night and statistical differences were not detected either. Another interesting feature draws attention on Figure 2. Daytime average depths form a slight U-shape, with the tagged sharks being in relative shallow waters at sunrise, gradually moving deeper as midday approaches and, finally, returning to shallow waters at dusk.

The U-shape can be observed even when day and night average depths do not differ, as is the case of shark AOCS3.

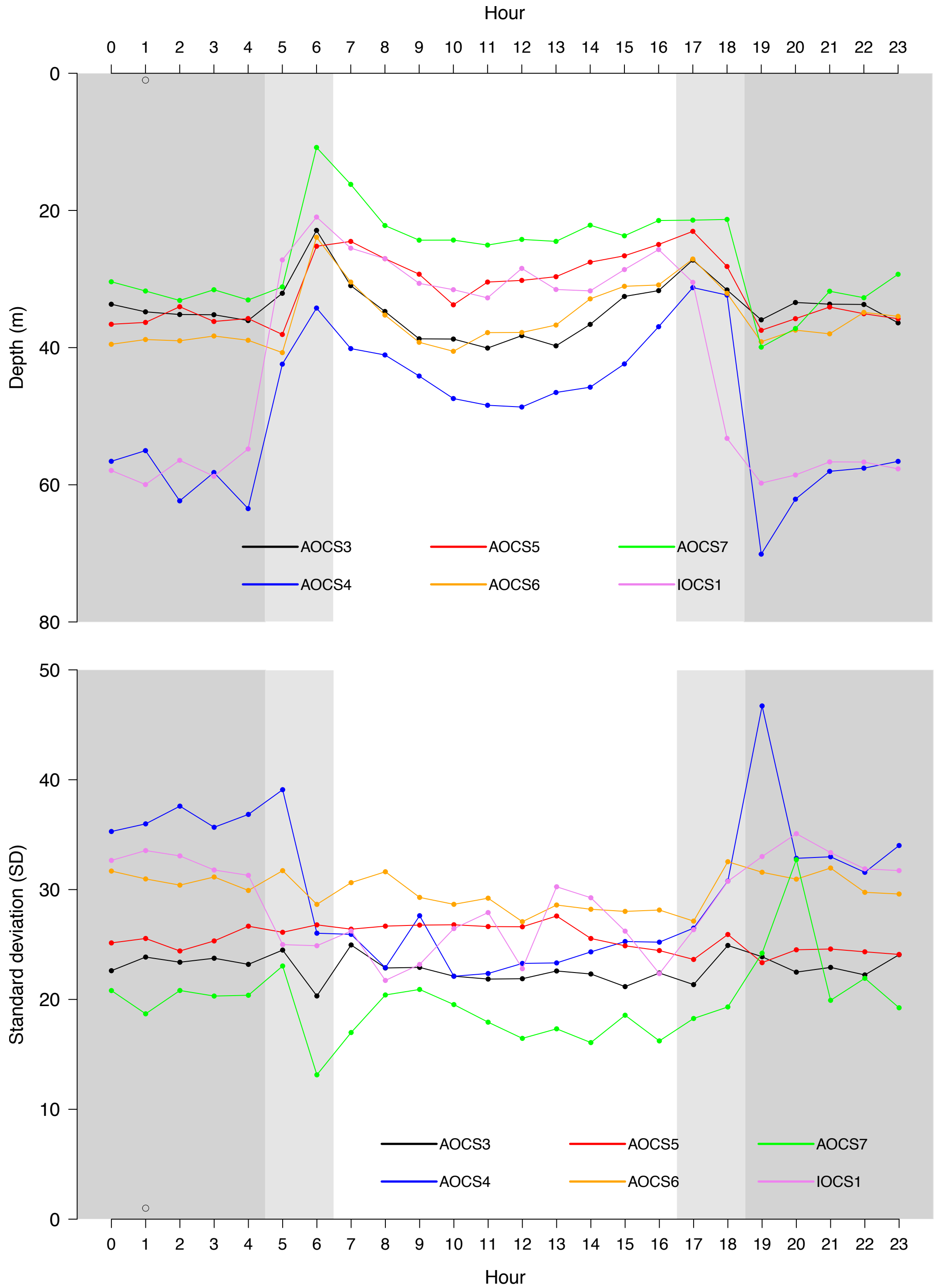

Figure 2. Hourly average depth and standard deviation of oceanic whitetip sharks tagged in the Atlantic and Indian oceans. Light shaded areas represent crepuscular periods, dark shaded areas represent night and white area represents day.

Table 2. P-values of Wilcoxon Tests comparing day and night depth values of oceanic whitetip sharks tagged in the Atlantic and Indian oceans.

Wilcoxon–Mann–Whitney Test (day ~ night, alpha=0.05)	p-value
AOCS3	0.5448
AOCS4	2.646e-05 *
AOCS5	2.646e-05 *
AOCS6	0.1087
AOCS7	2.646e-05 *
IOCS1	2.646e-05 *

*Statistically significant

Hourly standard deviation did not show the same marked trend as average depth (Figure 2). Overall, SD values did not vary much across the 24h cycle. Contrary to this overall trend, sharks IOCS1 and AOCS4 exhibited higher SD values during the night than during the day. Considering SD as a proxy for frequent vertical variations, these sharks seemed to be much more active during nighttime. Besides the marked difference between day and night activity, shark AOCS4 also exhibited a sharp SD peak shortly after sunset. Similarly, shark AOCS7 showed a sharp peak at around 20h.

The spectral analysis performed on the high resolution time series of AOCS3 revealed two distinct peaks, one at 12 hours and another at 24h (Figure 3). The sharp 12h peak most likely represents the crepuscular pattern described above. The sharpness of this peak also indicates a high degree of consistence of this diel pattern, meaning that the behavioral shift frequently occurs around the same time of the day. The 24h peak indicates that periodical behavioral shifts regarding daytime and nighttime depths are also occurring. The broad base of this peak, however, implies that there is a high degree of variability as to when these shifts occur. This is an interesting result that did not appear when the depth readings were aggregated by hour, since Figure 2 showed no differences between day and night average depths of this individual. The FFT leaves no doubt that this shark exhibited regular behavioral shifts between light and dark hours.

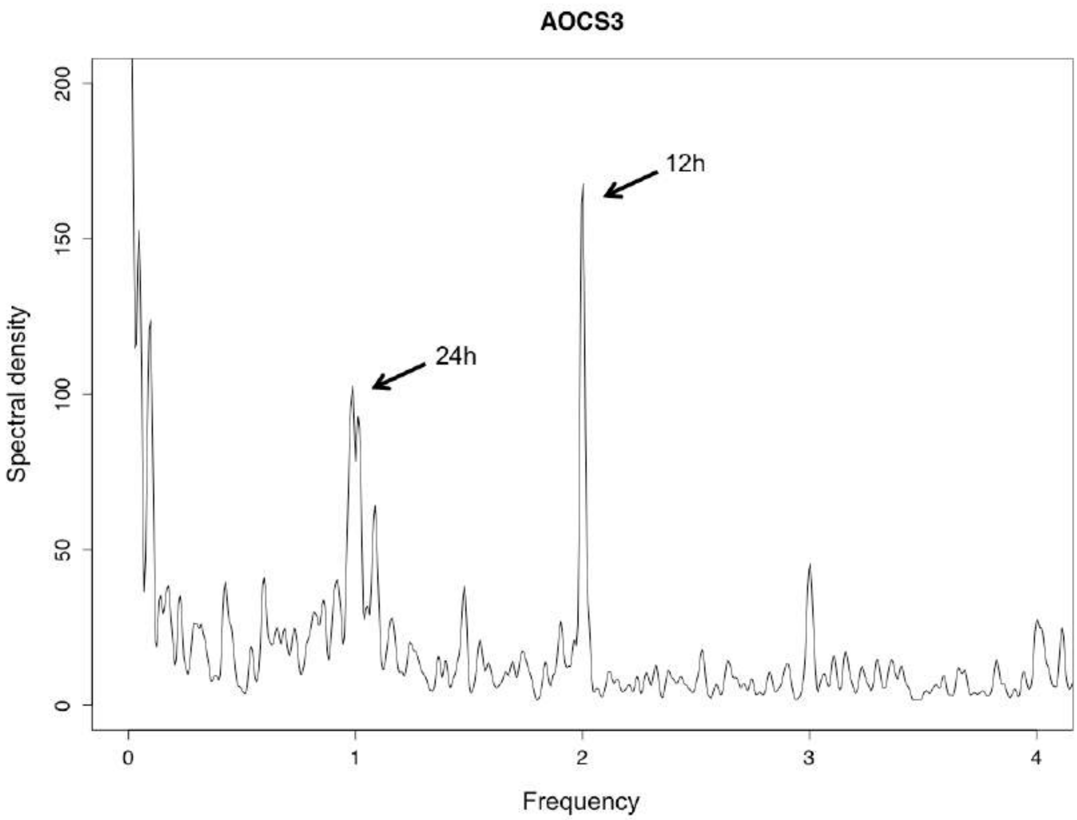

Figure 3. Periodogram generated by fast Fourier transforms of the continuous depth data of shark AOCS3. The cycles are expressed by 1/(frequency(x)).

The visual assessment of each time series allowed the identification of three main types of day/night behavioral patterns. Type I was characterized by a preference for shallower waters with some sporadic deep dives during the day, while during the night, sharks occupied deeper waters with regular up and down movements. Type II behavior features the inverse pattern observed on type I, with deeper waters occupied during daytime as opposed to nighttime, and also exhibiting regular up and down movements. On type III behavior no clear difference between day and night depth preferences was observed. Examples of each behavior type can be seen on Figure 4. All individuals exhibited the three behavioral patterns along their monitoring time, but the representativeness of each type varied largely among sharks (Figure 5). Type II was the least frequent behavior on all time series and occurred more often on AOCS3, representing 23.7% of this individual's time series. Type I behavior dominated the time series of sharks AOCS4 (41.0%) and IOCS1 (61.2%), while type III dominated the series of AOCS5 (62.8%) and 6 (50.5%). Note that due to gaps in the transmission data, some 24-h periods were not observed, and therefore could not be classified in one category.

