UNIVERSIDADE DE LISBOA
FACULDADE DE CIÊNCIAS
DEPARTAMENTO DE BIOLOGIA ANIMAL

Distribution patterns and habitat use of the smooth hammerhead shark (*Sphyrna zygaena*) in the Atlantic Ocean

Catarina Casaca Neves dos Santos

Mestrado em Ecologia Marinha

Dissertação orientada por:
Doutor Rui Coelho (IPMA)
Professor Doutor Carlos Assis (FCUL)

2017

ACKNOWLEGMENTS

I would like to express my deepest gratitude to all the people that contributed to make this work possible, especially to:

Dr. Rui Coelho, for accepting me into his research group and giving me the opportunity to learn. Without his guidance and constant feedback this thesis would not have been achievable.

Professor Carlos Assis, for accepting the co-orientation of this thesis, for always being available to answer my questions and for his constructive recommendations on this work.

The Presidency of IPMA, I.P. (Instituto Português do Mar e da Atmosfera), for allowing me to use their facilities during this study.

Oceanário de Lisboa, for the financial support through Project "SHARK-TAG: Migrations and habitat use of the smooth hammerhead shark in the Atlantic Ocean".

Scientific fishery observers Sérgio Goes and Carlos Barbosa, for collecting the data, and the crew of the fishing vessels *Alberto Miguel*, *Alma Lusa*, *Dário Filipe*, *Emibrupa*, *Estrela de Âncora*, *Mar Largo*, *Mar Português*, *Parma*, *Paula Filipa*, *Príncipe das Marés*, *Sonho de Infância*, *Sonho do Zeca* and *Virgem das Graças*, for their cooperation and commitment during this study.

All my colleagues at IPMA, for the encouragement and for setting such a nice working atmosphere. A special mention goes to the "Lunch gang" (Daniela, Rubén, André, David, Marina, Paula, Fábio, Paulo, João and Sérgio) – thank you for all the laughs and great moments!

My family and friends, for always standing by my side, giving me good advice and making my days brighter. Mom, Dad and Pedro, I love you with all my heart. Thank you for your unfailing support.

IPMA
Instituto Português do Mar e da Atmosfera

Oceanário de Lisboa

ABSTRACT

The smooth hammerhead shark, *Sphyrna zygaena*, is a cosmopolitan pelagic shark mostly captured as bycatch by industrial longline fleets targeting swordfish in the inter-tropical Atlantic Ocean. Listed by the IUCN as "Vulnerable", *S. zygaena* is currently under international protection. Nevertheless, the current information on life history, movement patterns, essential habitat and population dynamics is still scarce over most of its range. This study aimed to improve the knowledge on distribution patterns and habitat use of this species in the Atlantic Ocean. To this end, fishery observer data, collected between 2003 and 2016 from the Portuguese pelagic longline fishery in the Atlantic Ocean were analyzed. Datasets included information on the catch and effort (used to calculate CPUEs, catch per unit of effort), size and sex of the smooth hammerhead shark. A total effort of 2 523 288 hooks yielded 638 sharks, ranging in size from 123 cm to 275 cm fork length (FL). Results confirmed the wide latitudinal range of distribution of this species in the Atlantic Ocean, with higher CPUEs found closer inshore within the Tropical North and Equatorial regions. The larger sharks seemed to occur in the open ocean habitat and the smaller specimens in more coastal areas, while the sex ratio distribution showed a predominance of males in the sampled area of the Atlantic Ocean (overall sex ratio of 1.4 males for each female). Differences in CPUE and size distributions were also detected spatially and temporally. We highlight the increasing trend in the mean CPUE along with a decrease in the mean specimen size in the Equatorial region from 2012 onwards. Furthermore, eight smooth hammerheads were tagged with Pop-up Satellite Archival Tags (PSATs) in the inter-tropical region of the Northeast Atlantic Ocean, between 2012 and 2016, with successful transmissions received from seven tags (total of 319 tracking days). The findings of this work confirmed the ability of the species to travel significant distances, as the longest migration ever documented for the smooth hammerhead shark (> 6600 km) was recorded. The smooth hammerhead did not exhibit a diel vertical movement behavior, swimming mostly at surface waters (0-50 m) above 23 °C. However, differences in the vertical habitat utilization were found when comparing adults and juveniles, with the juveniles staying in deeper colder waters during nighttime. To assess the overlap between the species vertical distribution and the fishing depth of the Portuguese pelagic longline fishery, Minilog Temperature and Depth Recorders (TDRs) were deployed on 60 fishing sets. The overlap between species habitat and fishing gear deployment is taking place mainly during the night and is higher for juveniles. The results presented in this work provide a better understanding of the smooth hammerhead shark spatio-temporal dynamics, population structure, habitat use, and habitat overlap and potential impacts with pelagic longline fishing gear in the Atlantic Ocean. These results can now be used to provide better scientific advice and further improve the current species conservation measures.

Keywords: *Sphyrna zygaena*, Bycatch, Distribution patterns, Habitat use, Pop-up Satellite Archival Tags (PSATs)

RESUMO

Nos últimos anos, os peixes cartilagíneos (elasmobrânquios) têm ganho importância acrescida enquanto recursos pesqueiros face ao aumento das suas capturas. Este aumento deve-se à existência de pesca dirigida a algumas espécies de elasmobrânquios face à crescente procura de produtos derivados, como é o caso das barbatanas de tubarão muito procuradas nos mercados asiáticos. Por outro lado, a expansão de outras pescarias em que os elasmobrânquios são capturados de forma acessória e involuntária tem igualmente contribuído para o aumento das capturas destes peixes. O tubarão-martelo-liso, *Sphyrna zygaena*, é uma espécie pelágica e cosmopolita, que habita tanto áreas costeiras como águas oceânicas, sobretudo da zona intertropical do Oceano Atlântico. Ocasionalmente, o tubarão-martelo-liso é capturado como espécie acessória nas pescarias industriais de palangre de superfície, que dirigem maioritariamente a sua atividade para a captura do espadarte (*Xiphias gladius*) e atuns (*Thunnus* spp). Porém, é provável que os dados de capturas reportados sejam subestimativas da realidade, uma vez que as estatísticas de pesca dos tubarões-martelo são frequentemente agrupadas numa categorial geral - *Sphyrna* spp., devido à dificuldade de identificação ao nível de espécie dos exemplares capturados. Dados de capturas reportados à Comissão Internacional para a Conservação dos Tunídeos do Atlântico (ICCAT) indicam que no período entre 1987 e 2010 Portugal capturou cerca de 3,4 toneladas de tubarão-martelo-liso, revelando-se o quarto país com maiores capturas reportadas desta espécie no Oceano Atlântico. Dada a sua natureza altamente migratória, a gestão e conservação do tubarão-martelo-liso reveste-se de particular dificuldade. Por outro lado, tal como a maioria dos elasmobrânquios, o ciclo de vida desta espécie caracteriza-se por crescimento lento e relativamente baixo potencial reprodutivo, o que o torna particularmente vulnerável à pressão pesqueira. O tubarão-martelo-liso está incluído na categoria “Vulnerável” na Lista Vermelha de Espécies Ameaçadas da União Internacional para a Conservação da Natureza (IUCN), encontrando-se atualmente sob proteção internacional. Em 2010, a ICCAT implementou medidas de gestão que proíbem a retenção e comercialização do tubarão martelo liso, declarando ainda a necessidade de aprofundar o conhecimento científico sobre a espécie. Ainda assim, a informação sobre o tubarão-martelo-liso continua escassa, designadamente no que respeita a diferentes aspetos do ciclo de vida da espécie, padrões de migração, habitats essenciais e dinâmica de populações. Este estudo tem como objetivo aprofundar o conhecimento acerca dos padrões de distribuição e utilização do habitat do tubarão-martelo-liso no Oceano Atlântico. Para tal, foram analisados dados de capturas por unidade de esforço (CPUE), tamanho e sexo dos tubarões-martelo-liso capturados como espécie acessória pela frota Portuguesa de palangre de superfície. Estes dados foram recolhidos por observadores de pesca do Instituto Português do Mar e da Atmosfera (IPMA, I.P.), entre 2003 e 2016, contabilizando um total de 638 exemplares capturados em 2 523 288 anzóis. O tamanho dos exemplares capturados variou entre 123 cm e 275 cm de comprimento furcal. Os resultados confirmaram que o tubarão-martelo-liso apresenta uma ampla distribuição latitudinal (~ 45°N-35°S) no Oceano Atlântico. Os valores de CPUE foram mais elevados na zona Tropical Norte e Equatorial, junto ao continente africano, apesar do esforço de pesca amostrado ter sido superior na região Nordeste temperada e Equatorial, em zonas de oceano aberto. Os tubarões com maior comprimento furcal foram encontrados em zonas de oceano aberto, enquanto os exemplares de menores dimensões se concentraram maioritariamente em zonas costeiras. A análise da distribuição da proporção dos sexos revelou uma predominância de machos na população amostrada, tanto em zonas costeiras como em oceano aberto, resultando numa proporção de sexos global de 1,4 machos por cada fêmea. Foram ainda detetadas diferenças estatisticamente significativas nas distribuições espácio-temporais de CPUE e tamanhos. Destacou-se particularmente a evolução crescente no valor médio de CPUE, acompanhada por uma tendência decrescente do tamanho médio dos tubarões-martelo-liso, na região

Equatorial do Atlântico a partir de 2012. Na última década tem-se assistido à crescente utilização de marcas eletrónicas de arquivo de dados e transmissão via satélite (PSAT - *Pop-up Satellite Archival Tags*) para estudar os movimentos e comportamento de diferentes espécies de tubarões pelágicos oceânicos. Estas marcas são programadas para recolher dados de pressão (profundidade), temperatura e níveis de luminosidade durante um determinado período de tempo, após o qual a marca se solta automaticamente do peixe e fica a flutuar à superfície, possibilitando a transmissão dos dados acumulados através do sistema de satélites ARGOS. Uma vez recolhidos, os dados armazenados nas PSAT permitem estimar a geolocalização dos peixes e a sobreposição do seu habitat com as zonas de pesca. Ao longo dos últimos anos foram desenvolvidos estudos acerca de tubarões-martelo marcados com PSAT que descreveram os seus padrões de movimento, no entanto referem-se a exemplares marcados no Oceano Pacífico. Neste estudo foram marcados oito tubarões-martelo-liso de modo a conhecer os padrões de migração da espécie no Oceano Atlântico, nomeadamente em termos de movimentos horizontais e verticais, bem como a avaliar a sobreposição entre o habitat da espécie e a zona de colocação dos anzóis dos palangres (em termos verticais) utilizados na pescaria de espadarte. As marcações decorreram entre 2012 e 2016 nas zonas equatorial e tropical nordeste do Atlântico, no âmbito do Programa de observadores do IPMA, I.P. e com financiamento de um projeto do Oceanário de Lisboa, e com a colaboração de navios da frota Portuguesa de palangre de superfície. Sete das marcas colocadas produziram dados e uma falhou a transmissão, obtendo-se um total de 319 dias de dados de telemetria. Os resultados confirmaram a natureza altamente migratória do tubarão-martelo-liso, destacando-se o registo da mais longa migração já documentada para esta espécie (> 6600 km). Verificou-se que o tubarão-martelo-liso não possui um padrão de movimento vertical nictemeral e utiliza sobretudo as águas mais superficiais e quentes da coluna de água, passando a maioria do tempo entre os 0 m e 50 m de profundidade e em águas com temperatura acima dos 23 °C. Ocasionalmente, foram registados alguns mergulhos para águas mais profundas e frias, a que se sucederam subidas rápidas. Apesar de ténues, a comparação entre tubarões adultos e juvenis detetou diferenças estatisticamente significativas na utilização vertical do habitat, sendo que os tubarões juvenis permaneceram mais tempo em águas mais frias e profundas durante o período noturno. Para calcular a sobreposição entre o habitat vertical da espécie e a profundidade dos anzóis dos palangres de superfície da frota Portuguesa, foram colocados *Minilog Temperature and Depth Recorders* (TDR) em 60 lances de pesca. Os TDR são colocados junto aos anzóis e registam dados de profundidade através dos quais é possível caracterizar a profundidade da zona de operação dos palangres. Os dados de profundidade recolhidos pelas PSAT e pelos TDR foram então sobrepostos de modo a obter a percentagem de sobreposição entre o habitat vertical do tubarão-martelo-liso e a profundidade dos anzóis dos palangres. Os resultados mostraram que os tubarões se encontram mais suscetíveis à interação com os anzóis dos palangres durante o período noturno. Além disso, os tubarões juvenis apresentaram valores de sobreposição mais elevados em comparação com os tubarões adultos. Esta dissertação de Mestrado apresenta o estudo mais abrangente já efetuado acerca do tubarão-martelo-liso no Oceano Atlântico. A informação compilada neste estudo contribui significativamente para melhorar a qualidade da informação disponível acerca das dinâmicas espácio-temporais, estrutura populacional, utilização do habitat e sobreposição do habitat da espécie e potenciais interações com a pescaria de palangre de superfície. Apesar das limitações inerentes ao tipo de dados, os resultados apresentados podem agora ser utilizados como linha de orientação para os gestores, tendo em vista a implementação de medidas mais eficazes de gestão pesqueira e conservação do tubarão-martelo-liso.

Palavras-chave: Tubarão-martelo-liso, Espécie acessória, Padrões de distribuição, Utilização do habitat, Telemetria de satélite

CONTENTS

LIST OF FIGURES

LIST OF TABLES

Tables

CHAPTER 1: GENERAL INTRODUCTION

1.1 The smooth hammerhead shark

The smooth hammerhead shark, *Sphyrna zygaena* (Linnaeus, 1758) (Figure 1.1), is a Carcharhiniformes shark belonging to the Sphyrnidae family.

Figure 1.1 - Illustration of the smooth hammerhead shark, *Sphyrna zygaena* (Source: João T. Tavares/Gobius).

The smooth hammerhead shark is a coastal-pelagic and semi-oceanic shark occurring inshore and well offshore, over continental and insular shelves. Although preferring shallow waters (less than 20 m), this species inhabits a depth range from the surface down to 200 m and has a highly migratory nature (Compagno, 1984; Bester, 2008). The smooth hammerhead is found worldwide in temperate and tropical seas from latitudes of about 60°N to 55°S (Figure 1.2), with a wider range than other members of the Sphyrnidae family (Casper *et al*., 2005).

The hammerhead sharks are easily recognized by their laterally expanded head, known as the cephalofoil. Though similar in appearance, the three large-bodied hammerheads (*S. zygaena*, *S. lewini* and *S. mokarran*) are identified by the shape of their cephalofoil. In comparison to *S. lewini* and *S. mokarran*, *S. zygaena* lacks a median indentation on its cephalofoil, which helps to distinguish it from the other two species (Figure 1.3) (Bass *et al*., 1975).

Although few data are available on the smooth hammerhead life history characteristics, previous studies mention that this species reaches a maximum size of about 370 cm to 400 cm total length, and males and females become sexually mature when they reach an approximate length of 210 cm to 240 cm (Compagno, 1984). Despite the inexistence of longevity studies for *S. zygaena*, it is believed this species may have a lifespan of more than 20 years (Bester, 2008; Coelho *et al*., 2011; Rosa *et al*., 2017). Like many other Carcharhiniformes, the mode of reproduction for *S. zygaena* is viviparous, with the eggs hatching inside the body and the embryos nourished by a yolksac placenta (Bester, 2008). Females are thought to breed once every 2 years, and mating and birth both occur during the summer months with a gestation period of 10-11 months (Scandol *et al*. 2008; Bester, 2008). Litters of 20-40 pups have been reported, with each pup measuring around 50 cm in total length at birth (Bester, 2008). The smooth hammerhead shark is a high trophic level predator and its diet consists mainly of a variety of teleosts, including small scombrids, clupeids and carangids, crustaceans and cephalopods, as well as elasmobranchs, such as skates, stingrays and smaller sharks (including its own species) (Compagno, 1984; Bester, 2008). Opportunistic behavior has also been observed, with the sharks scavenging from fishing nets and hooks (Compagno, 1984; Bester, 2008).