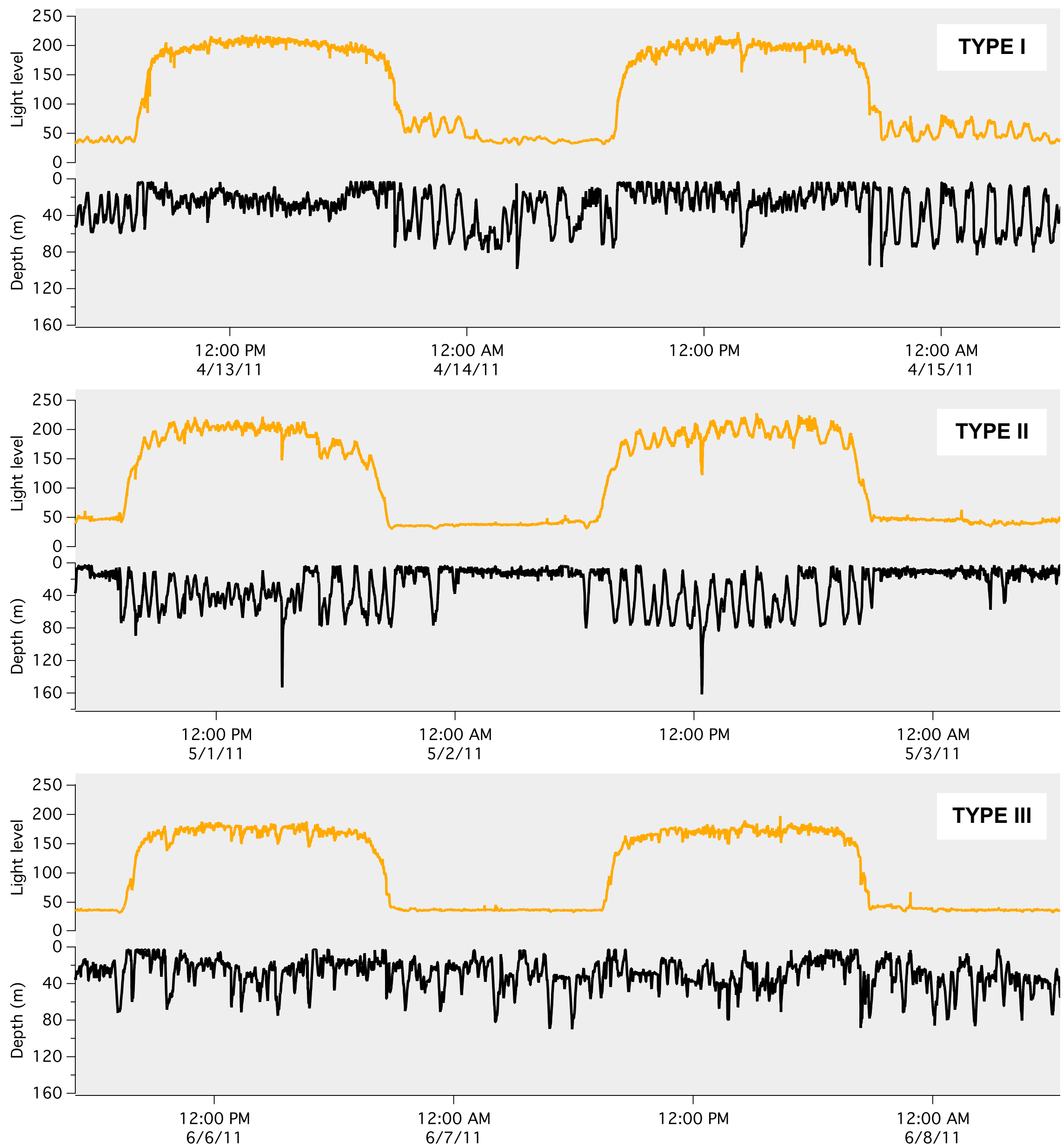

Figure 4. Behavior types identified during the visual assessment of the time series.

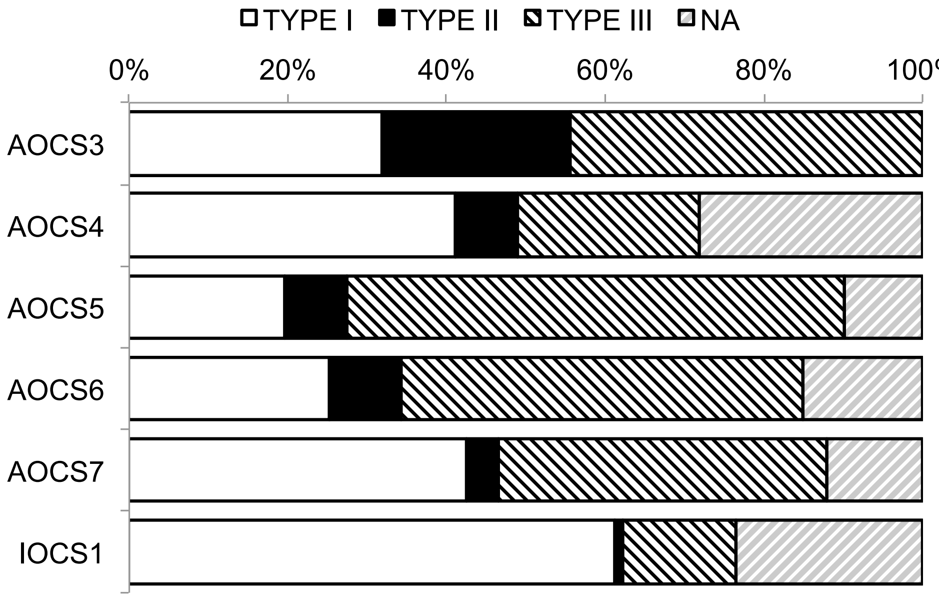

Figure 5. Proportion of the behavior types on the series of oceanic whitetip sharks.

The distribution of these types of behavior along the time did not appear to be uniform nor to follow a particular pattern (Figure 6). Shark AOCS3, for instance, exhibited the three types of behavior almost in the same proportion (Figure 5) and these behaviors were highly intercalated across its time series. Long sequences of the same behavior type were rare for this individual, the maximum being nine consecutive days of type I (Figure 6). In fact, long sequences of one behavior type were only seen when this particular behavior was already predominant for the individual, like type I for IOCS1 and type III for AOCS5. For all sharks, one isolated day of any behavior type occurred more frequently than any sequence. Only one individual, shark AOCS4, seemed to show a clear shift on behavior with time (Figure 6). During its first fifty days of monitoring, this shark exhibited type I behavior almost exclusively. After this period, shark AOCS4 started to intercalate type I with the other behavior types. At the same time, the amount of gaps present in the first 50 days of the time series weakens the representativeness of this constant pattern.

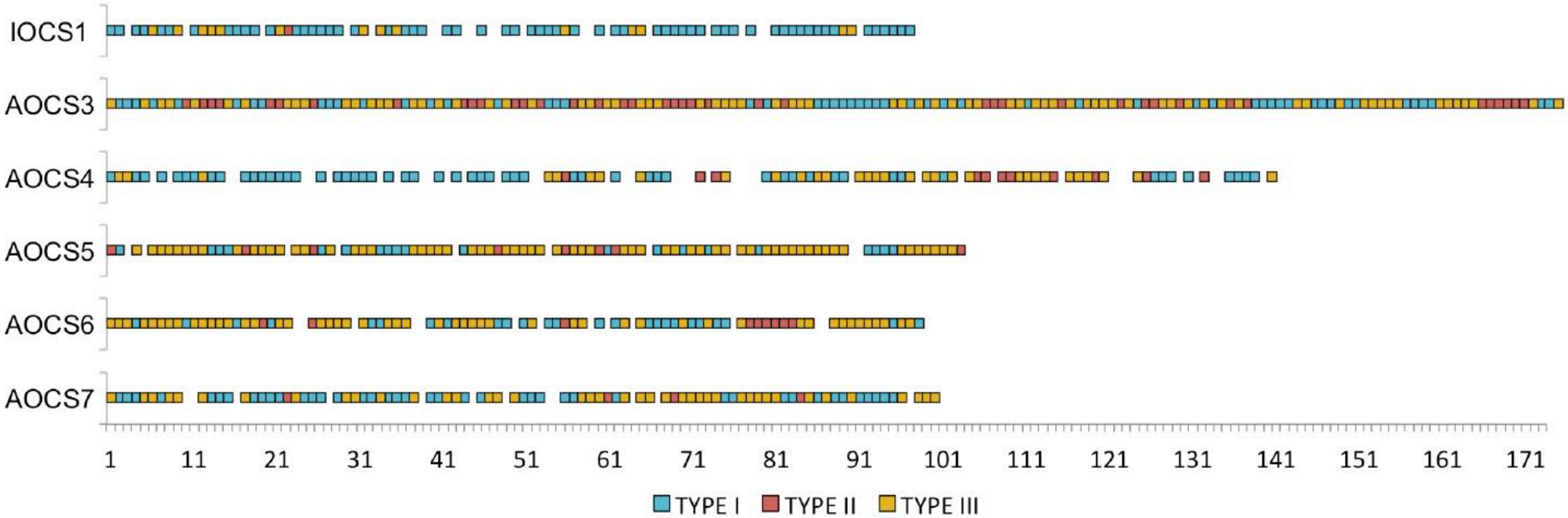

Figure 6. Sequence of the behavior types across the time series of oceanic whitetip sharks.

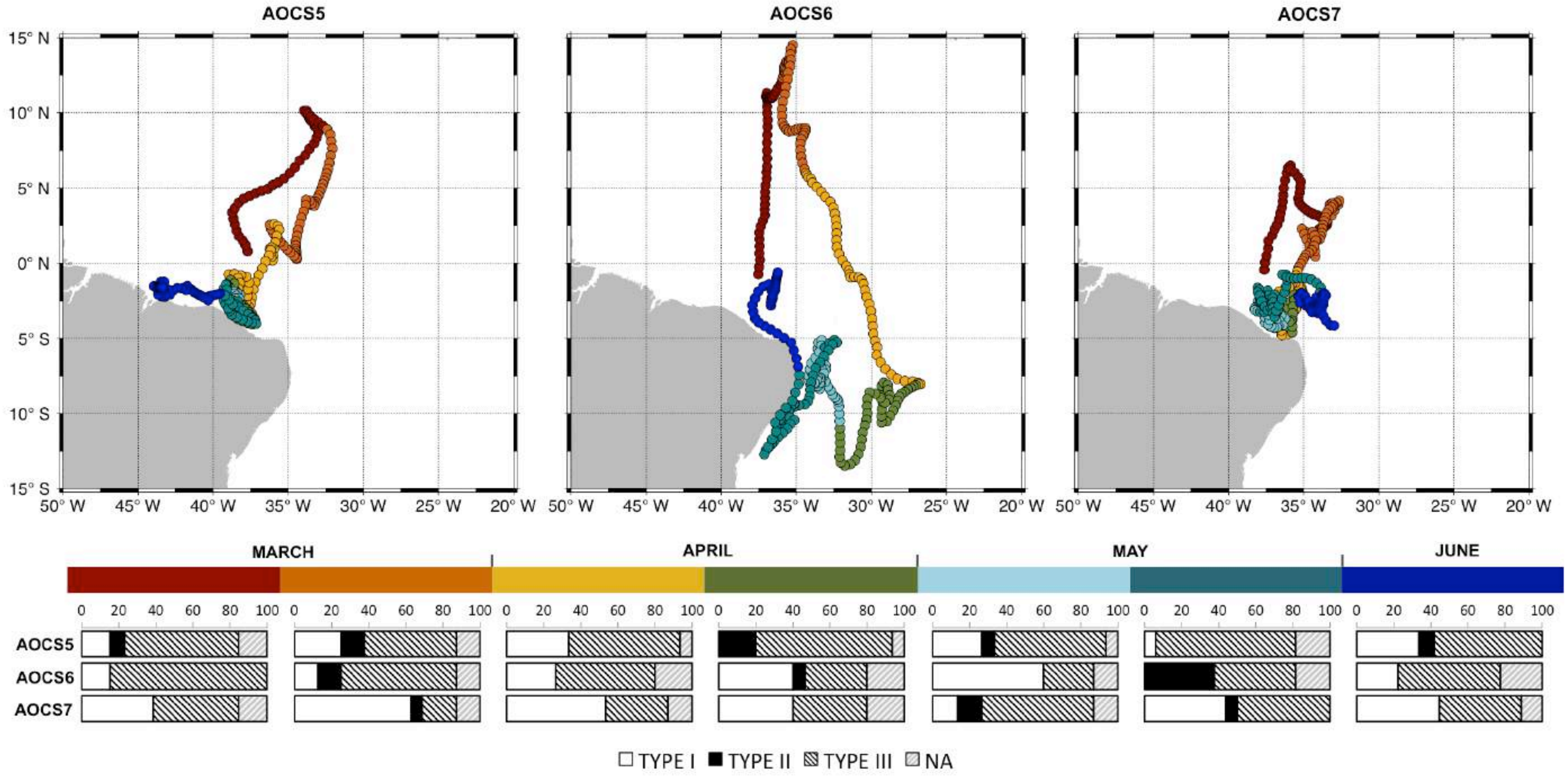

Figure 7. Proportion of the behavior types across the tracks of three oceanic whitetip sharks tagged on the same day.

Three sharks (AOCS5, 6 and 7) were tagged on the same day at similar locations and the duration of their monitoring period was equivalent. This unique situation enabled the incorporation of the spatial aspect into the discussion concerning the shifts between behavior types. The proportions between the three behavior types were linked across the tracks of these individuals (Figure 7). Considering that individuals that are simultaneously at the same location are also experiencing the same environment, this analysis evidenced moments where environmental factors could be the driver of their behavior. At the beginning of May, for example, sharks AOCS5 and 7 are at the same square of latitude and longitude and their behavioral pattern is also very similar. Shark AOCS6, on the other hand, is in another location exhibiting another behavioral pattern, indicating sharks' surroundings could be their behavioral driver. Shark AOCS6 remained in the same area for most of May, its behavior pattern, however, shifted completely between the first and second halves of the month. Again, an environmental factor could be the driver. However, during the second half of April, sharks AOCS5 and 7 are at the same location exhibiting completely different behavioral patterns. This trend appears again during the second half of May. This would suggest that the environment would not be the only driver of these behavioral modes.

3.1.2. Spike dives

While examining the time series it was noted that all individuals mainly stayed within the first 150 m, but descended on rare occasions to depths below 150 m. Looking closely at these rare events, that accounted for only 0.15% of their monitoring periods (Tolotti et al., 2015b), common features were identified. These features, denominated spike dives, were characterized by rapid descents to depths greater then 150 m, followed by considerably slower ascents. Two examples of spike dives are shown of Figure 8. All individuals performed spike dives during their monitoring period, with descent rates varying from 0.14 to 1.05 $m.s^{-1}$ and ascent rates varying form 0.08 to 0.26 $m.s^{-1}$ (Table 3). Most of spike dives lasted between 30 to 45 min, but dives that spanned for more than one hour were also registered. With the exception of shark AOCS7, spike dives occurred mostly during the day (Figure 9). Besides performing the great majority of its spike dives during nighttime, shark AOCS7 also exhibited this behavior much more frequently than the other individuals.

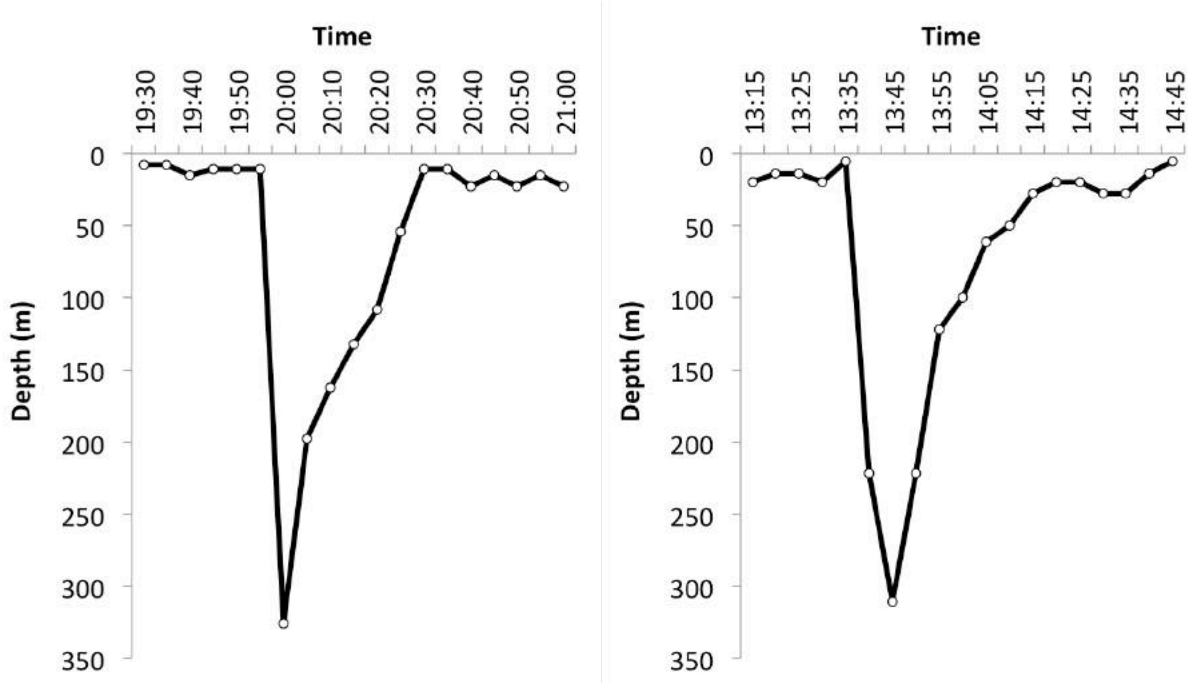

Figure 8. Examples of spike dives performed by oceanic whitetip sharks (right panel: AOCS7, left panel: IOCS1).

Table 3. Summary of the spike dives performed by oceanic whitetip sharks.

ID	Number of deep spike dives	Max depth range (m)	Duration (min)	Descent rate range ($m.s^{-1}$)	Ascent rate range ($m.s^{-1}$)
AOCS3	4	237 - 365	21 - 45	0.55 - 1.00	0.10 - 0.24
AOCS4	4	232 - 340	35 - 75	0.14 - 0.49	0.12 - 0.22
AOCS5	3	154 - 193	40 - 55	0.19 - 0.23	0.08 - 0.12
AOCS6	2	181 - 277	45	0.17 - 0.40	0.09 - 0.12
AOCS7	18	153 - 405	30 - 65	0.44 - 1.05	0.15 - 0.26
IOCS1	6	257 - 317	35 - 50	0.22 - 0.89	0.14 - 0.17