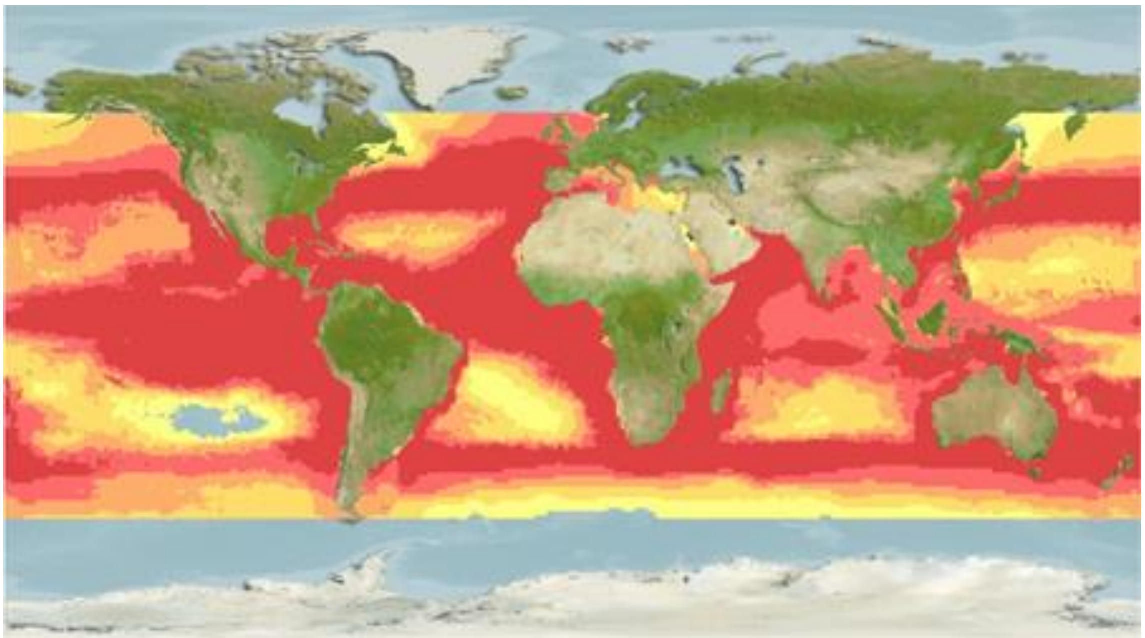

Figure 1.2 - Global distribution map for the smooth hammerhead shark, *Sphyrna zygaena*. The color scale represents the relative probabilities of occurrence, with red and yellow representing higher and lower probabilities of occurrence, respectively (Source: http://www.aquamaps.org/).

Despite being more tolerant to temperate waters than any other hammerhead shark, *S. zygaena* does make migrations towards warmer waters in the winter (Bester, 2008; Diemer *et al*., 2011). This is reversed in the summer, when it migrates towards higher latitudes into cooler water (Bester, 2008; Diemer *et al*., 2011). During these migrations, young sharks often form large schools, while adults usually occur singly or in small groups (Bester, 2008). However, and unlike other hammerheads, the smooth hammerhead is typically a solitary animal (Compagno, 1984).

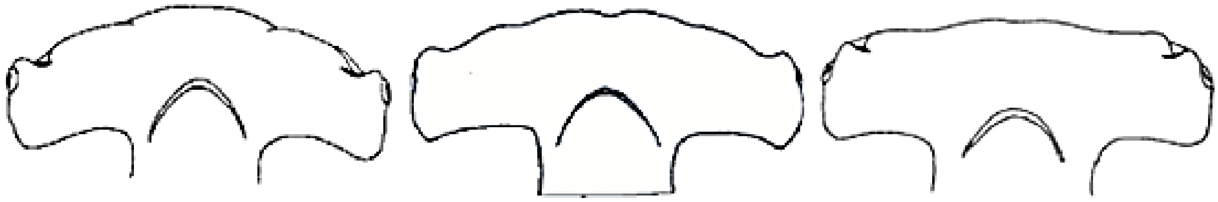

Figure 1.3 - Comparison of the cephalofoil shapes between the three large-bodied hammerheads (from the left to the right: *S. zygaena*, *S. lewini* and *S. mokarran*) (Source: Compagno, 1984).

1.2 Fisheries and status of the stocks

The smooth hammerhead is commonly captured in the Atlantic Ocean as bycatch by industrial longline fleets targeting swordfish (*Xiphias gladius*) and tunas (*Thunnus* spp.) (Buencuerpo *et al*., 1998; Cortés *et al*., 2010). Since species level identification is complex, the hammerhead sharks are usually not separately identified in the commercial catches. Instead, they are often grouped together in one general "hammerhead" category - *Sphyrna* spp. (Fowler *et al*., 2015; Camhi *et al*., 2009). Additionally, since the smooth hammerhead and the scalloped hammerhead (*S. lewini*) are often confused and misidentified, it is probable that significant and under-reported fishing mortality of *S. zygaena* is taking place in large-scale longline fisheries (Fowler *et al*., 2015; Coelho *et al*., 2011). Recent studies have demonstrated that, globally, the hammerheads (including *S. zygaena*) are estimated to have suffered considerable declines in abundance (Baum *et al*., 2003; Myers *et al*., 2007; Ferretti *et al*., 2008). Moreover, this situation is aggravated as the fins of hammerhead sharks, mostly used to make traditional shark fin soup, are highly valued on Asian markets because of their size and high needle count (Rose, 1996; Clarke *et al*., 2006). However, it is important to highlight that those studies suffer from data deficiencies, giving us little confidence concerning the magnitude of the estimates (Burgess *et al*., 2005).

The International Commission for the Conservation of Atlantic Tunas (ICCAT) is the inter-governmental organization responsible for the management and conservation of highly migratory tunas and tuna-like species (including pelagic sharks). ICCAT records provide nominal catch data for hammerhead sharks (Sphyrnidae) and specifically for the smooth hammerhead between 1987 and 2016. Although the different hammerhead sharks species are often confused and misidentified, the annual reported catches of hammerhead sharks ranged from 87 t, in 1987, and 2 375 t, in 2001 (Figure 1.4), with an annual average of 663 t. Prior to the adoption by ICCAT of Rec. [10-08] that established a no-retention measure for hammerheads in the Atlantic, with exceptions for *S. tiburo* and for hammerhead catches from coastal countries for own consumption, Spain had the highest mean annual catches (191 t) reported to ICCAT of hammerheads, followed by Senegal (172 t) and USA (49 t), whereas for Portugal the mean annual reported catch was of 7 t. As shown in Appendix A, this situation has changed substantially since 2011 after the adoption of the no-retention measures, as Ghana has been the country with the higher mean annual catches (310 t), followed by Trinidad & Tobago (143 t) and Senegal (113 t).

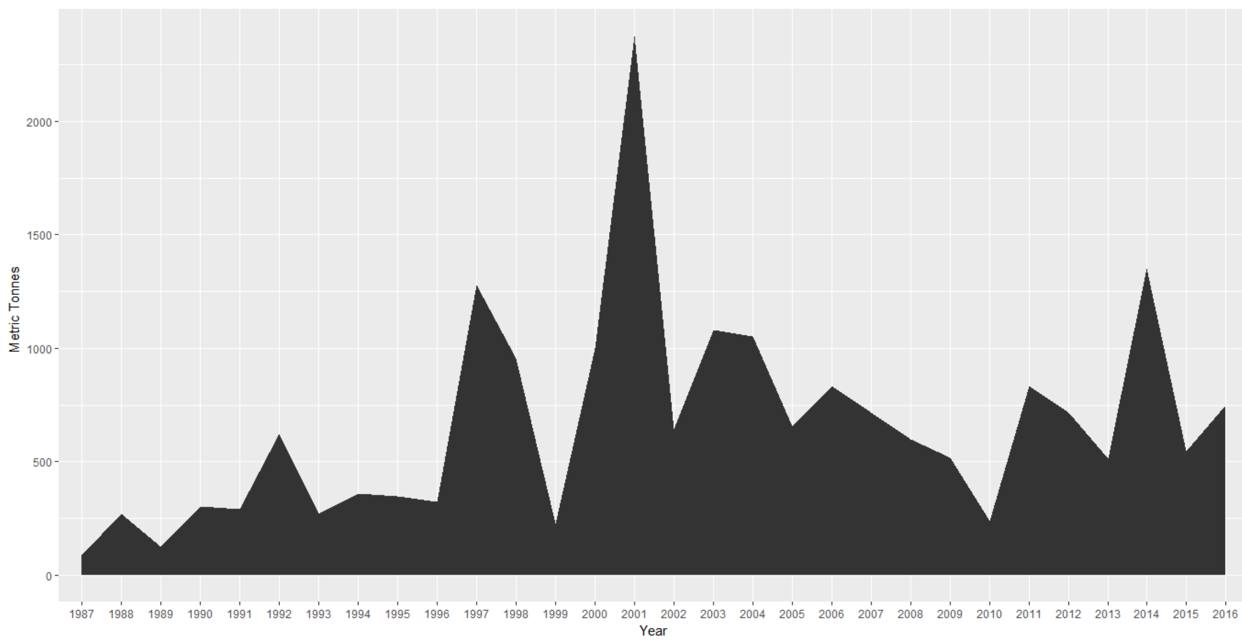

Figure 1.4 - Annual catches of Sphyrnidae sharks reported to ICCAT between 1987 and 2016 (Source: ICCAT, 2017).

Figure 1.5 shows the catches in the Atlantic Ocean of the four species of the genus *Sphyrna* reported to ICCAT for the period 1987-2016. Apart from the considerable annual fluctuations, it can be observed that the two species with the highest catches were *S. lewini* in the first half of the time series and *S. zygaena* on the most recent years. The reported catches of the smooth hammerhead shark have fluctuated considerably, showing a sharp increase on the reported catches since the mid-2000. Before the implementation of ICCAT Rec. [10-08] the mean annual reported catches were on the order of 50 t, but increase substantially thereafter (142 t/year between 2011 and 2016), particularly noticeable in between 2011 and 2013 (273 t/year). However, the catches have substantially decreased since 2014, being on the order of 11 t for the past three years. Before the adoption of the management regulation, Ivory Coast had the highest mean annual catches amounting to 17 t, followed by Guyana (14 t), Spain (3.5 t) and Portugal (3.4 t), while since 2011 the mean annual catches have substantially increased, being led by Senegal (77 t), Morocco (51 t) and Ivory Coast (9.3 t) (see Appendix A for additional information).

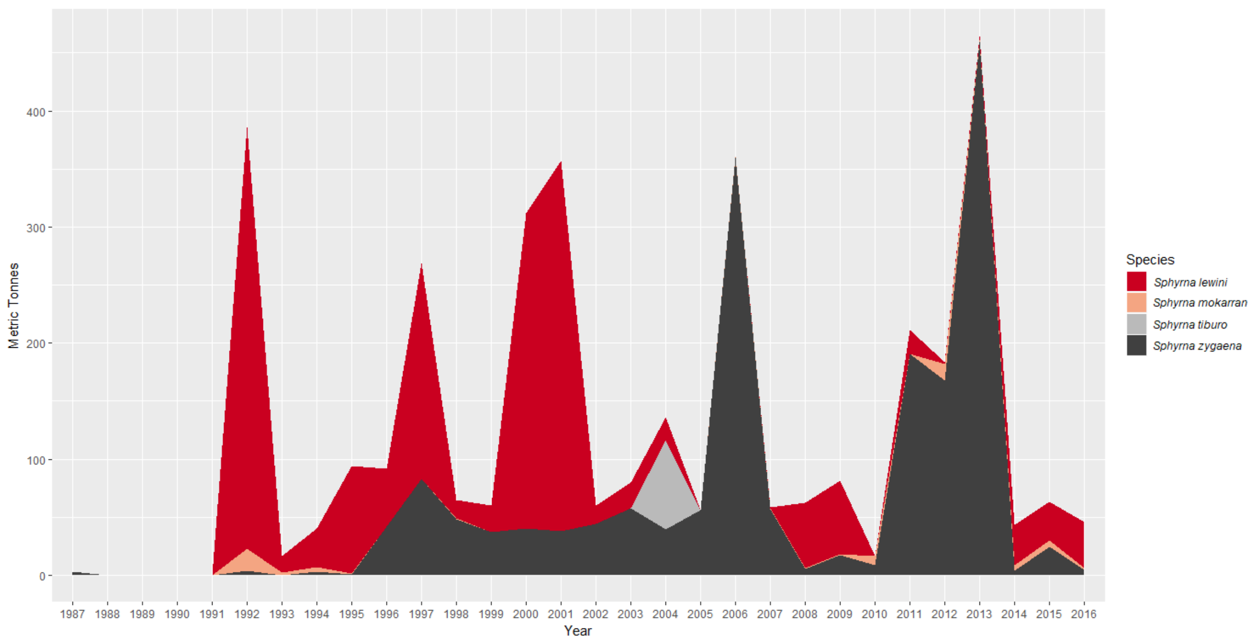

Figure 1.5 - Annual catches of *Sphyrna* spp. sharks reported to ICCAT between 1987 and 2016 (Source: ICCAT, 2017).

The International Union for the Conservation of Nature (IUCN) Red List Criteria classified the smooth hammerhead as being globally "Vulnerable", though it is recognized that additional studies are needed to determine whether it may warrant a higher risk category (Casper *et al*., 2005). In 2010, Cortés *et al*. conducted an Ecological Risk Assessment (ERA) for pelagic elasmobranchs in the Atlantic Ocean, where *S. zygaena* was classified as one of the least vulnerable. Ecological Risk Assessments are assessment tools that can be used to evaluate the overall vulnerability of a stock to overexploitation, taking into account its biological productivity and susceptibility to a fishery (Cortés *et al*., 2010). Cortés *et al*. (2015) revisited and expanded the latter study, though the relative vulnerability of the species did not change. However, these studies also mentioned that *S. zygaena* is amongst the pelagic shark species for which there is the most urgent need for better biological data, due to many uncertainties regarding its life history. As such, ICCAT stated the need to "implement research on hammerhead sharks in the Convention area" and prohibited since 2010 the "retention onboard, transship, land, store, sell, or offer for sale any part or whole carcass of hammerhead sharks of the family Sphyrnidae, (except for the *Sphyrna tiburo*), taken in the Convention area in association with ICCAT fisheries" [Rec. 10-08]. However, hammerhead sharks that are caught by ICCAT developing coastal Contracting Parties and Collaborators for local consumption are exempted from these measures. On the other hand, in March 2013, at the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) meeting in Bangkok, member nations voted in support of including the smooth hammerhead shark in its Appendix II, which lists "species that are not necessarily now threatened with extinction but that may become so unless trade is closely controlled" (CITES, 2013). To allow time for member nations to resolve the related technical and administrative issues, this CITES listing went into effect on September 2014.

1.3 Pop-up satellite archival tags

Tracking techniques and satellite tagging have experienced rapid development over the past decades, providing researchers the opportunity to improve the knowledge on habitat preferences, horizontal and vertical movements and home range of marine predators like pelagic sharks (Heithaus *et al*., 2007; Stevens *et al*., 2010; Abascal *et al*., 2011; Coelho *et al*., 2015; Queiroz *et al*., 2016), tunas (Wilson *et al*., 2005) and swordfish (Abascal *et al*., 2015). Pop-up satellite archival tags (PSATs) are electronic data storage devices that are attached externally to marine animals with a tether and an anchoring device (Musyl *et al*., 2011). In the case of sharks, PSATs are usually affixed to the animal in the musculature at the base of the first dorsal fin. These tags can be applied easily from a boat using a tagging lance (Hammerschlag *et al*., 2011). Once deployed, current-generation PSATs record data at set intervals of time on depth (pressure) and temperature, along with ambient light-level irradiance from which fish geolocations can be calculated (Musyl *et al*., 2001). Depth and temperature data are usually highly accurate. On the other hand, fish position calculations tend to be inaccurate due to natural variability in ambient light-levels induced by natural conditions such as water clarity, light attenuation with depth and shark diving behavior (Musyl *et al*., 2001; Hammerschlag *et al*., 2011). The PSATs are programmed to collect information for a predetermined amount of time. At the pre-determined date, the tag releases from its fish host and floats to the surface where it sends its broadcast of data to the ARGOS satellite-based system. Tag release and data transmission are also initiated if the tagged fish dies and sinks to 1200-1800 m or if the tag experiences no significant pressure change for a programmable number of days (2-4 days) (Musyl *et al*., 2011) (e.g., would allow detecting a lose tag drifting at the surface or a tag attached to a dead animal at the seabed ocean floor in depths shallower than 1200-1800m).

There are currently two main manufacturers of PSATs - Microwave Telemetry, Inc. and Wildlife Computers. These tags have different designs but are very similar in functionality (Figure 1.6). In addition, both have been used successfully on several pelagic species and able to reveal previous unknown insights about their biology (Arnold *et al*., 2001). For example, Bonfil *et al*. (2005) demonstrated white shark transoceanic migrations of over 10 000 km and Brunnschweiler *et al*. (2009) showed whale shark deep-diving behavior (dives exceeding 1000 m). Also, previous studies on hammerhead sharks tagged with PSATs described movement patterns and habitat use (Jorgensen *et al*., 2009; Ketchum *et al*., 2009; Bessudo *et al*., 2011; Hoffmayer *et al*., 2013), however the few ones that investigated the smooth hammerhead behavior were carried out in the Pacific Ocean (News - SWFSC, 2015; Francis *et al*., 2016).

Figure 1.6 - Pop-up Satellite Archival Tag (PSAT) built by Wildlife Computers.