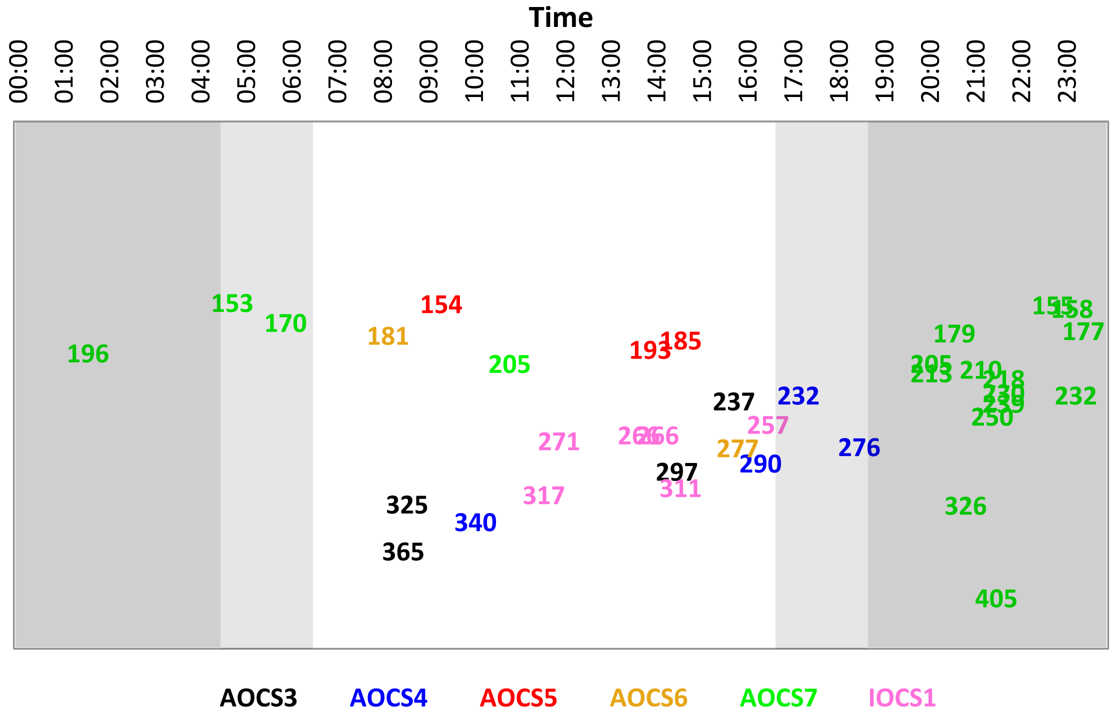

Figure 9. Maximum depth and time at which spike dives were performed. Light shaded areas represent crepuscular periods, dark shaded areas represent night and white area represents day.

3.2. Vertical movements and the environment

Daily average depth and standard deviation were plotted on top of water column temperature in order to identify possible links between behavior and environment. Although some environmental changes could be observed, the depth trend was overall stable for all sharks (Figure 10). The SD, in the other hand, exhibited some variation. On sharks IOCS1 and AOCS6, for example, higher values of SD were observed around June-July and early May, respectively. These higher values also corresponded with wider mixed layer, indicating more vertical amplitude when their preferred environment was expanded. SST also appears to influence sharks behavior. Looking at the figures of individuals AOCS3, 6 and 7 is possible to see that these sharks experienced colder waters during periods of higher SST. For AOCS3 this pattern mostly occurred between April and May.

Sharks AOCS 6 and 7 experienced cold waters more frequently between end of April and early May and between March and April, respectively.

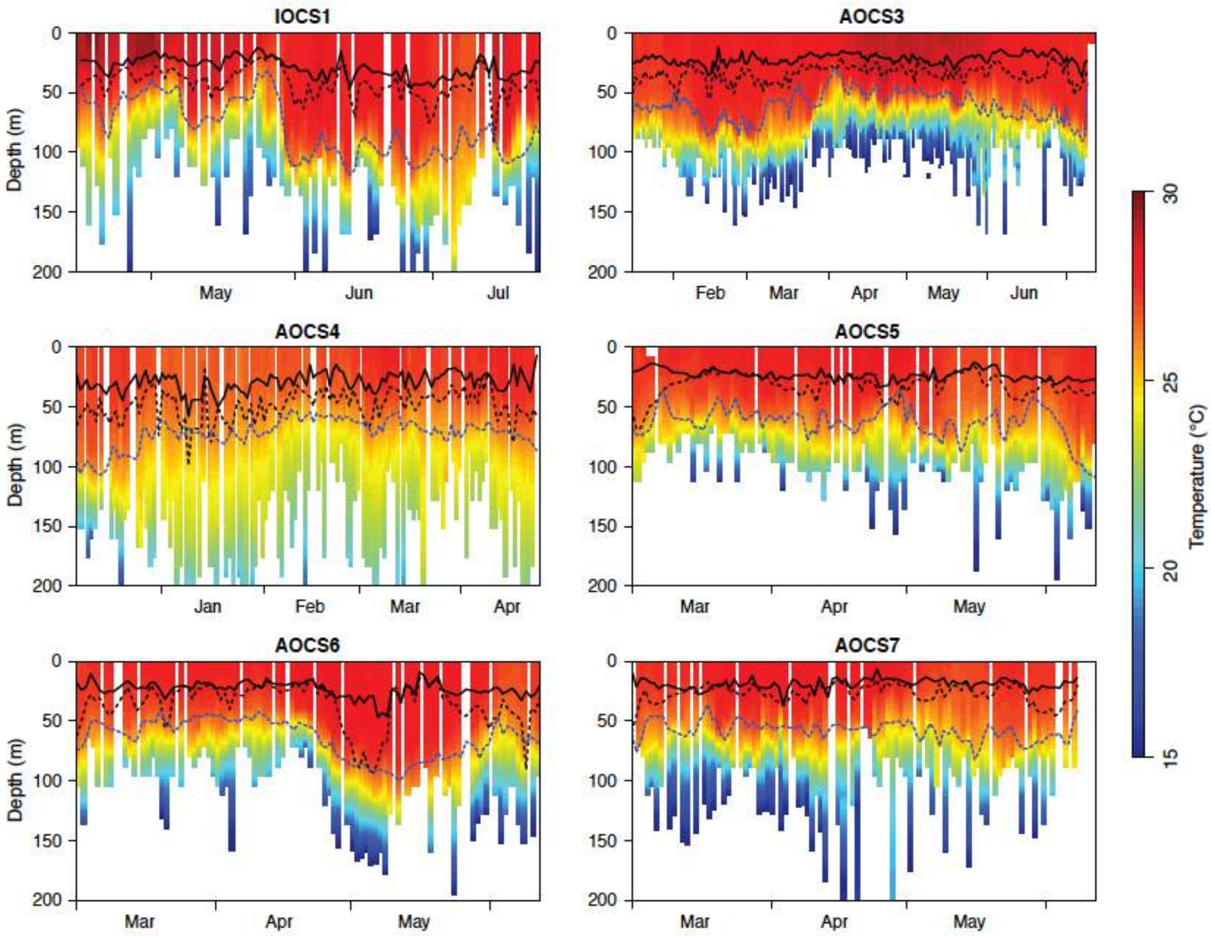

Figure 10. Daily temperature at depth profiles estimated using data transmitted by the tags. Continuous black line represents average depth, doted black line represents standard deviation and doted blue line represents mixed layer depth.

To better understand the relationship between behavioral trends and environment several GAMs were applied. The models results were not unexpected, reflecting the pattern observed in Figure 10. The best-fitted models consistently indicated a significant influence of horizontal position, mixed layer depth (MLD) and SST on the daily vertical activity (SD). The multiple-tag model suggested an additional effect of shark size and explained 50.1% of the deviance (R2=0.48, n=685). This model suggests an increase of vertical activity with the increase of the MLD and size. SST seems to follow the same trend, but it was the least significant factor on the multi-tag model (Figure 11). The individual models varied slightly between sharks, with horizontal positions being always significant as opposed to MLD and SST (Figure 11). The model of shark IOCS1 had 64.7% of the deviance explained (R2=0.63, n=97) and a positive linear effect of MLD was observed. Shark AOCS3 model also had a good fit with 68.6% of deviance explained (R2=0.63, n=165). Besides the positive relationship with MLD, the vertical activity of this individual was also positively correlated with SST. The models of AOCS5 and 6 were similar to AOCS3, but shark AOCS6 model had a weaker performance, with 40.1% of deviance explained (R2=0.34, n=98) as opposed to 68.3% for AOCS5 (R2=0.59, n=99). The model of AOCS4 had only horizontal position as a significant factor (dev. explained 51.0%, R2=0.41, n=129). Lastly, MLD was not a significant factor for AOCS7. Instead, this model suggested a non-linear effect with SST, exhibiting an overall negative trend with a slight increase close to 28°C (dev. explained 40.3%, R2=0.30, n=97).

To interpret the environment and movement variations more finely, cumulated sums of MLD, SST and SD were plotted for each individual. The cumulated sums were subtracted by the mean and re-scaled to highlight periods when values are above or below the mean (Figure 12). These plots reflected the models results and, in some cases, facilitated their understanding. Shark IOCS1, for instance, exhibited a perfect aligned correlation between MLD and vertical activity. When MLD is above average, and the species preferred environment expands, the SD is also above average. The opposite trend also remains true. It is not surprising that the GAM of this individual had MLD as a highly significant factor and a very good degree of deviance explained. An interesting case is shark AOCS3. In the beginning of its time series this shark exhibited the same trend observed for IOCS1. Around May, however, a major shift is seen. Instead of decreasing with MLD, vertical activity starts to increase disregarding the shrink of its preferred environment. During this moment it is SST that starts to reach values above average, hence its addition as a significant factor on the model of AOSC3. This same trend is observed for shark AOCS5. The MLD was not a significant factor for shark AOCS7 and SST was. Indeed, when looking to the cumulated sums, SD and

MLD do not follow the same direction, while SST and SD do. These two lines are not perfectly aligned, however, which could have reflected on the lower explained deviance of this shark's GAM.

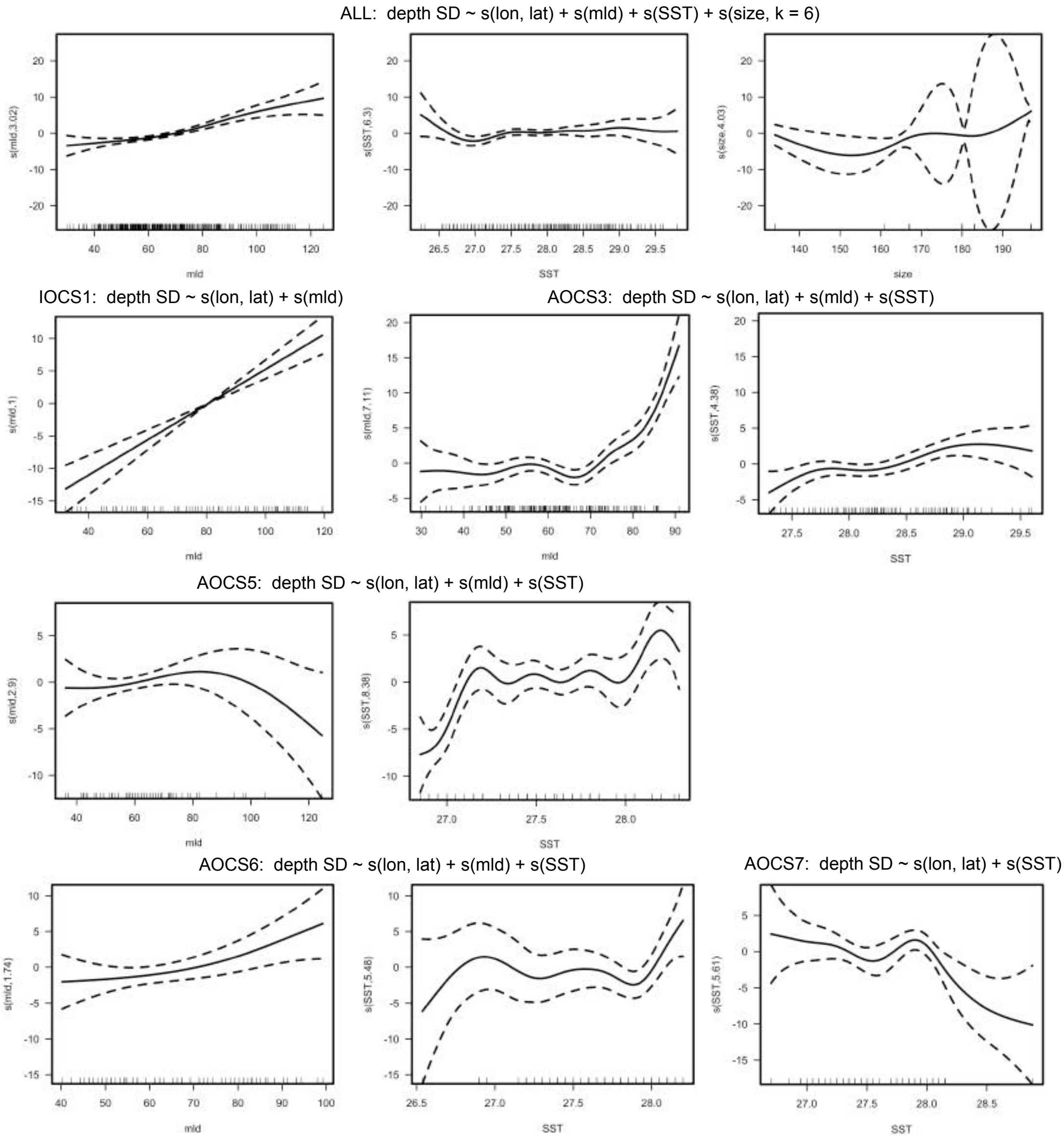

Figure 11. Main results of the best fitted GAMs.

Since AOCS3 is the only shark with temperature time series available, it was possible to take a closer look on the particularities of the long-term behavior of this individual. This shark experienced very high SST values (>29°C) and, at the same time, also experienced cold waters more frequently (Figure 10). Additionally, this shark did not decrease its vertical activity despite the shrinking of the mixed layer, which occurred during the same period as high SST (Figure 11). In fact, when plotting daily temperature range against daily SST it seems that there is a positive correlation: the higher the SST the greater the temperature range (Figure 13). The same does not seem to hold for daily depth range, which remains stable when SST increases. The temperatures experienced by this shark were summed by day as a way to represent daily-accumulated heat across its time series. Interestingly, despite the observed variations on temperature and SST, the accumulated heat remained rather stable (Figure 14).

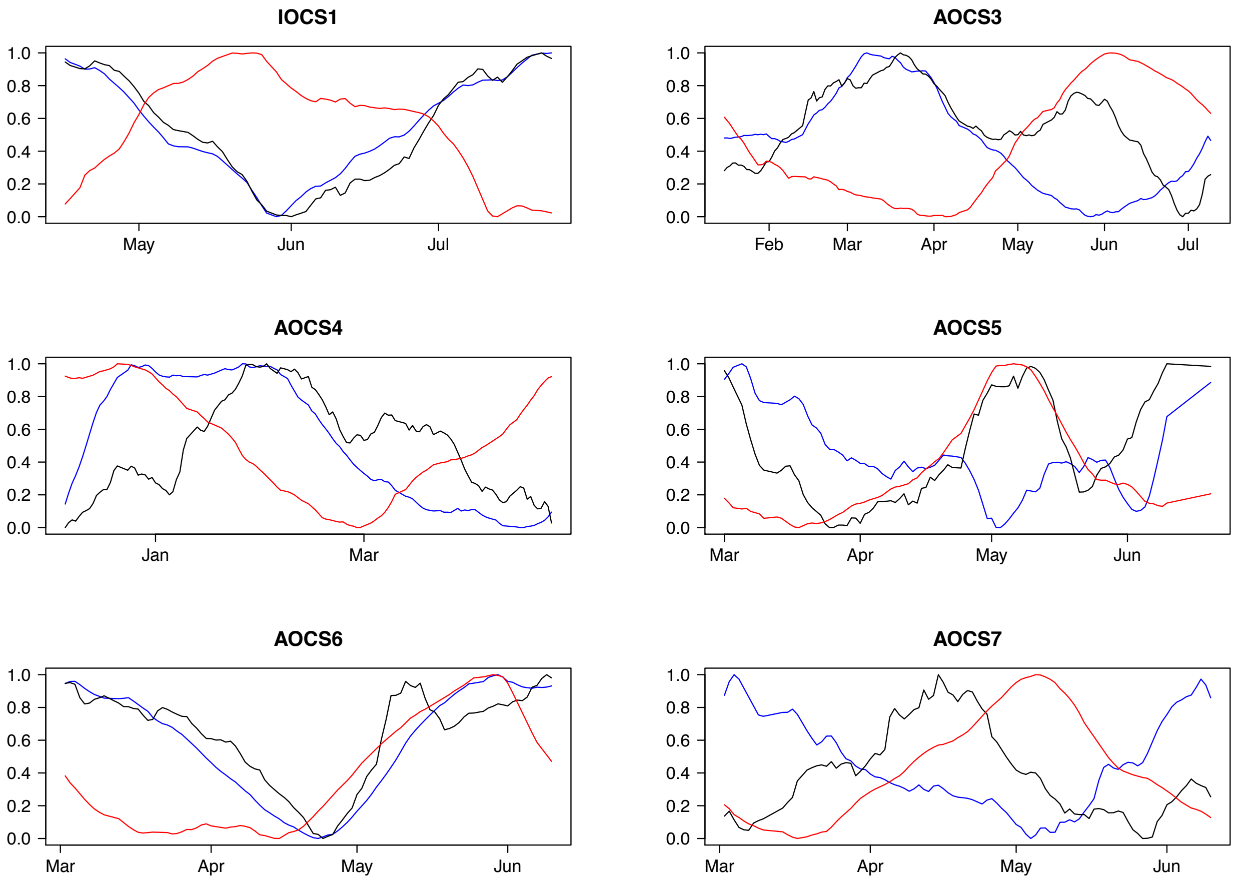

Figure 12. Cumulated sums subtracted by the mean of daily standard deviation (black), mixed layer depth (blue) and sea surface temperature (red).

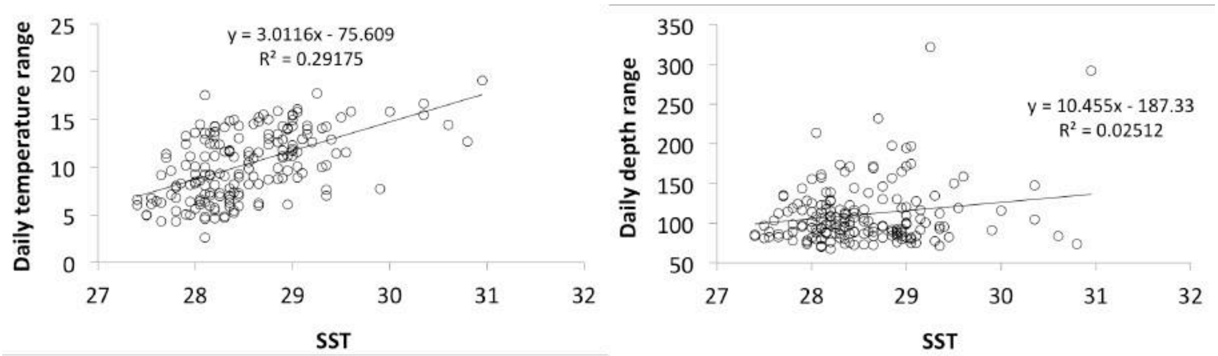

Figure 13. Daily temperature and depth ranges experienced by shark AOCS3.