Although PSATs have demonstrated to be useful and powerful tools in scientists' demand for information on pelagic species, they still suffer from several limitations mainly related to early tag detachment and tag failure in data transmission (Arnold *et al*., 2001; Gunn *et al*., 2001). Battery failure, antennae damage, expansion and contraction of electronic components, mortality of the tagged individual, predation, human error, and interferences in frequencies reserved for the Argos satellite system have been responsible for tag failure (Musyl *et al*., 2011). Early detachment is thought to be caused by mechanical failure of the tag head or tethers, biofouling agents, infection and tissue degradation at the site of the implanted anchoring device, entanglement, and social and sexual behaviors of the tagged individuals (Musyl *et al*., 2011). Therefore, in order to improve the performance and efficacy of the PSATs, it is crucial to understand the behavior of the target species, the attachment methodologies and the sampling design (Musyl *et al*., 2011).

1.4 General and specific objectives of this study

As stated above, there is a general lack of information on the smooth hammerhead shark, namely as regards its ecology and fisheries related issues. In the context described, the main objectives of this study were to improve the knowledge as regards the distributional patterns of this species, based on detailed fishery observer data; and the movement patterns of the smooth hammerhead shark on the inter-tropical area of the Atlantic Ocean, based on the information gathered by PSATs. For the detailed objectives, we intended i) to analyze the distribution of the catches per unit of effort (CPUE), sizes and sex ratio of the species bycaught by the Portuguese pelagic longline fishery in the Atlantic Ocean; ii) to investigate the vertical and horizontal migration patterns of the smooth hammerhead shark in the inter-tropical Atlantic; and iii) to assess the overlap between the species vertical distribution (habitat use) and fishing depth of the Portuguese pelagic longline fishery. The expected results will allow the provision of better scientific advice and further improving the current conservation measures for this species.

1.5 References

[Rec. 10-08] Recommendation by ICCAT on hammerhead sharks (family Sphyrnidae) caught in association with fisheries managed by ICCAT.

Abascal FJ, Mejuto J, Quintans M, García-Cortés B, Ramos-Cartelle A. Tracking of the broadbill swordfish, *Xiphias gladius*, in the central and eastern North Atlantic. Fisheries Research. 2015; 162:20-8.

Abascal FJ, Quintans M, Ramos-Cartelle A, Mejuto J. Movements and environmental preferences of the shortfin mako, *Isurus oxyrinchus*, in the southeastern Pacific Ocean. Marine Biology. 2011; 158:1175-84.

Arnold G, Dewar H. Electronic Tags in Marine Fisheries Research: A 30-Year Perspective. In: Electronic Tagging and Tracking in Marine Fisheries Reviews: Methods and Technologies in Fish Biology and Fisheries. J.R. Sibert & J.L. Nielsen (eds) Dordrecht: Kluwer Academic Press. 2001; 7–64.

Bass AJ, D'Aubrey JD, Kistnasamy N. Sharks of the east coast of Southern Africa. III. The families Carcharhinidae (excluding *Mustelus* and *Carcharhinus*) and Sphyrnidae. Durban, Republic of South Africa: Oceanographic Research Institute; 1975; 38:45-47.

Baum JK, Myers RA, Kehler DG, Worm B, Harley SJ, Doherty PA. Collapse and conservation of shark populations in the Northwest Atlantic. Science. 2003; 299:389-92.

Bessudo S, Soler GA, Klimley AP, Ketchum JT, Hearn A, Arauz R. Residency of the scalloped hammerhead shark (*Sphyrna lewini*) at Malpelo Island and evidence of migration to other islands in the Eastern Tropical Pacific. Environmental Biology of Fishes. 2011; 91:165-76.

Bester, C. Smooth Hammerhead. Florida Museum of Natural History. 2008. Available from: https://www.floridamuseum.ufl.edu/fish/discover/species-profiles/sphyrna-zygaena

Bonfil R, Meÿer M, Scholl MC, Johnson R, O'brien S, Oosthuizen H, Swanson S, Kotze D, Paterson M. Transoceanic migration, spatial dynamics, and population linkages of white sharks. Science. 2005; 310:100-3.

Brunnschweiler JM, Baensch H, Pierce SJ, Sims DW. Deep-diving behaviour of a whale shark *Rhincodon typus* during long-distance movement in the western Indian Ocean. Journal of Fish Biology. 2009; 74:706-14.

Buencuerpo V, Rios S, Morón J. Pelagic sharks associated with the swordfish, *Xiphias gladius*, fishery in the eastern North Atlantic Ocean and the Strait of Gibraltar. Fishery Bulletin. 1998; 96:667-85.

Burgess GH, Beerkircher LR, Cailliet GM, Carlson JK, Cortés E, Goldman KJ, Grubbs RD, Musick JA, Musyl MK, Simpfendorfer CA. Is the collapse of shark populations in the Northwest Atlantic Ocean and Gulf of Mexico real? Fisheries. 2005; 30:19-26.

Camhi MD, Valenti SV, Fordham SV, Fowler SL, Gibson C (comp. and ed.). The conservation status of pelagic sharks and rays: report of the IUCN Shark Specialist Group Pelagic Shark Red List Workshop, Tubney House, University of Oxford, UK, 19-23 February 2007. Newbury: IUCN Species Survival Commissions Shark Specialist Group; 2009.

Casper BM, Domingo A, Gaibor N, Heupel MR, Kotas E, Lamónaca AF, Pérez Jimenez JC, Simpfendorfer C, Smith WD, Stevens JD, Soldo A. *Sphyrna zygaena*: The IUCN Red List of Threatened Species 2005. 2005:e.T39388A10193797.
Available from: http://dx.doi.org/10.2305/IUCN.UK.2005.RLTS.T39388A10193797.en.

Clarke SC, McAllister MK, Milner-Gulland EJ, Kirkwood GP, Michielsens CG, Agnew DJ, Pikitch EK, Nakano H, Shivji MS. Global estimates of shark catches using trade records from commercial markets. Ecology Letters. 2006; 9:1115-26.

Coelho R, Fernandez-Carvalho J, Amorim S, Santos MN. Age and growth of the smooth hammerhead shark, *Sphyrna zygaena*, in the Eastern Equatorial Atlantic Ocean, using vertebral sections. Aquatic Living Resources. 2011; 24:351–7.

Coelho R, Fernandez-Carvalho J, Santos MN. Habitat use and diel vertical migration of bigeye thresher shark: Overlap with pelagic longline fishing gear. Marine Environmental Research. 2015; 112:91-9.

Compagno LJV. FAO species catalogue: sharks of the world: an annotated and illustrated catalogue of shark species known to date. Food and Agriculture Organization of the United Nations; 1984.

Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Proposal to include Hammerhead Sharks in Appendix II. Sixteenth meeting of the Conference of Parties. 2013. Available from: https://www.cites.org/sites/default/files/eng/cop/16/prop/E-CoP16-Prop-43.pdf

Cortés E, Arocha F, Beerkircher L, Carvalho F, Domingo A, Heupel M, Holtzhausen H, Santos MN, Ribera M, Simpfendorfer C. Ecological risk assessment of pelagic sharks caught in Atlantic pelagic longline fisheries. Aquatic Living Resources. 2010; 23:25-34.

Cortés E, Domingo A, Miller P, Forselledo R, Mas F, Arocha F, Campana S, Coelho R, Da Silva C, Hazin F, Holtzhausen H. Expanded ecological risk assessment of pelagic sharks caught in Atlantic pelagic longline fisheries. Collect Vol Sci Pap ICCAT. 2015; 71:2637-88.

Diemer KM, Mann BQ, Hussey NE. Distribution and movement of scalloped hammerhead *Sphryna lewini* and smooth hammerhead *Sphyrna zygaena* sharks along the east coast of southern Africa. African Journal of Marine Science. 2011; 33:229-38.

Ferretti F, Myers RA, Serena F, Lotze HK. Loss of large predatory sharks from the Mediterranean Sea. Conservation Biology. 2008; 22:952-64.

Fowler, SL, Cavanagh, RD, Camhi, M, Burgess, GH, Cailliet, GM, Fordham, SV, Simpfendorfer, CA, Musick, JA (comp. and ed.). Sharks, Rays and Chimaeras: The Status of the Chondrichthyan Fishes. Status Survey. IUCN/SSC Shark Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK. 2005.

Francis MP. Distribution, habitat and movement of juvenile smooth hammerhead sharks (*Sphyrna zygaena*) in northern New Zealand. New Zealand Journal of Marine and Freshwater Research. 2016; 50:506-25.

Gunn J, Block B. Advances in acoustic, archival, and satellite tagging of tunas. Fish Physiology Tuna: Physiology, Ecology, and Evolution. 2001; 167–224.

Hammerschlag N, Gallagher AJ, Lazarre DM. A review of shark satellite tagging studies. Journal of Experimental Marine Biology and Ecology. 2011; 398:1-8.

Heithaus MR, Wirsing AJ, Dill LM, Heithaus LI. Long-term movements of tiger sharks satellite-tagged in Shark Bay, Western Australia. Marine Biology. 2007; 151:1455-61.

Hoffmayer ER, Franks JS, Driggers WB, Howey PW. Diel vertical movements of a scalloped hammerhead, *Sphyrna lewini*, in the northern Gulf of Mexico. Bulletin of Marine Science. 2013; 89:551-7.

Jorgensen SJ, Klimley AP, Muhlia-Melo AF. Scalloped hammerhead shark *Sphyrna lewini*, utilizes deep-water, hypoxic zone in the Gulf of California. Journal of Fish Biology. 2009; 74:1682-7.

Ketchum J, Hearn A, Shillinger G, Espinoza E, Peñaherrera C, Klimley P. Shark movements and the design of protected pelagic environments within and beyond the Galapagos Marine Reserve. Proceedings of the Galapagos Science Symposium, Puerto Ayora. 2009; 127-130.

Musyl MK, Brill RW, Curran DS, Gunn JS, Hartog JR, Hill RD, Welch DW, Eveson JP, Boggs CH, Brainard RE. Ability of Archival Tags to Provide Estimates of Geographical Position Based on Light Intensity. In: Electronic Tagging and Tracking in Marine Fisheries Reviews: Methods and Technologies in Fish Biology and Fisheries. J.R. Sibert & J.L. Nielsen (eds) Dordrecht: Kluwer Academic Press. 2001; 343–68.

Musyl MK, Domeier ML, Nasby-Lucas N, Brill RW, McNaughton LM, Swimmer JY, Lutcavage MS, Wilson SG, Galuardi B, Liddle JB. Performance of pop-up satellite archival tags. Marine Ecology Progress Series. 2011; 433:1-28.

Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH. Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science. 2007; 315:1846-50.

News - SWFSC [Internet]. Swfsc.noaa.gov. 2015. Available from: https://swfsc.noaa.gov/news.aspx?ParentMenuId=39&id=20903

Queiroz N, Humphries NE, Mucientes G, Hammerschlag N, Lima FP, Scales KL, Miller PI, Sousa LL, Seabra R, Sims DW. Ocean-wide tracking of pelagic sharks reveals extent of overlap with longline fishing hotspots. Proceedings of the National Academy of Sciences. 2016; 113:1582-7.

Rosa D, Coelho R, Fernandez-Carvalho J, Santos MN. Age and growth of the smooth hammerhead, *Sphyrna zygaena*, in the Atlantic Ocean: comparison with other hammerhead species. Marine Biology Research. 2017; 13:300-13.

Rose DA. An overview of world trade in sharks and other cartilaginous fishes. TRAFFIC International, Cambridge. 1996.

Scandol J, Rowling K, Graham K. Status of Fisheries resources in NSW 2006/2007. NSW Department of Primary Industries, Cronulla. 2008; 334.

Stevens JD, Bradford RW, West GJ. Satellite tagging of blue sharks (*Prionace glauca*) and other pelagic sharks off eastern Australia: depth behaviour, temperature experience and movements. Marine Biology. 2010; 157:575-91.

Wilson SG, Lutcavage ME, Brill RW, Genovese MP, Cooper AB, Everly AW. Movements of bluefin tuna (*Thunnus thynnus*) in the northwestern Atlantic Ocean recorded by pop-up satellite archival tags. Marine Biology. 2005; 146:409-23.

CHAPTER 2: SPATIAL AND TEMPORAL DISTRIBUTION PATTERNS OF THE SMOOTH HAMMERHEAD SHARK IN THE ATLANTIC OCEAN

Abstract

The smooth hammerhead, *Sphyrna zygaena*, is a pelagic shark occasionally captured as bycatch by industrial pelagic longline fleets in the Atlantic Ocean. Fishery observer data on the catches per unit of effort (CPUEs), size and sex of the smooth hammerhead shark bycaught by the Portuguese pelagic longline fishery in the Atlantic Ocean, collected between 2003 and 2016, were considered in this study. A total effort of 2 523 288 hooks yielded 638 sharks, ranging in size from 123 cm to 275 cm (fork length). Results confirmed the species wide latitudinal range of distribution, although higher CPUEs appeared closer inshore within the Tropical North and Equatorial regions. Larger sharks tended to occur in the open ocean habitat and the smaller specimens in more coastal areas. The sex ratio distribution revealed the presence of more males in both inshore and offshore waters, with an overall sex ratio of 1.4 males for each female. Significant differences in CPUE and size distributions were found between regions, years and quarters of the year. Particularly, we emphasize the increasing tendency in the mean CPUE along with a decreasing trend in the mean specimen size in the Equatorial region from 2012 onwards. The distributional patterns presented in this study provide a better understanding of the smooth hammerhead shark spatio-temporal dynamics and population structure in the Atlantic Ocean, and can be used to improve management and conservation measures for this species.

Introduction

The smooth hammerhead shark, *Sphyrna zygaena*, is a widespread pelagic species that can be found in temperate and tropical waters, from latitudes of about 60°N to 55°S (Compagno, 1984; Casper *et al*., 2005). This species generally occurs close inshore, however it may also be found over continental and insular shelves to offshore areas, being described as the most oceanic of the hammerhead species (Compagno, 1984; Bester, 2008; Clarke *et al*., 2015).

As with other pelagic species, although in much lower numbers in comparison to the blue shark (*Prionace glauca*) and shortfin mako shark (*Isurus oxyrinchus*), *S. zygaena* is commonly captured as bycatch in pelagic longline fisheries (Buencuerpo *et al*., 1998; Cortés *et al*., 2010). Nevertheless, information on the global population structure of the smooth hammerhead is still very limited (Coelho *et al*., 2011). Moreover, this problem is aggravated due to the lack of reliable species-specific data, since hammerhead sharks are often grouped together under the category *Sphyrna* spp. or included in the general sharks group.

The International Commission for the Conservation of Atlantic Tunas (ICCAT) is the Regional Fisheries Management Organization (RFMO) responsible for the management and conservation of migratory tunas and tuna-like species (including pelagic sharks, such as *S. zygaena*) in the Atlantic Ocean and adjacent seas. In 2010, ICCAT adopted several management recommendations to protect the smooth hammerhead shark, prohibiting the retention onboard, transshipment, landing, storing, selling, or offering for sale any part or the whole carcass of hammerhead sharks, family Sphyrnidae, (except for *Sphyrna tiburo*) taken in the

Convention area in association with ICCAT fisheries. Furthermore, ICCAT stated the need of research focused on hammerhead sharks in the Convention area [Rec. 10-08]. Still within the ICCAT scientific community work, Cortés *et al*. (2010) conducted an Ecological Risk Assessment for eleven species of pelagic elasmobranchs commonly caught in tuna fisheries in the Atlantic Ocean, concluding that *S. zygaena* is amongst the less vulnerable to overexploitation. This was mainly due to a relatively high productivity and relatively low interaction with pelagic fisheries, as the species spends part of its cycle in more coastal waters and is therefore less susceptible to capture in those oceanic fisheries. However, Cortés *et al*. (2010) also highlighted the urgent need for better biological and distributional information, since there is a high level of uncertainty regarding the life cycle parameters and distribution patterns on this species.

Studying the spatio-temporal dynamics and population structure of marine species is crucial for the development of effective fisheries management and conservation strategies, as it allows to understand the species distribution and predict potential fishing impacts. Recent studies have shown evidence of probable severe decline in the global population of smooth hammerhead sharks (Baum *et al.* 2003; Myers *et al.* 2007; Ferretti *et al.* 2008), however these findings may not represent a full and accurate portrayal of the species status, as many were based on limited data from logbooks, research surveys and public sighting records, which may not adequately sample the smooth hammerhead population. In fact, several flaws were identified, mostly related to insufficient sample sizes, poor geographical coverage, misidentification of the species and oversight of the fishing gear specifications and modifications through time (Burgess *et al*., 2005).

The general objective of this study was to provide information on the distributional patterns of the smooth hammerhead shark aiming to fill some of the knowledge gaps for the species in the Atlantic Ocean. For that purpose, detailed fishery observer data collected by the Portuguese Institute for the Ocean and Atmosphere, I.P. (IPMA) between 2003 and 2016 were analyzed. Specific objectives of the study were to analyze the catch per unit of effort (CPUE), size and sex ratio distribution, and to provide time series trends and analyze the seasonal patterns of the catch per unit of effort (CPUE) and size distributions of the smooth hammerhead shark in the Portuguese pelagic longline fishery in the Atlantic Ocean.

Material and methods

Data collection

The data used for this study were collected across the Atlantic Ocean by IPMA from national scientific fishery observers onboard Portuguese pelagic longline vessels, from 2003 to 2016.

For all specimens caught, fishery observers recorded data on fork length (FL), sex, capture location (latitude and longitude), water temperature and date. Additionally, the status of the specimens upon retrieval of the gear (i.e., dead or alive, commonly referred to as at-haulback mortality) was recorded, as was the status if discarded. Catch and effort data were available from 2003 to 2016, while data on smooth hammerhead sizes and sex ratio were available from 2006 to 2015.

Between 2003 and 2016, data from a total of 2110 longline sets were collected, which amounted to a total effort of 2 523 288 million hooks and yielded 638 smooth hammerhead sharks.

Data analysis

The spatial CPUE (number of inds. caught /1000 hooks), the effort (total number of hooks per set) and the sex ratio distributions were calculated and expressed geographically using 5° x 5° resolution grids of latitude and longitude (e.g., see Lee *et al*., 2005; Fernandez-Carvalho *et al*., 2015).

CPUE and size data were tested for normality using the Kolmogorov-Smirnov normality test with the Lilliefors correction (Lilliefors, 1967), and for homogeneity of variances with Levene test (Levene, 1960). Given the lack of normality in the data and heterogeneity of variances, CPUE and specimen size were compared between years, quarters of the year, and regions with nonparametric Kruskal–Wallis tests, Wilcoxon-Man-Whitney tests and k-sample permutation tests using the permutational central limit theorem (Manly, 2007). Sex ratios were compared among regions with contingency tables and Pearson's Chi-squared tests.

The sample was composed mostly of specimens captured in the Equatorial and Tropical North regions of the Atlantic Ocean, hence only these two regions were considered for the sex ratio analysis and the CPUE and specimen size yearly and quarterly analysis. The Tropical North area was delimited between 10°N and 30°N, while 10°S and 10°N were the limits set for the Equatorial region.

All statistical analyses in this work were carried out with the R Project for Statistical Computing version 3.3.2 (R Core Team, 2016). Additional packages used included the following libraries: "car" (Fox *et al*., 2011), "ggplot2" (Wickham, 2009), "gmodels" (Warnes *et al.*, 2015), "mapdata" (Becker *et al*., 2016), "maps" (Becker *et al*., 2016), "mapplots" (Gerritsen, 2014), "maptools" (Bivand *et al*., 2017), "nortest" (Gross *et al*., 2015), "perm" (Fay *et al*., 2010), "pgirmess" (Giraudoux, 2017), "plyr" (Wickham, 2011), RColorBrewer (Neuwirth, 2014) "scales" (Wickham, 2016) and "shapefiles" (Stabler, 2013).

Results

CPUE distribution

The spatial distribution of the sampled fishing sets showed that the fishing effort sampled over the 14-year period took place between 50°N and 40°S, approximately (Figure 2.1). The temperate Northeast (30°N-45°N) and the Equatorial (10°N-5°S) regions represented the major areas of operation of the Portuguese pelagic longline fleet in the Atlantic Ocean. Particularly, the fishing effort was higher in offshore waters within these regions. The fishing effort ranged between 668 and 2300 hooks per set, with and average effort of 1196 hooks per set.

The smooth hammerhead CPUEs ranged from 0.0 to 8.61 fish per 1000 hooks, with an average CPUE of 0.24 fish per 1000 hooks. A high proportion of the sets (85%) showed zero smooth hammerhead catches, whereas 13% of the sets showed a CPUE between 1 and 3 fish per 1000 hooks, and only in 2% of the sets 4 or more fish were caught per 1000 hooks. The CPUEs geographical distribution are shown in Figure 2.2, indicating smooth hammerhead sharks were distributed throughout the Atlantic Ocean between 45°N and 35°S, approximately. Higher CPUE values were found closer to the African continent, within the Tropical North and Equatorial regions.

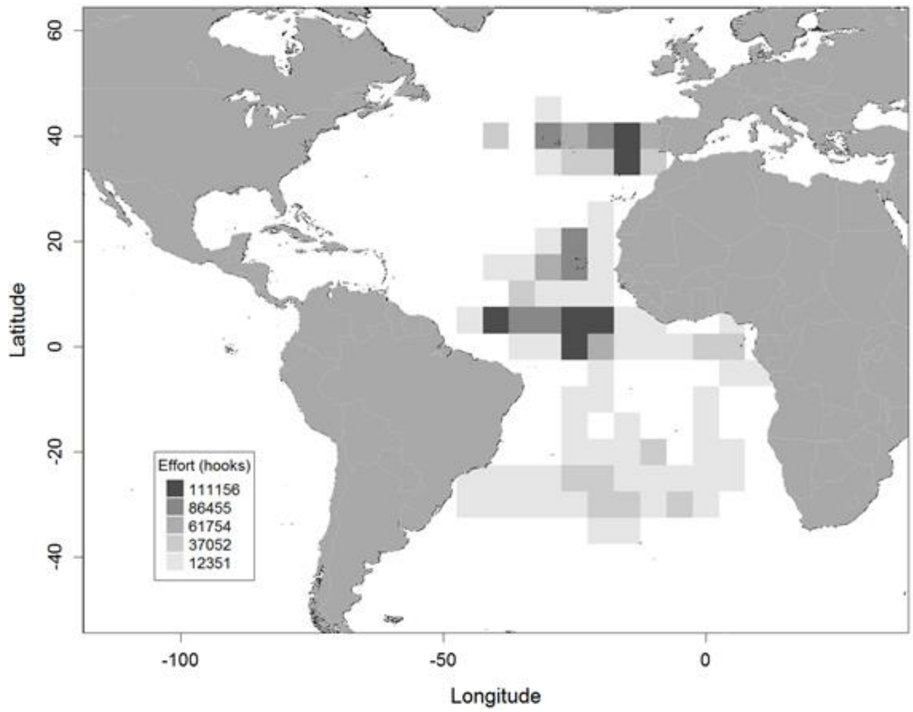

Figure 2.1 - Spatial distribution of the sampling effort (fishing effort in number of hooks) analyzed for this work, from the Portuguese pelagic longline fleet in the Atlantic Ocean, between 2003 and 2016.

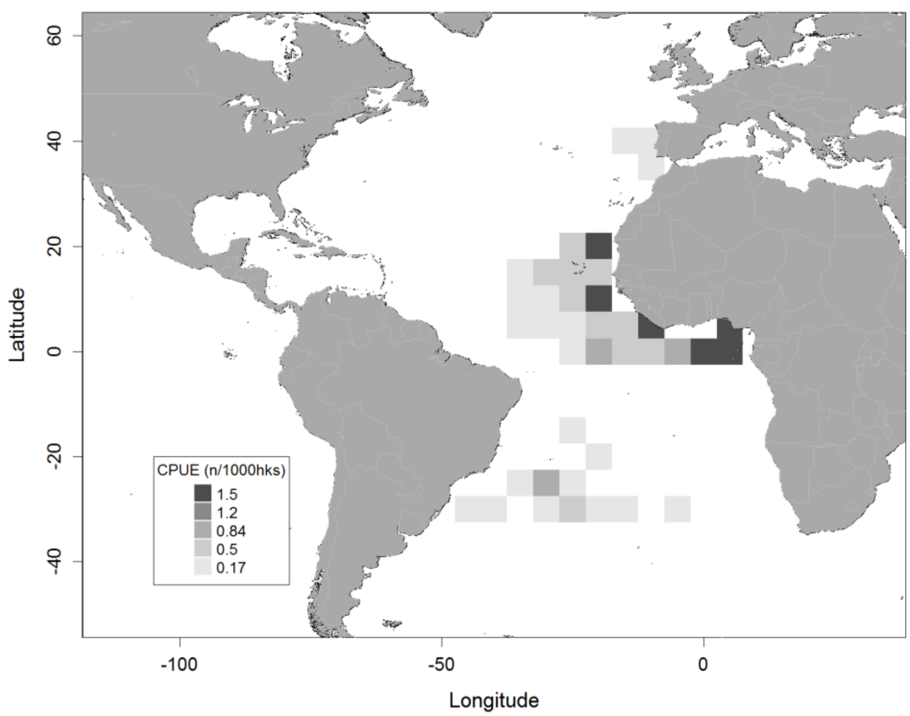

Figure 2.2 - Spatial distribution of smooth hammerhead, *Sphyrna zygaena*, CPUE (n/1000 hooks) by the Portuguese pelagic longline fleet in the Atlantic Ocean, analyzed for this work between 2003 and 2016.

Size distribution

Fishery observers recorded data on specimen size for 559 sharks caught between 40°N and 30°S, approximately (Figure 2.3). The specimens ranged in size from 123 cm to 275 cm FL, with an average size of 195 cm FL. Typically, larger-sized specimens tended to be caught offshore, contrarily to small-sized specimens found on more inshore waters, particularly in the Gulf of Guinea. Furthermore, in the South region of the Atlantic Ocean (15°S-30°S, offshore waters), all sharks caught were larger than 187 cm FL.

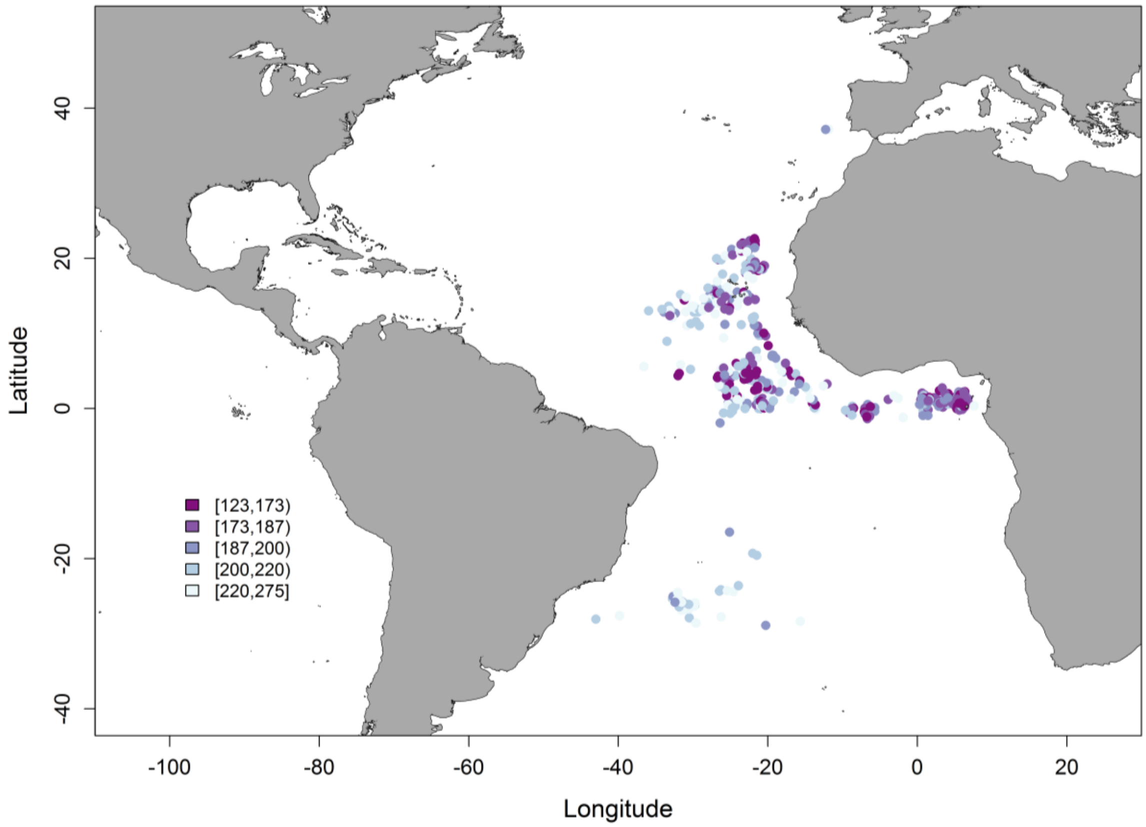

Figure 2.3- Location and size distribution (FL, cm) of the smooth hammerhead shark, *Sphyrna zygaena*, recorded for this study between 2006 and 2015. The color scale of the dots represents specimen sizes, with darker colors representing smaller specimens and lighter colors, larger specimens. The categorization of size classes was carried out using the 0.2 quantiles of the data (values in the legend represent the lower and upper limits of each size class).

Sex ratio distribution

Data on sex was recorded for 562 specimens, caught between 40°N and 30°S, approximately (Figure 2.4). Of all the smooth hammerhead sharks with sex recorded, 238 (42.3%) were females and 324 (57.7%) were males, representing an overall sex ratio of 1.4 males for each female. Particularly, there seemed to be some evidence of the presence of more males in both inshore and offshore waters of the Atlantic Ocean.

The differences observed when comparing the Equatorial and Tropical North regions of the Atlantic Ocean were not statistically significant (proportion test: Chi-squared = 0.541, df = 1, p-value = 0.462).

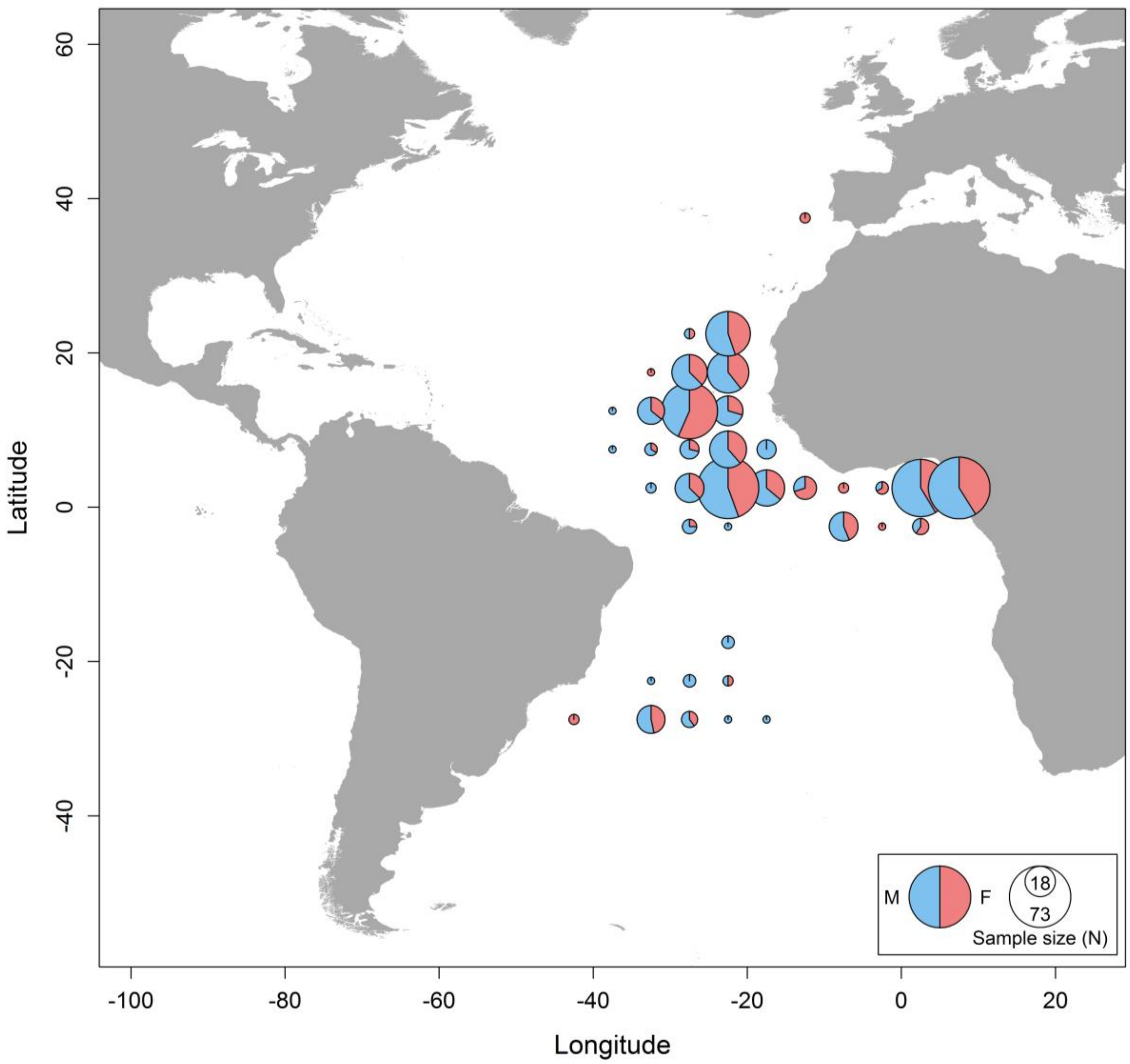

Figure 2.4 – Smooth hammerhead shark, *Sphyrna zygaena*, sex ratios recorded in 5°x5° squares, between 2006 and 2015. The circle diameter is proportional to the sample size (N) in each square.