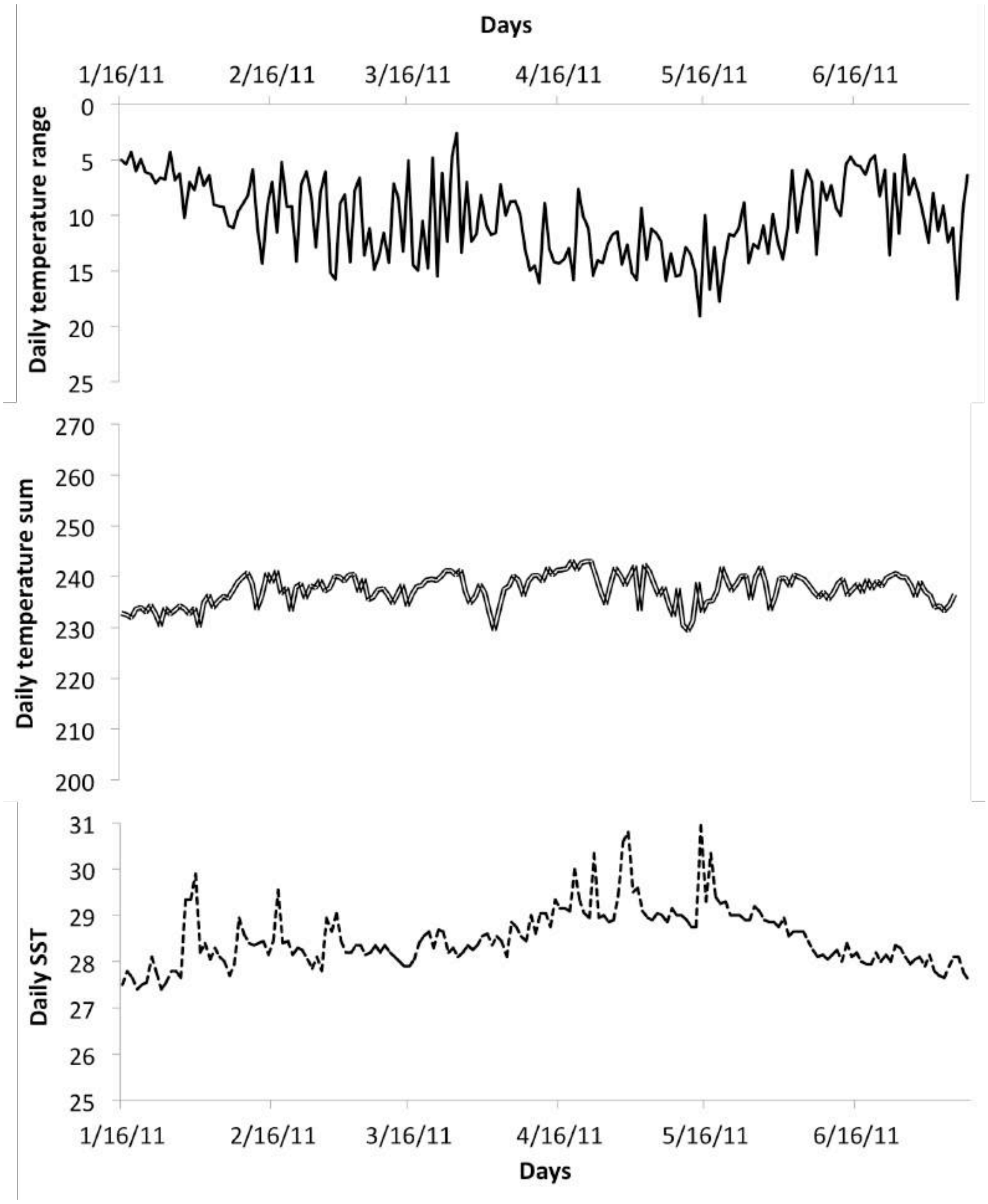

Figure 14. Daily-accumulated heat expressed as the sum of temperatures experienced by shark AOCS3.

4. Discussion

Recent studies have shown that the oceanic whitetip shark is an epipelagic predator largely confined to the mixed layer (Howey-Jordan et al., 2013; Musyl et al., 2011; Tolotti et al., 2015b), a result that was also confirmed by this study. Up until now, however, detailed information on how this species occupies the epipelagic environment was lacking. The present study revealed complex movement patterns, including marked diel changes, behavior shifts and environmental influence on vertical activity. The combination of several analysis tools was key to identify this variety of vertical movement patterns. This work also represents the first description of satellite archival data form an oceanic whitetip shark in the Indian Ocean.

4.1. Diel patterns

Previous research on vertical movements of oceanic whitetip sharks has not reported the occurrence of diel behavior (Howey-Jordan et al., 2013). Conversely, diel patterns were observed for all six individuals analyzed in the present study. While variability was also noted, diel patterns occurred for at least one moment of their monitored time series. The most frequent pattern, classified as type I behavior (Figure 4), was characterized by shallower depths during the day and deeper vertical expansion during the night, resulting in deeper average depths. The exact opposite of this diel pattern was also observed, characterized by deeper occupation of the water column during daytime than during nighttime (type II behavior). Periods of no distinct diel patterns ware also observed (type III behavior). Diel vertical movements are very common on species with vertical ranges that exceed that of oceanic whitetips, such as blue sharks (*Prionace glauca*), bigeye thresher sharks (*Alopias superciliosus*), swordfish (*Xiphias gladius*) and bigeye tuna (*Thunnus obesus*) (Abecassis et al., 2012; Coelho et al., 2015; Lam et al., 2014; Musyl et al., 2011, 2003). These species usually occupy deep waters during the day and remain in the mixed layer during the night and are believed to be following the vertical migration of meso-pelagic prey species within the deep scattering layer (DSL) (Bernal et al., 2009).

Epipelagic predators, such as oceanic whitetips, have also been reported to display diel patterns. Silky sharks (*C. falciformis*) and mahi-mahis (*Coryphaena hippurus*), for example, exhibited vertical movements similar to the type I behavior described above (Filmalter et al., 2015; Merten and Appeldoorn, 2014). Although inverse to the general diel migration pattern described for pelagic species with wide vertical ranges, type I behavior could also be linked to feeding on mesopelagic prey from the DSL. Filmalter et al. (2015) reported that silky sharks were more vertically active during the night and at a similar depth to the nocturnal range of pelagic species known to track the migration of the DSL. The authors hypothesized that these increased vertical oscillations were associated with feeding activity. In the present study, indication of an increased vertical activity during the night was also found, as some individuals (AOCS4, 7 and IOCS1) exhibited higher standard deviation values during this period. Oceanic whitetip sharks are known to feed on mesopelagic squids (Backus et al., 1956) and a recent study using stable isotopes has estimated a nearly equal importance between squids (44%) and larger pelagic teleosts (47%) on its diet (Madigan et al., 2015). Deep excursions of oceanic whitetips are rare and could not account for such a significant portion of a mesopelagic species in its diet, suggesting that type I behavior can indeed be linked to feeding on prey from the DSL during the night.

Variability on vertical movement patterns is also often reported for pelagic species. Five behavior types have recently been described for blue sharks, a species known for its marked diel migration to shallower waters during the night (Queiroz et al., 2012). These behaviors ranged from the general known diel pattern to its inverse and included patterns where no diel differences were apparent, just like what was observed for the oceanic whitetip sharks from this study (type III behavior). Mako (*Lamna nasus*) and the plankton feeding basking shark (*Cetorhinus maximus*) have been reported to perform opposite diel patterns during their monitoring period too (Pade et al., 2009; Sims et al., 2005). These behavior shifts are also believed to be linked with the availability of prey. The cited studies were able to observe that changes in the diel pattern occurred when sharks changed environments, moving from mixed coastal to well stratified off shore waters, for example (Pade et al., 2009; Queiroz et al., 2012), or because they were mirroring prey behavior (Sims et al., 2005). For the oceanic whitetip sharks tagged in the present work, it was not possible to identify clear temporal or spatial patterns in the occurrence of the different behaviors. The types of behavior were highly intercalated and showed no consistency across their time series (Figures 6 and 7). Oceanic whitetips are opportunistic predators (Backus et al., 1956; Compagno, 1984) and the great variability seen on their vertical movement patterns could very well be linked to prey distribution, as it has been proved for other pelagic sharks. To move forward on this matter, however, additional research is required, as information on prey distribution in the studied areas is lacking. Data on other pelagic sharks tagged in the same areas could also provide good insights.

The Fast Fourier Transform analysis of the recovered tag (AOCS3) revealed two peaks, indicating periodicity on vertical movements (Figure 3). The peak at 24 hours confirms the diel behavior and its broad base indicates variability. This result is in accordance with what was observed in the previous analysis, as shark AOCS3 frequently intercalated the three types of behavior across its time series (Figure 6). Other pelagic shark species have also shown peaks corresponding to a 24h cycle, which are typically interpreted as evidence of diel behavior (Brunnschweiler and Sims, 2012; Filmalter et al., 2015; Tyminski et al., 2015). The peak at 12h, however, is not reported as often for pelagic species. Usually, a spectral peak at 12h is seen on coastal species and they are linked to tidal cycles (Urmy et al., 2012). Similar to shark AOCS3, the strongest spectral peak in the periodogram of a basking shark had a period of 12.35h (Shepard et al., 2006).

The authors found that the peak also matched the tidal cycle, since the shark remained in the continental shelf for the duration of its monitoring. Shark AOCS3, on the other hand, remained at oceanic waters (Figure 1). Thus, it is unlikely that the 12h spectral peak observed for this oceanic whitetip shark has any link to the tidal cycle. Instead, the 12h peak could be related to the crepuscular pattern. Oceanic whitetip sharks occupied considerable shallower depths during crepuscular hours (Figure 2). Coincidentally, at equatorial latitudes day and night have similar lengths, resulting in a crepuscular event every 12h (World of Earth Science, 2003). Shark AOCS3 stayed at equatorial latitudes for the totality of its track, indicating that 12h spectral peak of vertical movement matches the crepuscular cycle. The crepuscular pattern of vertical movements was consistent throughout the time series of all six individuals, and was also identified for oceanic whitetips tagged in the Pacific Ocean (Musyl et al., 2011). The sharpness of the 12h peak suggests that this crepuscular pattern is a major part of oceanic whitetip behavioral repertoire. Southern bluefin tunas (*T. maccoyii*) exhibited increased activity during crepuscular hours, including pronounced ascents to the surface at civil twilight (Willis et al., 2009). The authors hypothesized that this behavior had orientation purposes because twilight is the best-suited moment for the detection of celestial polarization patterns, and also because birds and marine mammals are known to use this patterns as navigational cues. This orientation hypothesis could explain the crepuscular behavior of oceanic whitetip sharks, especially considering that they spent considerably more time at the firsts 10 m of the water column during crepuscular hours. It is important to note, however, that studies about the sensitivity of oceanic whitetips to polarized light have never been conducted.