Yearly and quarterly trends in the CPUEs

CPUEs were not normally distributed (Lilliefors test: D = 0.501, p value < 0.001) and variances were heterogeneous between years (Levene test: F = 7.121, df = 10, p value < 0.001) and quarters of the year (Levene test: F = 19.031, df = 3, p value<0.001), and homogenous between regions (Levene test: F = 3.854, df = 1, p value = 0.050). Univariate nonparametric statistical tests revealed that CPUEs were significantly different between years (K–W: Chi-squared = 124.86, df = 10, p-value < 0.001; permutation test: Chi-squared = 67.67, df = 10, p-value < 0.001) and quarters of the year (K–W: Chi-squared = 100.89, df = 3, p-value < 0.001; permutation test: Chi-squared = 54.57, df = 3, p-value < 0.001). The differences between regions were less clear, as the differences were statistically significant when using Wilcoxon-Man-Whitney tests (W-M-W: W = 117870, p-value < 0.001) but not when using permutation tests (permutation test: Chi-squared = 3.85, df = 1, p-value = 0.050)

The mean CPUE yearly trend followed an oscillatory pattern in both Tropical North and Equatorial regions (Figure 2.5). However, in the Equatorial region there was a tendency for increasing CPUEs from 2012 onwards. Additionally, the mean CPUE values were generally lower in the Equatorial region in comparison to the Tropical North area.

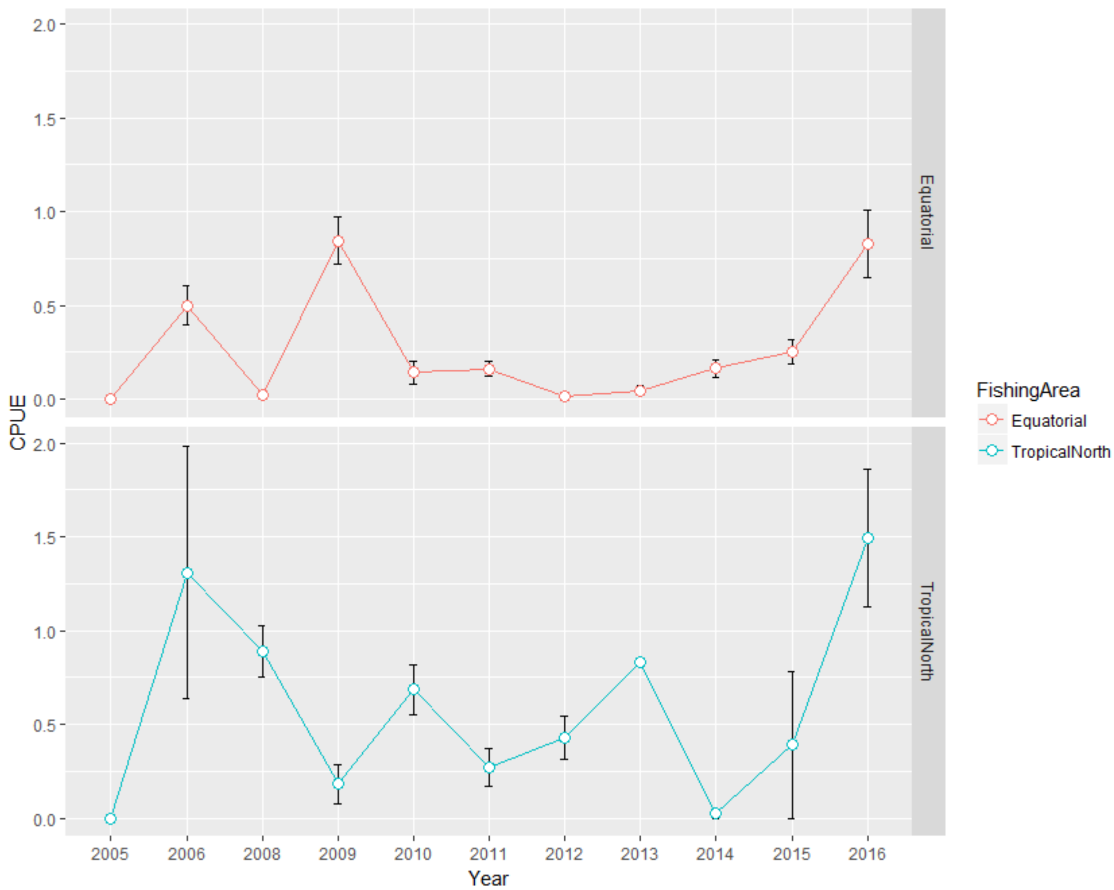

Figure 2.5 - Time series of the mean CPUEs of the smooth hammerhead shark, *Sphyrna zygaena*, caught in the Tropical North and Equatorial regions of the Atlantic Ocean, between 2005 and 2016. The error bars are ± 1 standard error.

Seasonality also seemed to influence CPUEs (Figure 2.6). Higher mean CPUE values were registered in the 3rd quarter of year for the Equatorial region. In the Tropical North, mean CPUEs tended to increase along the year, reaching a peak in the 4th quarter of year.

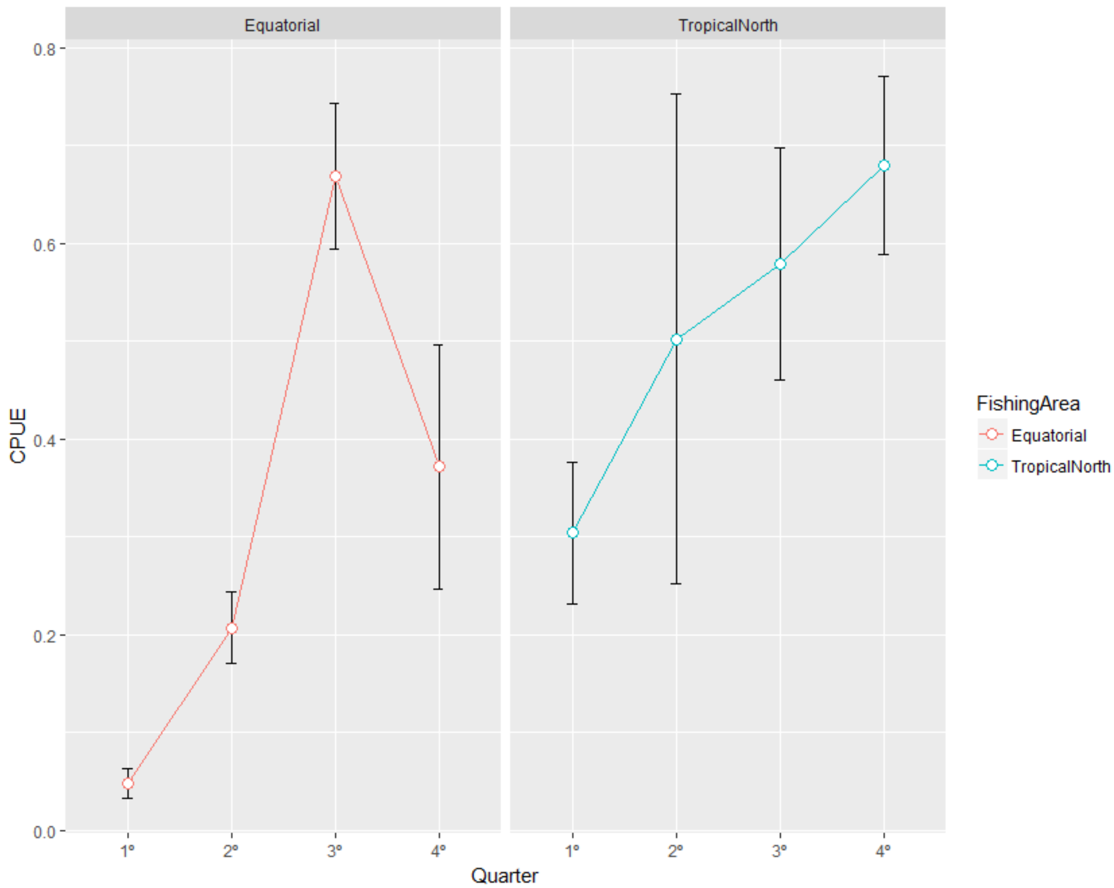

Figure 2.6 - Mean CPUEs of the smooth hammerhead shark, *Sphyrna zygaena*, caught in the Tropical North and Equatorial regions of the Atlantic Ocean during the four quarters of the year, between 2005 and 2016. The error bars are ± 1 standard error.

Yearly and quarterly trends in the size distribution

Size data were not normally distributed (Lilliefors test: D = 0.059, p value < 0.001) and variances were heterogeneous between years (Levene test: F = 6.988, df = 8, p value < 0.001) and quarters of the year (Levene test: F = 4.8207, df = 3, p value<0.01), but not between regions (Levene test: F = 2.774, df = 1, p value = 0.096). Sizes were compared with univariate nonparametric statistical tests among years (K–W: Chi-squared = 101.74, df = 8, p-value < 0.001; permutation test: Chi-squared = 100.94, df = 8, p-value < 0.001), quarters of the year (K–W: Chi-squared = 14.737, df = 3, p-value < 0.01; permutation test: Chi-squared = 18.987, df = 3, p-value < 0.001) and regions (W-M-W: W = 23964, p-value < 0.001; permutation test: Chi-squared = 25.81, df = 1, p-value < 0.001), with statistical differences detected for all cases.

The time series of the mean size distribution showed a persistent decreasing trend of the sharks' sizes in the Equatorial region from 2012 onwards (Figure 2.7). Moreover, the variability was higher in the Tropical North Atlantic when compared to the Equatorial region. However, it is worth noting that only one specimen was sized in 2009 and 2015 and no size data was recorded between 2013 and 2014. In terms of seasonality, mean sizes were higher and more regular in the Tropical North region in comparison to the Equatorial region, although no specimen has been sized during the 2^{nd} quarter of the year in the Tropical North region (Figure 2.8).

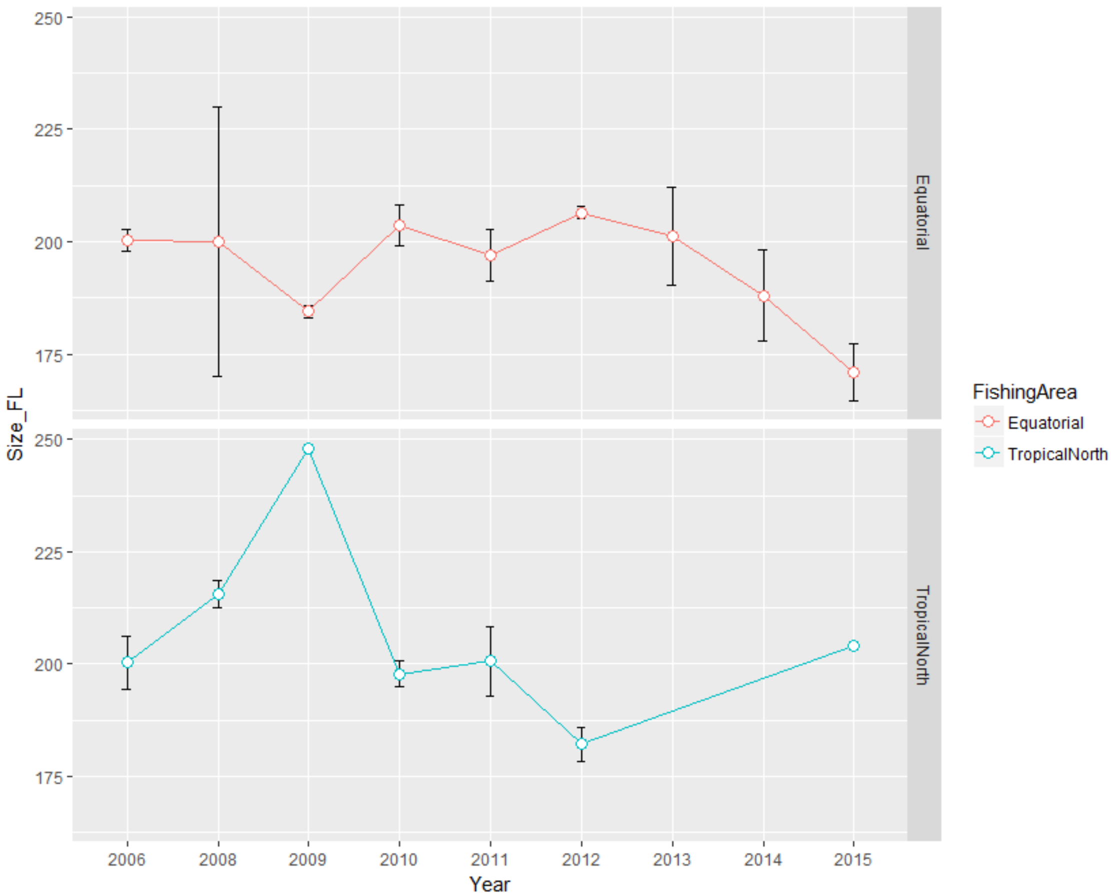

Figure 2.7 - Time series of the mean size (FL, cm) of the smooth hammerhead shark, *Sphyrna zygaena*, caught in the Tropical North and Equatorial regions of the Atlantic Ocean, between 2006 and 2015. The error bars are ± 1 standard error.

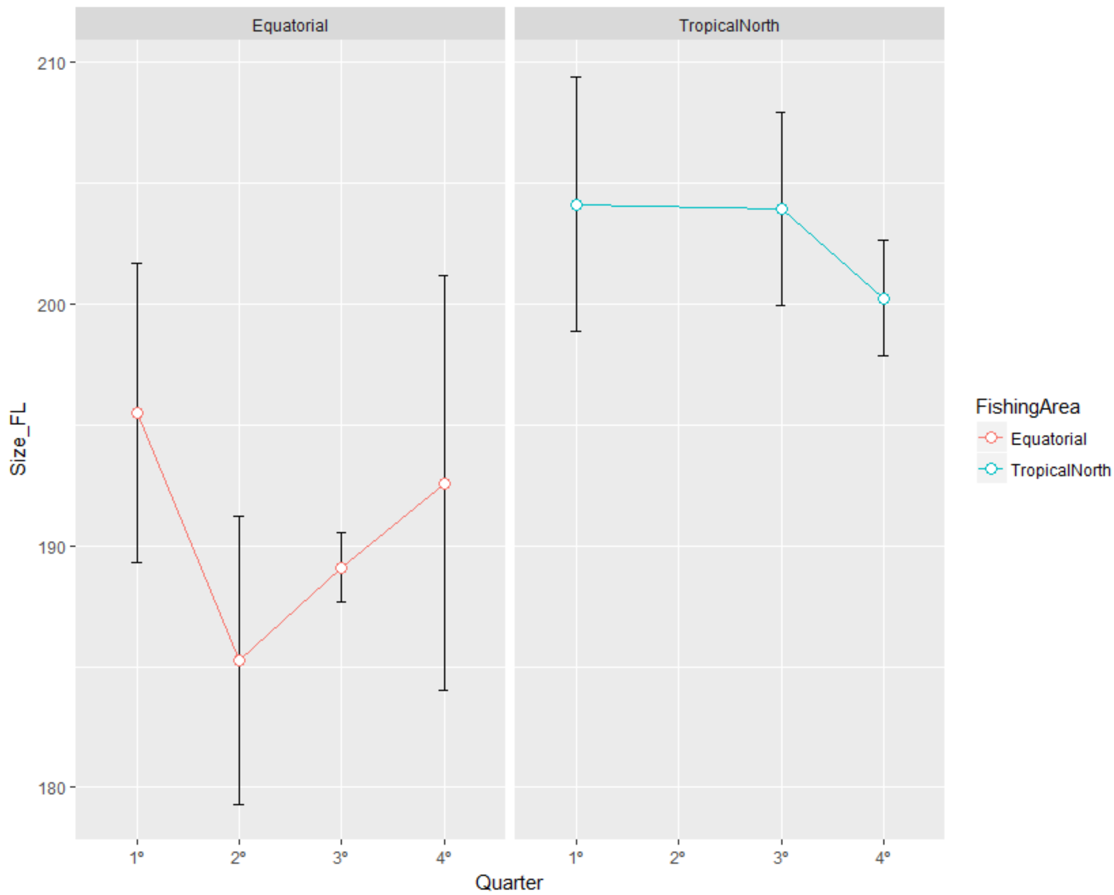

Figure 2.8 - Mean size (FL, cm) of the smooth hammerhead shark, *Sphyrna zygaena*, caught in the Tropical North and Equatorial regions of the Atlantic Ocean during the four quarters of the year, between 2006 and 2015. The error bars are ± 1 standard error.

Discussion

In the light of the global declining trend of several shark stocks worldwide, improving the limited information available for the smooth hammerhead becomes critical for the species conservation and fisheries management. This work provides detailed information on the spatio-temporal dynamics and population structure of the smooth hammerhead shark in the Atlantic Ocean. Specifically, catch per unit of effort (CPUE), catch at size and sex ratio distributions were analyzed based on detailed data collected from fishery observers from the Portuguese pelagic longline fishery operating in the Atlantic Ocean, between 2003 and 2016. In addition, time series trends and seasonal patterns of CPUEs and size distributions were also analyzed.

Similar to what was previously reported by Coelho *et al*. (2012), our results showed that the Portuguese longline fleet operates throughout a wide area of the Atlantic Ocean, with spots of high fishing effort around the temperate Northeast and Equatorial regions in offshore waters. The spatial distribution of the fishing effort is associated with the targeted species - swordfish and, to a lesser extent, blue shark -, however the characteristics of the vessels of the fleet differ between regions. Specifically, the vessels that operate in the Northeast region of the Atlantic (closer to mainland Portugal and the Azores archipelago) are commonly smaller in size and mostly do not have freezing capacity. In contrast, the vessels that concentrate their activity in the more distant regions of the equatorial Atlantic are usually larger vessels with freezing capacity (Coelho *et al*., 2012).

In terms of the spatial distribution of CPUEs, records of catches ranging from 45°N to 35°S, approximately were provided, confirming the species wide latitudinal range of distribution in the Atlantic Ocean (Compagno, 1984; Cortés *et al*., 2015). Higher CPUEs were found closer inshore within the Tropical North and Equatorial regions. Within these regions, the African west coast (including the Gulf of Guinea) represented an important area of high CPUEs for the smooth hammerhead shark. Near-shore waters, as well as islands and seamounts tend to aggregate many shark species and may be used as nursery areas, feeding grounds and/or protection sites (Olson *et al*., 1994; Castro *et al*., 1995; Beck *et al*., 2001; Queiroz *et al*., 2012; Knip *et al*., 2010). In addition, smooth hammerhead sharks are reported to occur generally close inshore and in shallow waters, and the Gulf of Guinea is thought to be a possible nursery area for this species (Compagno, 1984; Bester, 2008; Castro *et al*., 1995). Consequently, the spatial distribution of CPUEs is possibly related to environmental conditions of the African west coast and the species habitat preferences. Moreover, it is important to highlight that a high percentage of the sets showed zero catches of smooth hammerheads, corroborating previous results by Cortés *et al*. (2010) that demonstrated *S. zygaena* was amongst some of the less vulnerable sharks to pelagic longline fisheries in the Atlantic Ocean, due to less likely interactions with the fishing gear.

The specimens caught ranged in size from 123 cm to 275 cm FL. The larger sharks tended to occur in the open ocean habitat, while the smaller sized specimens seemed to concentrate in more coastal areas. This distribution pattern may be linked to habitat characteristics and migratory behavior, which are in turn related to growth and reproductive state (Coelho *et al*., 2017). Another possible hypothesis for the size distribution observed is that it may also be affected by fishing gear selectivity (Fernandez-Carvalho *et al*., 2015). Nevertheless, given that for this study the fishing gear analyzed was always shallow pelagic longlines targeting swordfish, without likely size selectivity issues, and the considerable size of the smaller specimens caught, the hypothesis of a life history cycle with the occurrence of smaller specimens in more inshore waters and larger specimens in more oceanic waters is more likely for the smooth hammerhead.

In general, the sex ratio distribution indicated that there was a tendency for the presence of more males in the sampled area, representing an overall sex ratio of 1.4 males for each female. The predominance of one sex over the other may be related to selectivity of the fishing gear, through greater attraction to bait and/or larger sizes (White *et al*., 2008). Also, partial segregation of the sexes has been associated with differential selection of habitats for social, thermal or forage-related reasons (Mucientes *et al*., 2009), which may explain the tendency for females to move to areas outside those in which the Portuguese pelagic longline fleet tends to operate.

Since the sample was composed mostly of specimens captured in the Equatorial and Tropical North regions of the Atlantic Ocean, the specimens caught in the temperate North and Southern Atlantic were not used for the detailed CPUE and size distribution analysis. Significant differences in CPUE and size distributions were found between regions, years and quarters of the year. We emphasize the increase in the mean CPUE along with a decreasing tendency in the mean specimen size in the Equatorial region from 2012 onwards. These results may be related with the fishing pressure and the capture of larger specimens over the years, which would cause a decrease in the mean specimen size. However, it is important to note that the data used in our study may not reflect the trends in the smooth hammerhead shark population in the Atlantic Ocean, since data from only a fraction of the Portuguese pelagic longline fleet were considered. Previous studies suggested that the population of smooth hammerhead sharks in the Atlantic Ocean has likely experienced a decline (Baum *et al*., 2003; Myers *et al*., 2007; Ferretti *et al*., 2008), however the lack of quality species-specific data prevents reliable evaluation of the species spatio-temporal trends.

A limitation to our study was that the data used were fishery-dependent, thus numerous factors can affect the reliability of the results. Some of the factors that commonly cause biases are the change in the efficiency of the fleet, targeting species, environment, gear selectivity, area coverage and dynamics of the population or fishing fleet (Maunder *et al*., 2006). The data used in this work came from oceanic pelagic longlines, set in oceanic waters and targeting mainly swordfish. As such, the results obtained provide mainly a snapshot of the smooth hammerhead shark population that is present in these waters and is selected by the shallow setting longline gear used in the Portuguese fishery. Also, the possibility of occurrence of *S. zygaena* in the areas not covered cannot be excluded.

Despite all the limitations inherent to the fishery-dependent nature of the data, the distribution patterns presented in our study provide an improvement on the understanding of the spatio-temporal dynamics and population structure of the smooth hammerhead shark in the Atlantic Ocean that can be used to better inform future management decisions and implement efficient conservation measures for the species. Regardless, further work is needed to further fill knowledge gaps on this species.

References

[Rec. 10-08] Recommendation by ICCAT on hammerhead sharks (family Sphyrnidae) caught in association with fisheries managed by ICCAT.

Baum JK, Myers RA, Kehler DG, Worm B, Harley SJ, Doherty PA. Collapse and conservation of shark populations in the Northwest Atlantic. Science. 2003; 299:389-92.

Beck MW, Heck Jr KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates: a better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. Bioscience. 2001; 51:633-41.

Becker RA, Wilks AR, Brownrigg R, Minka TP. Original S code. R version by Ray Brownrigg. maps: Draw Geographical Maps. R package version 3.1.1. 2016. Available from: https://CRAN.R-project.org/package=maps.

Becker RA, Wilks AR. Original S code. R version by Ray Brownrigg. mapdata: Extra Map Databases. R package version 2.2-6. 2016. Available from: https://CRAN.R-project.org/package=mapdata.

Bester, C. Smooth Hammerhead. Florida Museum of Natural History. 2008. Available from: https://www.floridamuseum.ufl.edu/fish/discover/species-profiles/sphyrna-zygaena.

Bivand R, Lewin-Koh N. maptools: Tools for Reading and Handling Spatial Objects. R package version 0.8-41. 2017. Available from: https://CRAN.R-project.org/package=maptools.

Buencuerpo V, Rios S, Morón J. Pelagic sharks associated with the swordfish, *Xiphias gladius*, fishery in the eastern North Atlantic Ocean and the Strait of Gibraltar. Fishery Bulletin. 1998; 96:667-85.

Burgess GH, Beerkircher LR, Cailliet GM, Carlson JK, Cortés E, Goldman KJ, Grubbs RD, Musick JA, Musyl MK, Simpfendorfer CA. Is the collapse of shark populations in the Northwest Atlantic Ocean and Gulf of Mexico real? Fisheries. 2005; 30:19-26.

Casper BM, Domingo A, Gaibor N, Heupel MR, Kotas E, Lamónaca AF, Pérez Jimenez JC, Simpfendorfer C, Smith WD, Stevens JD, Soldo A. *Sphyrna zygaena*: The IUCN Red List of Threatened Species 2005. 2005:e.T39388A10193797.
Available from: http://dx.doi.org/10.2305/IUCN.UK.2005.RLTS.T39388A10193797.en.

Castro JA, Mejuto J. Reproductive parameters of blue shark, *Prionace glauca*, and other sharks in the Gulf of Guinea. Marine and Freshwater Research. 1995; 46:967-73.

Clarke SC, Coelho R, Francis MP, Kai M, Kohin S, Liu K, Simpendorfer C, Tovar-Availa J, Rigby C, Smart JJ. Report of the Pacific Shark Life History Expert Panel Workshop. Western and Central Pacific Fisheries Commission. 2015.

Coelho R, Fernandez-Carvalho J, Amorim S, Santos MN. Age and growth of the smooth hammerhead shark, *Sphyrna zygaena*, in the Eastern Equatorial Atlantic Ocean, using vertebral sections. Aquatic Living Resources. 2011; 24:351–7.

Coelho R, Fernandez-Carvalho J, Lino PG, Santos MN. An overview of the hooking mortality of elasmobranchs caught in a swordfish pelagic longline fishery in the Atlantic Ocean. Aquatic Living Resources. 2012; 25:311-9.

Coelho R, Mejuto J, Domingo A, Yokawa K, Liu KM, Cortés E, Romanov EV, Silva C, Hazin F, Arocha F, Mwilima AM, Bach P, Zárate VO, Roche W, Lino PG, García-Cortés B, Ramos-Cartelle AM, Forselledo R, Mas F, Ohshimo S, Courtney D, Sabarros PS, Perez B, Wogerbauer C, Tsai WP, Carvalho F, Santos MN. Distribution patterns and population structure of the blue shark (*Prionace glauca*) in the Atlantic and Indian Oceans. Fish and Fisheries. 2017.

Compagno LJV. FAO species catalogue: sharks of the world: an annotated and illustrated catalogue of shark species known to date. Food and Agriculture Organization of the United Nations; 1984.

Cortés E, Arocha F, Beerkircher L, Carvalho F, Domingo A, Heupel M, Holtzhausen H, Santos MN, Ribera M, Simpfendorfer C. Ecological risk assessment of pelagic sharks caught in Atlantic pelagic longline fisheries. Aquatic Living Resources. 2010; 23:25-34.

Cortés E, Domingo A, Miller P, Forselledo R, Mas F, Arocha F, Campana S, Coelho R, Da Silva C, Hazin F, Holtzhausen H. Expanded ecological risk assessment of pelagic sharks caught in Atlantic pelagic longline fisheries. Collect Vol. Sci. Pap. ICCAT. 2015; 71:2637-88.

Fay MP, Shaw PA. Exact and Asymptotic Weighted Logrank Tests for Interval Censored Data: the interval R Package. Journal of Statistical Software. 2010; 36:1–34. Available from: https://CRAN.R-project.org/package=perm.

Fernandez-Carvalho J, Coelho R, Mejuto J, Cortés E, Domingo A, Yokawa K, Liu KM, García-Cortés B, Forselledo R, Ohshimo S, Ramos-Cartelle A. Pan-Atlantic distribution patterns and reproductive biology of the bigeye thresher, *Alopias superciliosus*. Reviews in Fish Biology and Fisheries. 2015; 25:551-68.

Ferretti F, Myers RA, Serena F, Lotze HK. Loss of large predatory sharks from the Mediterranean Sea. Conservation Biology. 2008; 22:952-64.

Fox J, Weisberg S. An R companion to applied regression. 2nd ed. Los Angeles, CA: Sage; 2011. Available from: https://CRAN.R-project.org/package=car.

Gerritsen H. mapplots: Data Visualisation on Maps. R package version 1.5. 2014. Available from: https://CRAN.R-project.org/package=mapplots.

Giraudoux P. pgirmess: Data analysis in ecology. R package version 1.6.7. 2017. Available from: https://CRAN.R-project.org/package=pgirmess.

Gross J, Ligges U. nortest: Tests for Normality. R package version 1.0-4. 2015. Available from: https://CRAN.R-project.org/package=nortest.

Knip DM, Heupel MR, Simpfendorfer CA. Sharks in nearshore environments: models, importance, and consequences. Marine Ecology Progress Series. 2010; 402:1-11.

Lee PF, Chen IC, Tzeng WN. Spatial and temporal distribution patterns of Bigeye tuna (*Thunnus obesus*) in the Indian Ocean. Zoological Studies. 2005; 44: 260–70.

Levene H. Robust tests for equality of variances. Contributions to Probability and Statistics. 1960; 1:278-92.

Lilliefors HW. On the Kolmogorov-Smirnov test for normality with mean and variance unknown. Journal of the American Statistical Association. 1967; 62:399-402.

Manly BFJ. Randomization, bootstrap and Monte Carlo methods in biology. 3rd ed. New York: Chapman & Hall/CRC; 2007.

Maunder MN, Sibert JR, Fonteneau A, Hampton J, Kleiber P, Harley SJ. Interpreting catch per unit effort data to assess the status of individual stocks and communities. Ices Journal of Marine Science. 2006; 63:1373-85.

Mucientes GR, Queiroz N, Sousa LL, Tarroso P, Sims DW. Sexual segregation of pelagic sharks and the potential threat from fisheries. Biology Letters. 2009; 5: 156-9.

Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH. Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science. 2007; 315:1846-50.

Neuwirth E. RColorBrewer: ColorBrewer palettes. R package version 1.1-2. 2014. Available from: https://CRAN.R-project.org/package=RColorBrewer.

Olson DB, Hitchcock GL, Mariano AJ, Ashjian CJ, Peng G, Nero RW, Podestá GP. Life on the edge: marine life and fronts. Oceanography. 1994; 7:52-60.

Queiroz N, Humphries NE, Noble LR, Santos AM, Sims DW. Spatial dynamics and expanded vertical niche of blue sharks in oceanographic fronts reveal habitat targets for conservation. PLoS One. 2012 Feb 29; 7:e32374.

R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria 2016. Available from: http://www.R-project.org/.

Stabler B. Shapefiles: Read and Write ESRI Shapefiles. R package version 0.7. 2013. Available from: https://CRAN.R-project.org/package=shapefiles.

Warnes GR, Bolker B, Lumley T, Johnson RC. gmodels: Various R Programming Tools for Model Fitting. R package version 2.16. 2. 2015. Available from: https://CRAN.R-project.org/package=gmodels.

White WT, Bartron C, Potter IC. Catch composition and reproductive biology of *Sphyrna lewini* (Griffith & Smith) (Carcharhiniformes, Sphyrnidae) in Indonesian waters. Journal of Fish Biology. 2008; 72:1675-89.

Wickham H. ggplot2: elegant graphics for data analysis Springer; New York; 2009. Available from: https://CRAN.R-project.org/package=ggplot2.

Wickham H. scales: Scale Functions for Visualization. R package version 0.4.1. 2016. Available from: https://CRAN.R-project.org/package=scales.

Wickham H. The Split-Apply-Combine Strategy for Data Analysis. Journal of Statistical Software. 2011; 40:1-29. Available from: https://CRAN.R-project.org/package=plyr.

CHAPTER 3: MIGRATIONS AND HABITAT USE OF THE SMOOTH HAMMERHEAD SHARK IN THE ATLANTIC OCEAN

Abstract

The smooth hammerhead shark, *Sphyrna zygaena*, is a cosmopolitan pelagic shark captured as bycatch in pelagic oceanic fisheries, especially pelagic longlines targeting swordfish and/or tunas. From 2012 to 2016, eight smooth hammerheads were tagged with Pop-up Satellite Archival Tags (PSATs) in the inter-tropical region of the Northeast Atlantic Ocean, with successful transmissions received from seven tags (total of 319 tracking days). Results confirmed *S. zygaena* is a highly migratory species, as the longest migration ever documented for this species (> 6600 km) was recorded. An absence of a diel vertical movement behavior was noted, with the sharks spending most of its time at surface waters (0-50 m) above 23 °C. The operating depth of the pelagic longline gear was measured with Minilog Temperature and Depth Recorders (TDRs), and the overlap with the species vertical distribution was calculated. The overlap is taking place mainly during the night and is higher for juveniles (~40% of overlap time). The information presented can now be used to provide sustainable management tools and serve as input for Ecological Risk Assessments for smooth hammerheads caught in Atlantic pelagic longline fisheries.

Introduction

With the rapid expansion of fishing fleets and the increasing exploitation of the open ocean, many marine predators have experienced a decline over the past decades (Musick *et al*., 2000; Hilborn *et al*., 2003). Among the impacted species, large elasmobranchs (including sharks) have been of particular concern (Poisson *et al*., 2016). Pelagic sharks are caught by a variety of fishing gear and are common as bycatch of pelagic longline fleets targeting mainly swordfish (*Xiphias gladius*) and tunas (*Thunnus* spp.) (Compagno, 1984; Buencuerpo *et al*., 1998; Stevens *et al*., 2000; Petersen *et al*., 2009; Camhi *et al*., 2009). Since apex predators play a major role in marine communities' structure and function, widespread decline of sharks across the world's oceans are expected to strongly influence the equilibrium of marine ecosystems (Stevens *et al*., 2000; Myers *et al*., 2007). Therefore, understanding habitat use and ecology of sharks is crucial to evaluate the fishing impacts on them and throughout the food web. Additionally, for many pelagic shark species, important information on their life history and ecology is still missing, which hinders higher level scientific-based management advice.