4.2. Spike dives

Oceanic whitetip sharks tagged in the North Atlantic (Bahamas) were reported to perform sporadic deep dives to the mesopelagic zone, down to 1082m (Howey-Jordan et al., 2013). Similar to the deep dives observed in the present work, dives of oceanic whitetips from the Bahamas study had descent rates significantly faster than ascent rates, forming a v-shaped profile. However, unlike most sharks of the present study, Bahamian sharks performed deep dives mostly at night. The difference between the period of when oceanic whitetips performed deep dives could simply be due to area particularities, however one of the South Atlantic sharks also performed spike dives mostly during the night (shark AOCS7). These contrasting periods and the rarity of these deep events make it difficult to understand what is driving them. In any case, similar shaped deep dives are relatively common among pelagic sharks and are often believed to be associated with prey searching behavior (Hoffmayer et al., 2013; Howey-Jordan et al., 2013; Sepulveda et al., 2004; Tyminski et al., 2015). Gleiss et al. (2011) suggested that v-shaped dives might help sharks to efficiently scan the water column for food patches while expending minimal energy. They also suggested that slower ascent rates might improve the chances of pelagic predators to detect prey because backlighting is improved during ascents.

If prey searching is the driver behind the occasional spike dives observed for oceanic whitetip sharks, they could have been triggered after sharks remained in less productive surface waters for prolonged periods. It has been hypothesized that deep dives observed on whale sharks in the Indian Ocean were triggered when individuals were crossing less productive areas (Brunnschweiler and Sims, 2012). Another possible hypothesis for the occurrence of spike dives is the search for navigational cues through magnetic gradients (Willis et al., 2009). Sea floor magnetic anomalies associated with bathymetric features form a predictable gridded pattern believed to aid navigation (Walker et al., 2002). Sharks can detect magnetic fields (Kalmijn, 1982) and deep dives might be a mechanism to acquire these magnetic cues (Gleiss et al., 2011; Tyminski et al., 2015). The two proposed hypotheses behind deep dives are plausible and not mutually exclusive. Therefore, it is possible that the isolated spike dives performed by oceanic whitetip sharks can be triggered by both foraging and navigational purposes depending on the circumstances.

4.3. Vertical movements and the environment

Water temperature is a limiting factor for species whose body temperature is dependent on the external environment, as it represents a central factor controlling their physiological processes (Sims, 2003). For a species like the oceanic whitetip shark, which occupies the tropical epipelagic niche (Howey-Jordan et al., 2013; Musyl et al., 2011; Tolotti et al., 2015b), variations of the warm mixed layer are expected to play a major role on the species vertical movements. The present research confirmed this strong relationship by modeling the daily standard deviation of depth readings as proxy of vertical movement amplitude. The GAMs showed that tagged oceanic whitetips tended to be more widely dispersed in the water column as the depth of the mixed layer increased and, consequently, their preferred habitat expanded. This same relationship was recently observed for another tropical epipelagic species. Mahi-mahis tagged in the Pacific Ocean extended their vertical depth ranges as the thermocline depth increased (Furukawa et al., 2014). Only one shark (AOCS7) displayed a different behavior. Although tagged with other two sharks and remaining in similar areas, shark AOS7 vertical movements did not follow MLD variations. This shark was also the only individual to perform spike dives mostly at night. Given the small sample size of the present work, it is interesting to see such remarkable differences in behavioral patterns.

Besides mixed layer depth, other factors were found to influence the vertical movements of tagged oceanic whitetip sharks. The combined GAM indicated an effect of individual size, where larger individuals tended to have wider utilization of the water column. Figure 2, displaying average depth per hour, also suggests that vertical distribution might vary with shark size. This effect is likely a reflex of the increased thermal inertia that results from larger body mass, enabling larger individuals to expand their thermal habitat (Neill et al., 1976, 1974; Wilson et al., 2006). A possible effect of size on the vertical movements of oceanic whitetips and silky sharks has also been reported on a tagging study conducted off Hawaii

(Musyl et al., 2011). Large individuals (>200 m) of these two closely related species were separated form the juveniles in a cluster analysis based on their vertical movements.

Oceanic whitetip sharks tagged in the Bahamas exhibited a correlation between average daily depth and sea surface temperature (Howey-Jordan et al., 2013). The authors observed that when individuals experienced warmer SST, average daily depth increased. For the oceanic whitetips from the present study, most GAMs also indicated a positive relationship between vertical movement and SST. Interestingly, for two individuals (AOCS3 and 5), this relationship occurred at the same time when the relationship between mixed layer depth and vertical movement was inverted. In short, when SST was above average these two sharks increased their vertical activity disregarding the shrink of the mixed layer. This pattern might indicate behavioral thermoregulation. The oceanic whitetips could be either using the warmer SST to accumulate heat and explore cooler deep waters or diving below the thermocline to cool down. Howey-Jordan et al. (2013) also suggested that the correlation between SST and average depth observed for the Bahamian oceanic whitetips could be evidence for thermoregulation. In fact, the use or active avoidance of heat sources to regulate body temperature has been reported for other shark species (Campana et al., 2011; Speed et al., 2012; Vianna et al., 2013). There is evidence supporting that behavioral thermoregulation optimizes physiological and metabolic processes (Sims, 2003). For the oceanic whitetip shark where high-resolution temperature data was available, a significant relationship between the daily temperature range and SST was observed. When SST increased the temperature range increased too. A similar relationship was reported for blue sharks (Campana et al., 2011). The authors also reported an increase in maximum depth with SST. In contrast, shark AOCS3 depth range did not vary significantly with SST (Figure 13). Campana et al. (2011) hypothesized that blue sharks exhibited behavioral thermoregulation to reduce metabolic losses and increase foraging efficiency. The reduced sample size of the present work prevents further discussion concerning behavioral thermoregulation on oceanic whitetip sharks. Still, even with the clear need for more data, results indicate that the accumulation of heat plays an important role on the species vertical movement. It seems that the warmer SST allows oceanic whitetips to tolerate greater temperature gradients without limiting their vertical movements.

Longline is the main gear responsible for the fishing impacts on oceanic whitetip shark populations (Rice and Harley, 2012). Given that this fishing gear considerably overlaps with the vertical behavior of the species (Tolotti et al., 2015b), it is important to continue our efforts to better understand its behavioral patterns and the drivers behind these patterns. When dealing with rare threatened animals, such as the oceanic whitetip shark, sample size is constrained by opportunity. This study was based on only 6 individuals, but the total of 538 days of observations in the Atlantic Ocean and 100 days of observations in the Indian Ocean already provided new information on the species. Nevertheless, the scientific community should direct its efforts to increase the number of tagged individuals, including different areas. Electronic tags are resourceful non-lethal instruments that can significantly improve our knowledge on the ecology of this threatened species and, consequently, aid its conservation.

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Appendix I

Summary results of best fitted GAMs:

(Significance codes: 0 '***'; 0.001 '**'; 0.01 '*' ;0.05 '.')

MULTI-TAG	depth SD ~ s(lon, lat) + s(mld) + s(SST) + s(size, k = 6)						
	Estimate	Std. error	Pr(>|t|)	Dev. Explained	R2	AIC	
Intercept	24.2282	0.1967	<2e-16	0.501	0.475	3979.3638	***
		Approximate significance of smooth terms:					
		edf	F	p-value			
	lon : lat	20.976	2.951	2.24E-06	***		
	MLD	3.019	15.797	8.57E-12	***		
	SST	6.297	2.122	0.0364	*		
	size	4.028	7.377	7.74E-06	***		

IOCS1	depth SD ~ s(lon, lat) + s(mld)						
	Estimate	Std. error	Pr(>|t|)	Dev. Explained	R2	AIC	
Intercept	29.0068	0.5143	<2e-16	0.647	0.629	404.9074	***
		Approximate significance of smooth terms:					
		edf	F	p-value			
	lon : lat	3.79	1.013	0.42			
	MLD	1	52.395	6.03E-11	***		

AOCS3	depth SD ~ s(lon, lat) + s(mld) + s(SST)						
	Estimate	Std. error	Pr(>|t|)	Dev. Explained	R2	AIC	
Intercept	21.6832	0.2083	<2e-16	0.647	0.686	822.7224	***
		Approximate significance of smooth terms:					
		edf	F	p-value			
	lon : lat	18.505	5.621	1.64E-12	***		
	MLD	7.106	12.264	3.12E-14	***		
	SST	4.381	3.685	0.00308	**		

AOCS4	depth SD ~ s(lon, lat)						
	Estimate	Std. error	Pr(>|t|)	Dev. Explained	R2	AIC	
Intercept	28.9803	0.5295	<2e-16	0.51	0.412	806.36	***
		Approximate significance of smooth terms:					
		edf	F	p-value			
	lon : lat	21.31	3.741	3.00E-07	***		

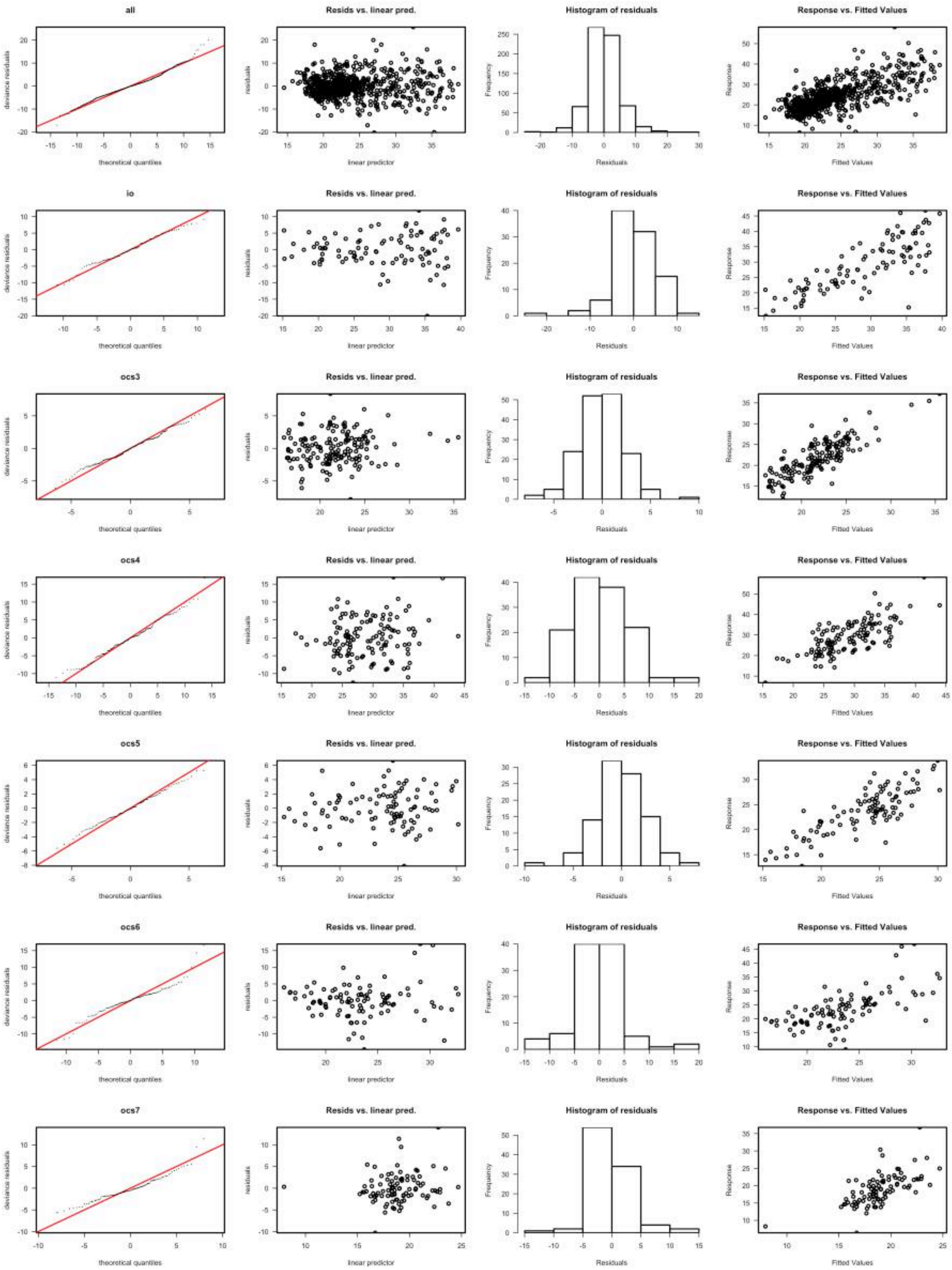
AOCS5	depth SD ~ s(lon, lat) + s(mld) + s(SST)						
	Estimate	Std. error	Pr(>|t|)	Dev. Explained	R2	AIC	
Intercept	23.6277	0.2909	<2e-16	0.683	0.59	500.8115	***
Approximate significance of smooth terms:							
		edf	F	p-value			
	lon : lat	10.97	4.202	9.80E-06	***		
	MLD	2.895	1.584	0.19			
	SST	8.379	7.041	1.28E-07	**		

AOCS6	depth SD ~ s(lon, lat) + s(mld) + s(SST)						
	Estimate	Std. error	Pr(>|t|)	Dev. Explained	R2	AIC	
Intercept	23.3922	0.5326	<2e-16	0.401	0.338	615.6109	***
Approximate significance of smooth terms:							
		edf	F	p-value			
	lon : lat	2	2.478	0.09	.		
	MLD	1.738	2.788	0.06	.		
	SST	5.476	2.335	0.03	*		

AOCS7	depth SD ~ s(lon, lat) + s(SST)						
	Estimate	Std. error	Pr(>|t|)	Dev. Explained	R2	AIC	
Intercept	18.9165	0.3744	<2e-16	0.403	0.302	544.0799	***
Approximate significance of smooth terms:							
		edf	F	p-value			
	lon : lat	8.345	2.083	0.03	*		
	SST	5.608	2.481	0.03	*		

Appendix II

Residual plots of best fitted GAMs:



Chapter 7

Final remarks

1. Main findings

Management of pelagic sharks is a complex issue. Their mortality is primarily due to incidental catches from tuna fisheries worldwide, but, despite incidental, catch rates are high. The shared habitat between pelagic sharks and target species is the primary cause of their incidental captures, but they are also considered a welcome bycatch. Shark fins are a luxury commodity in the Asian cuisine and their trade is very profitable (Clarke, 2007). The legislation set out by tuna RFMOs only prevents retention, and not actual capture. Given this scenario, banning measures will have little impact on fisher-behavior and the high-level of pelagic shark mortality is likely to continue. A set of integrated measures will more effectively aid in the conservation and recovery of threatened pelagic sharks. These measures should mainly include: (1) the development of alternative fishing techniques; and (2) the reduction of fishing effort, e.g. developing spatial or temporal management measures such as closed areas/seasons. Monitoring is also vital for any successful management system and the implementation and/or expansion of observer programs must be encouraged (Chapter 2).

Analysis of observer data from the Brazilian longline fleet reveled that the oceanic whitetip shark is frequently captured by this fishery (Chapter 3). The data also reveled that oceanic whitetip catches are mainly constituted of individuals under the size at first maturity. It was not possible, however, to establish a population trend because the observer program only dates back to 2004 and OCS catches were not reported on the fishery's logbooks. In addition to the short time series, the lack of a homogeneous distribution of fishing effort and strategy also hampered the utilization of CPUE as a proxy of actual abundance. It was observed that the catchability of the species varied greatly with gear configuration (fishing strategy). CPUE values were significantly higher for vessels using shallow longline configuration than those deploying hooks at greater depths. This result was later linked with the vertical distribution of the species.

Observer data from the French purse seine fishery in the Atlantic Ocean was also analyzed in an attempt to establish a population trend for the oceanic whitetip shark (Chapter 4). The population status of the species in the south Atlantic, however, remained unclear. While in the western Atlantic the analyzed time series was too short (Chapter 3), in the eastern Atlantic the occurrence index derived from the purse seine fishery was very low and did not exhibited any trend (Chapter 4). For the western Indian Ocean, besides the observer data from the French purse seine fleet, a historical dataset from the Soviet Union was also available. The analysis suggested that OCS population have declined since mid 1990's in this ocean (Chapter 4).

The combined analysis between tagging and fishery data from the equatorial Atlantic (Brazilian longline fleet) provided good insights towards the development of mitigation measures (Chapter 5). The results of this study indicate that oceanic whitetip sharks spent 95% of their time above 120 m depth. This result perfectly illustrates the variations on CPUE values described in Chapter 3, as the depth range of the longline with shallow configuration corresponds exactly to the species vertical distribution. Despite spending most of the time inside of the mixed layer oceanic whitetip sharks exhibited complex vertical movement patterns, including distinct diel behavioral patterns and deep diving (Chapter 6). Oceanic whitetip vertical movements were also influenced by the sea surface temperature, which suggests the occurrence of thermoregulation for the species (Chapter 6).

The evidence regarding oceanic whitetip shark vertical distribution is solid and corroborated by other recently published works (Howey-Jordan et al., 2013; Musyl et al., 2011). This information suggests that the removal of the shallow hooks from the longline gear could be proposed as technique to mitigate OCS bycatch (Beverly et al., 2009; Walsh et al., 2009). The fact that CPUE variations were already observed suggests that this might be an effective measure. The movement data also reveled that oceanic whitetips have some degree of philopatry to the main fishing ground of the Brazilian longline fleet (Chapter 5). The horizontal and vertical overlap between oceanic whitetip sharks and the Brazilian longline fleet raises concerns regarding the vulnerability of the species. Furthermore, fine-scale data collection for this fishery has ceased in 2012 with the suspension of its observer program. This current situation will certainly jeopardize future analysis of OCS population trends.

2. Future research

This thesis provides new information on the ecology of the oceanic shark ad raises important conservation issues. But, as with many poorly studied species, knowledge gaps still remain and new questions have emerged. In light of what was presented a few research initiatives are suggested.

Due to the clustering of tagged oceanic whitetip sharks on the equatorial Atlantic Ocean and on the first half of the year, more tagging is encouraged. It would be particularly interesting to tag sharks outside the main fishing ground of the Brazilian longline fleet. This would provide new information to fuel the discussion regarding the philopatric behavior observed for the species and maybe evidence of other hotspots in the Atlantic. Movement patterns of oceanic whitetip sharks in the Indian Ocean remain unknown, thus tagging efforts should also be directed to this ocean.

There is a general consensus amongst fisheries scientists that oceanic whitetip populations are declining at dangerous rates, if not already overfished (Baum et al., 2006; Rice and Harley, 2012). The lack of fisheries data, however, prevents a clear understanding of the situation. Historical reference points are limited and systematic monitoring is still scarce. So far, estimations of oceanic whitetip population trends have relied on longline fishery data, since the species is more frequently caught on this gear. The issue with this fishery's database is that catchability is highly sensitive to variations on the gear, making standardization a challenge (Burgess et al., 2005; Ward and Myers, 2005; Ward, 2008). For species with a high proportion of zero catches results are often inconclusive, which was the case with the analysis presented in Chapter 3. In the purse seine fishery catchability is not as sensitive, as modifications of this gear are mostly related with decreasing searching time for tuna schools. The analysis of observer data from the French purse seine fleet combined with historical data from the Soviet Union indicated that purse seine fishery databases could provide reliable abundance trends (Chapter 4). Using a simple occurrence index, many data sources, especially historic ones, could be integrated for a more robust analysis.

A global assessment, including as many historical data as possible, should be conducted for the oceanic whitetip shark, but there are two main issues that need to be considered. The associative behavior of oceanic whitetip sharks around floating objects is key for the development of abundance indexes derived from the tuna purse seine databases. Therefore, studies on this front also need to be conducted (see Filmalter et al., 2015). Another issue is how FAD densities have evolved along the years. It is still unclear by how much FAD densities have augmented and modified the oceanic habitat, and also on how this could have affected species behavior (Dagorn et al., 2013a, 2013b; Maufroy et al., 2015). In order to estimate reliable abundance trends based on purse seine fishery data the FAD issue needs to be addressed as well.

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