The smooth hammerhead shark, *Sphyrna zygaena*, is a pelagic coastal and oceanic shark distributed worldwide in temperate and tropical waters, most commonly in depths of up to 20 m along the water column (Compagno, 1984; Casper *et al*., 2005). Such as most elasmobranchs, *S. zygaena* is characterized by having slow-growth, late maturity and relatively low fecundity, which makes the species relatively vulnerable to fishing mortality (Compagno, 1984; Stevens *et al*., 2000; Bester, 2008; Cortés *et al*., 2015; Rosa *et al*., 2017). Cortés *et al*. (2015) conducted an Ecological Risk Assessment (ERA) and concluded that smooth hammerheads' stocks had one of the lowest vulnerabilities specific to pelagic longline fisheries in the Atlantic Ocean. Ecological Risk Assessments are assessment tools that can be used to evaluate the overall vulnerability of a stock to overexploitation, taking into account its biological productivity and susceptibility to a fishery (Cortés *et al*., 2010). In this way, out of the 20 assessed shark stocks, smooth hammerheads ranked 13th in terms of their overall vulnerability to the pelagic longline fisheries (Cortés *et al*., 2015).

The smooth hammerhead is listed as "Vulnerable" by the International Union for the Conservation of Nature (IUCN) (Casper *et al*., 2005) and was given international level protection in terms of trade under Appendix II of the Convention for International Trade in Endangered Species (CITES) (CITES, 2013). Also, sustainability concerns regarding this species led the International Commission for the Conservation of Atlantic Tunas (ICCAT) to issue several management regulations concerning the conservation of the smooth hammerhead in the Atlantic Ocean. Specifically, fishing vessels are prohibited from "retaining onboard, transshipping, landing, storing, selling, or offering for sale any part or whole carcass of hammerhead sharks of the family Sphyrnidae (except for the *Sphyrna tiburo*), taken in the Convention area in association with ICCAT fisheries" [Rec. 10-08]. Although *S. zygaena* is occasionally captured as bycatch by industrial longline fleets targeting swordfish and tunas in the Atlantic Ocean (Buencuerpo *et al*., 1998; Cortés *et al*., 2010), very limited information is currently available on its life history parameters, movement patterns, essential habitat and population dynamics (Coelho *et al.*, 2011; Rosa *et al*., 2017).

Studying pelagic species in their natural environment is a difficult task, however tracking techniques and satellite tagging have experienced rapid development over the past decades, providing scientists the opportunity to improve the knowledge on spatial ecology of marine predators, like pelagic sharks (e.g., Heithaus *et al*., 2007; Stevens *et al*., 2010; Abascal *et al*., 2011; Coelho *et al*., 2015; Queiroz *et al*., 2016), tunas (e.g., Wilson *et al*., 2005) and swordfish (e.g., Abascal *et al*., 2015). Apart from providing estimates of fish position, current-generation Pop-up Satellite Archival Tags (PSATs) also collect and record environmental data, such as pressure (depth) and environmental water temperature, at set intervals of a few seconds to several hours (Musyl *et al*., 2001). After being programmed to collect information for a predetermined amount of time, the PSAT releases from its host and floats to the surface where it sends its broadcast of data to the ARGOS satellite-based system (Musyl *et al*., 2001; Musyl *et al*., 2011). The data transmitted from the satellite tags can then be used to understand distribution ranges, movement patterns and calculate overlaps between the vertical habitat utilization and depths of hooks of pelagic longline fishing gear. Such information can therefore improve the knowledge needed to provide advice on optimizing species management and conservation.

Previous studies using satellite telemetry on smooth hammerhead sharks are very limited and none was so far carried out in the Atlantic. In the Pacific, a smooth hammerhead shark tagged in June 2015 off San Clemente Island, California, was documented to travel more than 600 km south to the central Baja Peninsula and then returned north to waters off Ventura, California, travelling a total distance of more than 1600 km (News - SWFSC, 2015). More recently, five smooth hammerheads were tagged in northern New Zealand, with information from three tags successfully transmitted. Besides noting the ability of the species to travel significant distances, the study also revealed that smooth hammerhead sharks generally occurred in shallow waters (Francis *et al*., 2016). For other hammerhead species, particularly for the scalloped hammerhead (*Sphyrna lewini*), some previous studies using PSATs were carried out in the Pacific and Atlantic Oceans (Gulf of Mexico) that described vertical and horizontal movement patterns (Jorgensen *et al*., 2009; Ketchum *et al*., 2009; Bessudo *et al*., 2011; Hoffmayer *et al*., 2013).

Given the limited data currently available on the habitat use and vulnerability to fisheries for the smooth hammerhead shark, and the need of such information to provide informed advice for management and conservation of the species, the objectives of this study were 1) to improve the knowledge of movement patterns in the inter-tropical Atlantic Ocean, 2) to investigate vertical habitat utilization in terms of diel movements and 3) to calculate the overlap between the vertical habitat utilization and the depth of hooks of pelagic longline fishing gear, specifically from surface longlines targeting swordfish.

Materials and methods

Tagging procedure

A total of 8 PSATs were used in this study. Tagging was carried out by scientific fisheries observers from the Portuguese Institute for the Ocean and Atmosphere, I.P. (IPMA) onboard vessels from the Portuguese pelagic longline fleet. The PSAT deployment took place in the inter-tropical region of the Northeast Atlantic Ocean, between September 2012 and August 2016 (Figure 3.1).

The PSATs were rigged with monofilament leaders (aprox. 15 cm in length) secured with copper crimps and encased in surgical silicone tubing. The copper crimps were at a distance from the tag sufficient to prevent any accidental contact with the PSATs detachment mechanism and were covered with silicone tubing. An umbrella-type nylon dart (Domeier *et al*., 2005) was used to insert the tag laterally to the dorsal musculature below the first dorsal fin, using the methodology described by Howey-Jordan *et al*. (2013). Before tag attaching, the PSATs were programmed to collect information for periods between 31 and 150 days (Table 3.1), tested and positively buoyant in the sea water. The pelagic longline gear used J-style hooks and steel leaders. Sharks were either hoisted alongside the vessel or brought on board for tagging. In addition, the animals were sexed, measured for fork length (FL), and GPS tagging location (latitude and longitude), date and time were recorded. The leaders were cut and hooks removed if possible.

Four models of PSATs were used. Standard, X-tags and high rate (MTI-HR) X-tags manufactured by Microwave Telemetry, Inc. (MTI) and MiniPAT tags built by Wildlife Computers (WC). Standard tags and X-tags record data on depth and temperature every 2 min, daily minimum and maximum depths and temperatures, as well as the light levels and times of sunrise and sunset. The temperature range of these tags is -4 °C to +40 °C, with a resolution of 0.16-0.23 °C. The depth range is 0 m to 1296 m, with a resolution of 5.4 m (via Argos) for Standard tags and a resolution of 0.34-5.5 m (via Argos) and 0.34 m (archived data) for X-tags. After pop-up, the transmitting tags attempt to transmit one depth and temperature data-pair within each 15 min period in the time series, as well as the full minimum and maximum daily depths and times of sunrise and sunset. The HR X-tags record data on depth, temperature and light levels every 5 min and after pop-up attempt to transmit the entire time series of data. The temperature range of these tags is -4 °C to +40 °C, with a resolution of 0.16-0.23 °C, and the depth range is 0 m to 1296 m, with a resolution of 1.34 m (via Argos) and 0.34 m (archived data). The MiniPAT tags work in a similar way, collecting data on light intensity, depth and temperature at pre-determined time intervals which depend on the length of the pre-programmed deployment. In this case, the WC tags were programmed for 120-150 days deployment periods and all sensors were sampling at a rate of 5 seconds. The temperature range is -20 °C to +50 °C, with a resolution of 0.05 °C, and the depth range is 0 m to 1700 m, with a resolution of 0.5 m (via Argos). After pop-up, the tags attempt to transmit time series of depth and temperature measurements at 10 min intervals in order to have the full coverage of the entire time series. If the tag is physically recovered the entire data recorded can be downloaded directly to a PC.

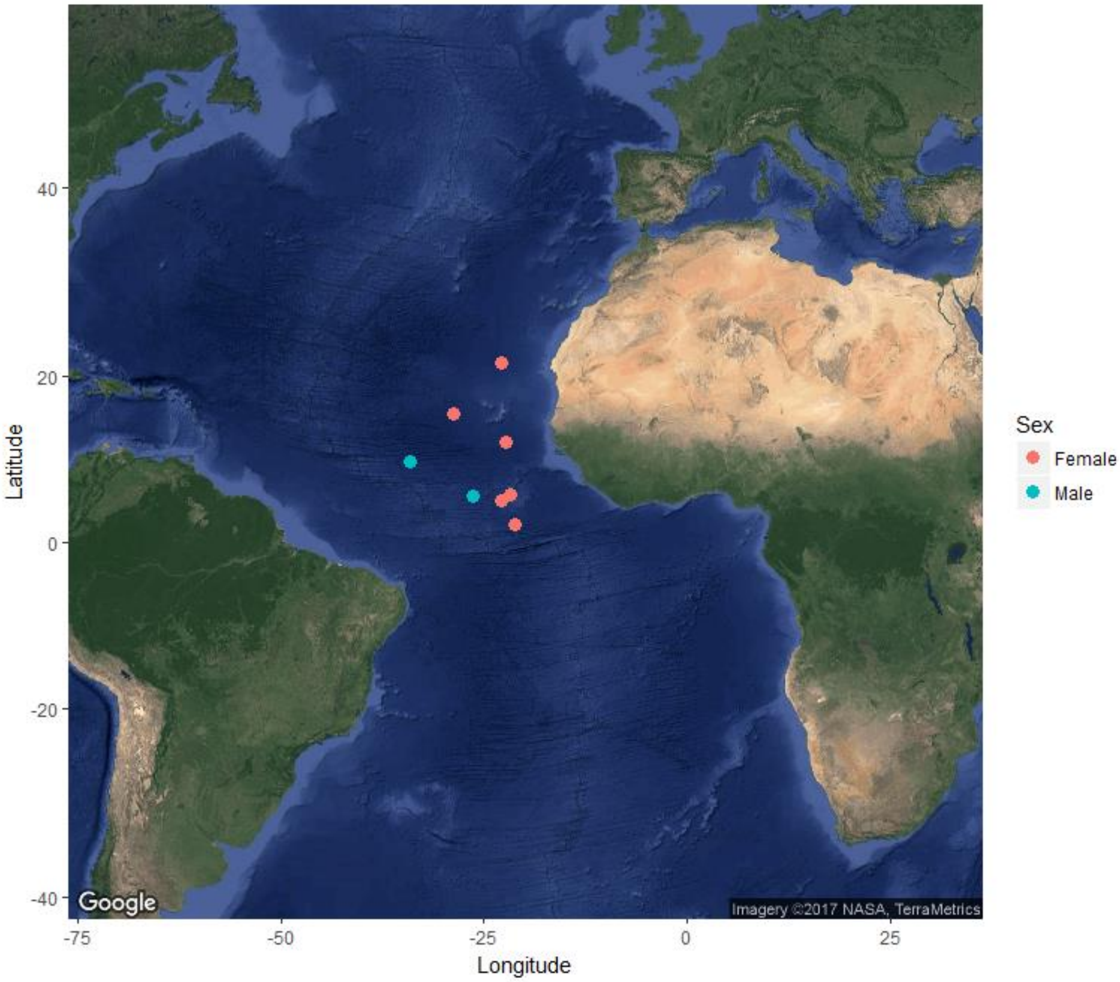

Figure 3.1 – Tagging locations of the smooth hammerhead sharks, *Sphyrna zygaena*, tagged with Pop-up Satellite Archival Tags (PSATs) in the Atlantic Ocean.

Table 3.1 - Characteristics of tagged smooth hammerhead sharks, *Sphyrna zygaena*, and Pop-up Satellite Archival Tags (PSATs) used in this study, with information on specimen size, sex, maturation state, tag type, planned duration, effective tracking days and % of transmitted data. FL = fork length.

ID	Tag Model	Size (FL, cm)	Sex	Maturation state	Tagging date	Planned duration (days)	Tracking days	Transmitted data (%)
113781	MTI Standard	170	Male	Adult	3-Sep-2012	90	28	100
113784	MTI Standard	170	Female	Juvenile	11-Oct-2012	120		
127998	MTI X-tag-HR	175	Female	Juvenile	1-Oct-2013	31	31	56
127999	MTI X-tag-HR	130	Female	Juvenile	17-Nov-2013	31	31	7
136856	WC MiniPAT	123	Female	Juvenile	27-Jul-2014	120	6	44
136143	MTI X-tag	180	Male	Adult	18-Sep-2014	60	6	100
160917	WC MiniPAT	180	Female	Juvenile	27-May-2016	150	67	74
162392	WC MiniPAT	205	Female	Adult	2-Aug-2016	150	150	78

Depth of longline gear operation

In order to characterize the depth of pelagic longline operations, Minilog Temperature and Depth Recorders (TDRs) made by Vemco (Bedford, Nova Scotia, Canada) were deployed on 60 fishing sets. Six TDRs were used per fishing set and were programmed to record data at every 1 min interval, with a resolution of 1.2 m. TDRs were attached immediately adjacent to the hooks and placed on all hooks between floats.

The fishing sets were carried out following the general practices of the European shallow pelagic longline fleet that targets mainly swordfish, with gear setting typically starting in the late afternoon, and retrieval commencing at dawn of the next morning. Details of the fishing gear are described in Coelho *et al*. (2015), basically consisting of a standard US-style polyamide monofilament mainline, with five branch lines (~ 18 m long and with a J-style hook in the terminal tackle) between floats. Two different size options for the float line are typically used by this fleet: either 12 m or 16 m. Consequently, this variability of the fleet fishing strategy was considered in the study design, with the TDRs equally deployed on sections using both sizes of float lines.

Data analysis

The habitat use was investigated as the percentage of time-at-depth and time-at-temperature and was separately analyzed for daytime and nighttime. Sunset and sunrise were calculated taking into account the date (Julian day), latitude and longitude (Teets, 2003), using library "RAtmosphere" in R (Biavati, 2014). Habitat utilization was also analyzed separately for juvenile and adult specimens. The definition of juvenile and adult stages was based on the Compagno (1984) values of size at first maturity of 210-240 cm total length.

The time-at-depth and time-at-temperature data were aggregated into 10 m and 1°C bins, respectively, based on the above analyses. These data were subsequently expressed as a fraction of the total time of observation for each shark, and the fractional data bins averaged across all sharks within each category. The depth and temperature data were tested for normality with Kolmogorov-Smirnov tests with Lilliefors correction (Lilliefors, 1967) and for homogeneity of variances with Levene tests (Levene, 1960). Given the lack of normality in the data and heterogeneity of variances, time-at-depth and time-at-temperature were compared between the daily period (daytime *vs*. nighttime) and maturity stage (adults *vs*. juveniles) with nonparametric k-sample permutation tests (Manly, 2007), using library "perm" in R (Fay *et al*., 2010). For this, a Monte Carlo approach was used with the data randomized and re-sampled 9999 times to build the expected distribution of the differences under a random distribution, which was then used to determine the significance of the differences in the time-at-depth and time-at-temperature for the sample.

Geographic positions at tagging were determined by Global Positioning System (GPS), while the pop-up locations of transmitting PSATs were established as the first point of transmission with an Argos satellite. The most probable tracks between tagging and pop-up locations were calculated from PSATs light level data using astronomical algorithms provided by the tag manufacturers. To improve the geolocation quality, the unscented Kalman filter state-space model incorporating a sea surface temperature field was then applied (Lam *et al*., 2008), using library "ukfsst" in R (Nielsen *et al*., 2012). In the case of HR X-tags, light level data cannot be used for geolocation estimates because it is stored at a lower resolution than in standard rate tags. Therefore, the distances travelled by the sharks tagged with HR X-tags were measured in straight lines between the tagging and the pop-up locations.

The overlap between the habitat use and depth of fishing gear was calculated by analyzing the results from the TDRs and PSATs. The mean depth of the hooks was calculated, and the differences between hooks set with 12 m or 16 m float lines tested with permutation tests (Manly, 2007). The 90% percentiles of the recorded hook depths were calculated and the depth distribution of the specimens PSAT data were overlapped with the depth distribution of the fishing gear in order to calculate the percentage of overlap time.

All statistical analyses for this paper were carried out with the R Project for Statistical Computing version 3.3.2 (R Core Team, 2016). Plots were created using libraries "plotrix" (Lemon, 2006) and "ggplot2" (Wickham, 2009).

Results

Tag performance

Eight tags were deployed during this study, with data from seven tags successfully transmitted and one tag failing data transmission. A total of 319 tracking days were registered, of which 285 and 34 days corresponded to females and males (including adults and juveniles of each sex), respectively (Table 3.2).

Table 3.2 - Total tracking days of smooth hammerhead sharks, *Sphyrna zygaena*, per sex (males and females) and maturity stage (juveniles and adults).

Sex	Maturity stage		Total
	Adults (N=3)	Juveniles (N=4)	
Females (N=5)	150	135	285
Males (N=2)	34		34
Total	184	135	319

Horizontal movements

Estimated courses taken by smooth hammerhead sharks are shown in Figure 3.2. The data indicates that *S. zygaena* seems to be mainly a tropical and equatorial species, swimming in both open and coastal waters in the Atlantic Ocean. The distances travelled ranged from 131.7 km to 6610 km (for 6 and 150 tracking days, respectively), corresponding to an average daily distance of 33.5 km/day (Table 3.3).

Since HR X-tags don't record the times of sunrise and sunset, the distances travelled by the sharks 127998 and 127999 were measured in straight lines between the tagging and pop-up locations. Shark 127998 migrated north, while shark 127999 swam towards southeast. Both these sharks seem to have migrated inshore towards Cape Verde archipelago coastal waters. During their migrations, shark 113781 and shark

160917 followed an oscillatory track heading south and east, respectively. Shark 136143 moved northeast and shark 136856 swam in a steady northeasterly direction. Finally, shark 162392 travelled around the African west coast towards southeast. This shark's course represented a trans-equatorial migration since the shark moved from northern to southern hemisphere.

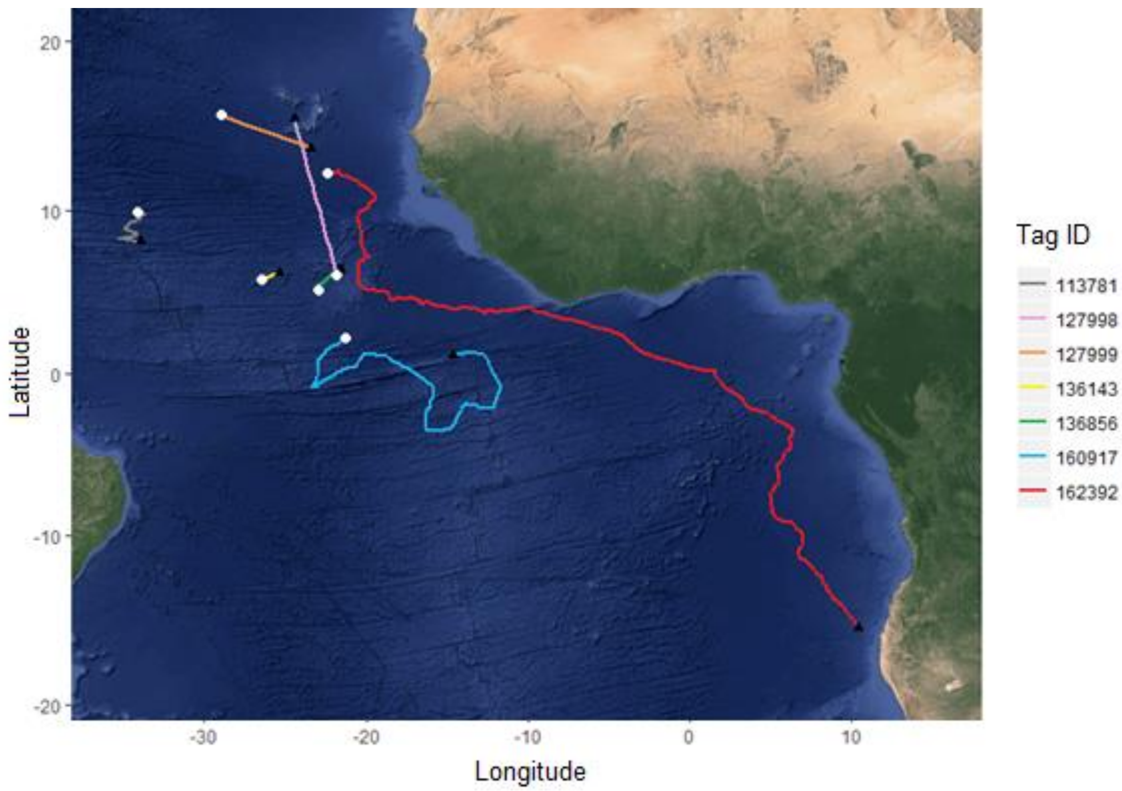

Figure 3.2 - Tagging and pop-up locations of smooth hammerhead sharks, *Sphyrna zygaena*, tracked with pop-up satellite archival tags (PSATs) in this study. The tagging locations are represented with white circles and the pop-up locations are represented with black triangles.

Table 3.3 - Characteristics of the courses taken by smooth hammerhead sharks, *Sphyrna zygaena*, with information on effective tracking days, distance travelled and average daily distance.

Shark ID	Tracking days	Distance travelled (km)	Average daily distance (km/day)
127998	31	1092	35.2
127999	31	636	20.5
113781	28	683	24.4
136143	6	132	22
160917	67	3037	45.3
136856	6	257	42.8
162392	150	6610	44.1

Vertical habitat utilization

The vertical movements of the smooth hammerhead sharks did not exhibit diel cyclicity. Although significant differences on habitat use between night and day were found (depth: permutation test differences = 3.19, p-value < 0.001; temperature: permutation test differences = -0.66, p-value < 0.001), sharks spent most of both their day and nighttime close to the surface (mean depth = 13.62 m; mean temperature = 26.28 °C) within the depth-interval 0-50 m and preferred a warmer environment with water temperature above 23 °C (Figure 3.3). Occasionally, deeper dives followed by rapid ascends were recorded. The maximum depth reached was 260.90 m and the minimum temperature recorded was 12.80 °C (Figure 3.4).

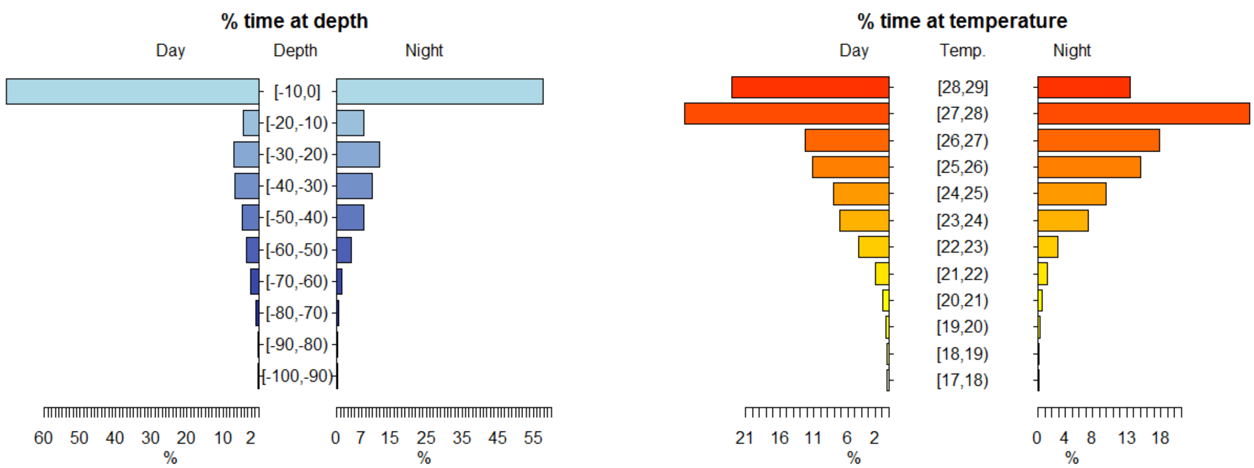

Figure 3.3 - Habitat utilization of smooth hammerhead shark, *Sphyrna zygaena*, for daytime and nighttime in terms of depth and temperature. Depth classes are categorized in 10 m intervals and temperature classes in 1 °C intervals.

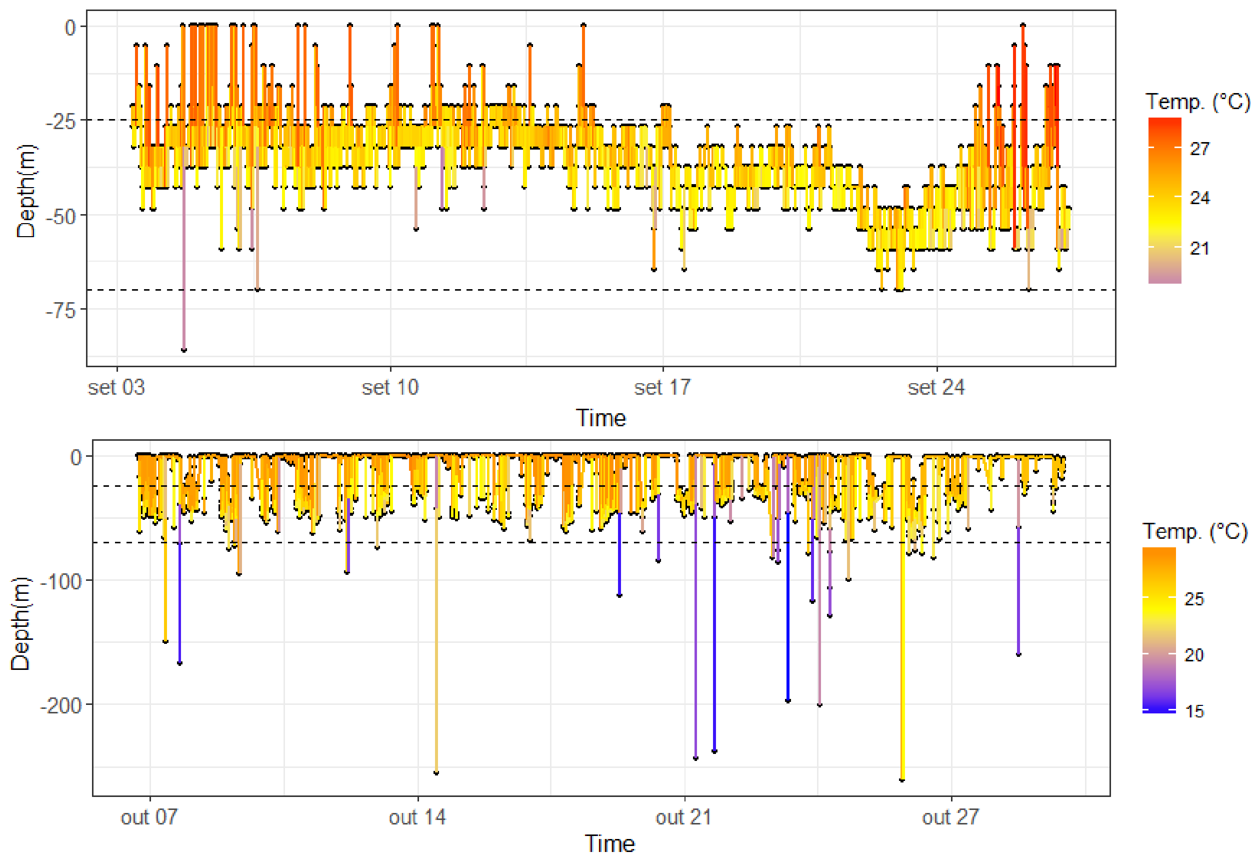

Figure 3.4 - Details of diving behavior profiles of smooth hammerhead sharks, *Sphyrna zygaena*, tagged with pop-up satellite archival tags (PSATs). The plot on the top (shark 113781) represents the most common behavior movements. The plot on the bottom (shark 127998) shows occasional deep dives. Horizontal dashed lines represent the 90% percentile depth distribution of the hooks (~25-70 m).

Although both adults and juveniles showed a preference for shallow waters, different habitat utilization patterns were observed during both daytime and nighttime. Specifically, the juveniles occupied a wider range of vertical habitat than the adults, with the juveniles staying in deeper colder waters during the night (Figure 3.5). The mean depth during daytime was 10.99 m for adults and 13.72 m for juveniles (permutation tests: daytime differences= -2.73, p-value < 0.001), while during nighttime the mean depth was 11.23 m for adults and 21.81 m for juveniles (permutation tests: nighttime differences= -10.58, p-value < 0.001). Similar results were obtained regarding the water temperature. The mean temperature during daytime was 26.43 °C for adults and 26.28 °C for juveniles (permutation tests: daytime differences= 0.15, p-value < 0.001), while during nighttime the mean temperature was 26.41 °C for adults and 25.84 °C for juveniles (permutation tests: nighttime differences= 0.57, p-value < 0.001).

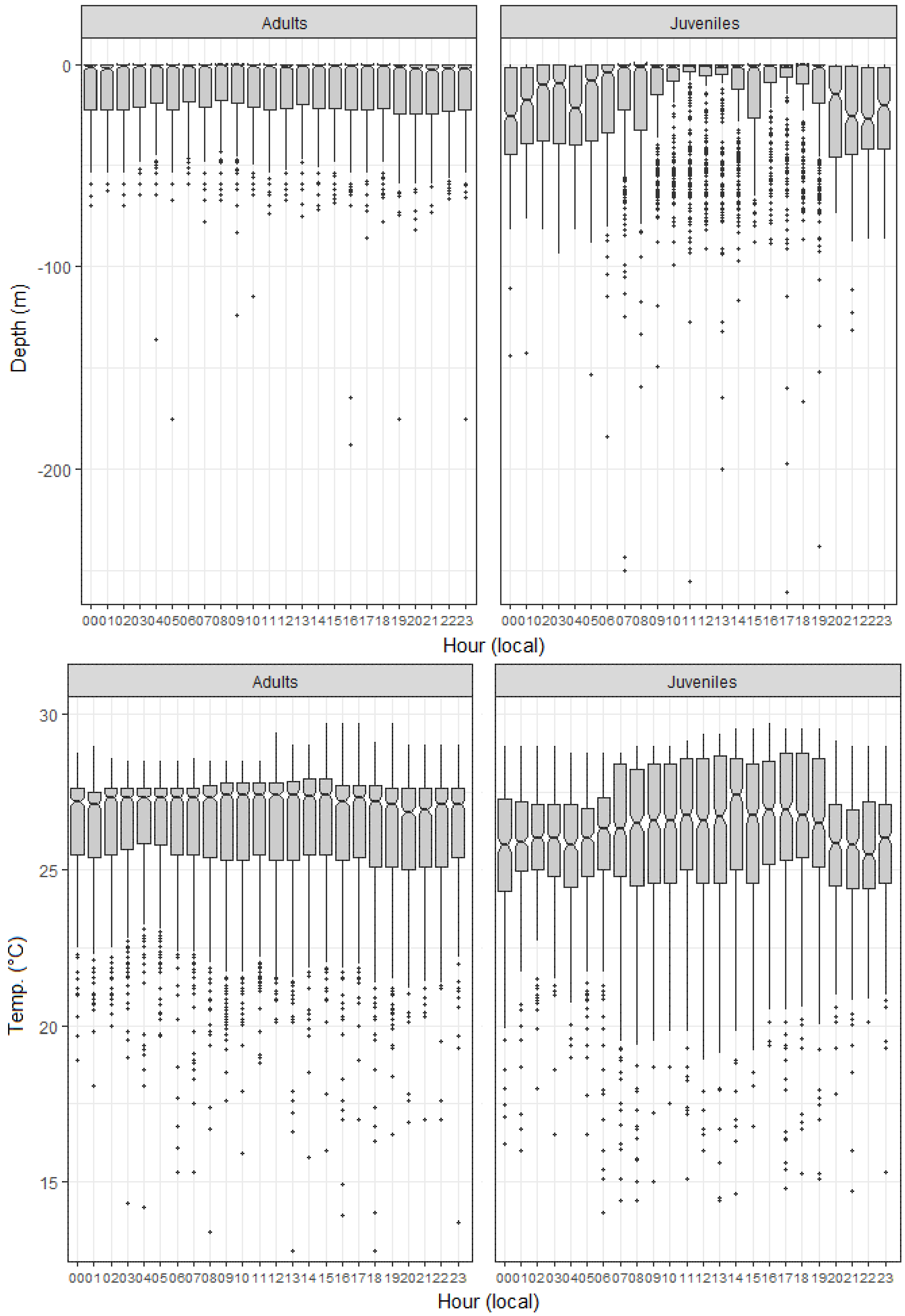

Figure 3.5 - Smooth hammerhead shark, *Sphyrna zygaena*, habitat utilization with the data categorized in one-hour time classes, separated by maturity stage. The data represented is the median, the 1st and 3rd quartiles, the 95% confidence intervals of the median and the outliers.

Time-at-depth data revealed that the 0-10 m depth class was the most often occupied during the day and night, independently of the maturity stage of the sharks. The adults spent 67.86% and 63.86% of their day and nighttime, respectively, at 0-10 m, while the juveniles displayed peaks of 74.76% and 47.78% at such depth for day and nighttime, respectively (Figure 3.6). In addition, adults showed a preference for water layers of 27-28 °C, with 41.45% and 44.44% of their day and nighttime, respectively, spent there. Juveniles preferred slightly warmer water temperatures (28-29 °C) during daytime (31.62% of the daytime), whereas during nighttime the modal water temperature shifted to colder waters (26-27 °C) where juveniles spent 22.03% of their nighttime (Figure 3.6).

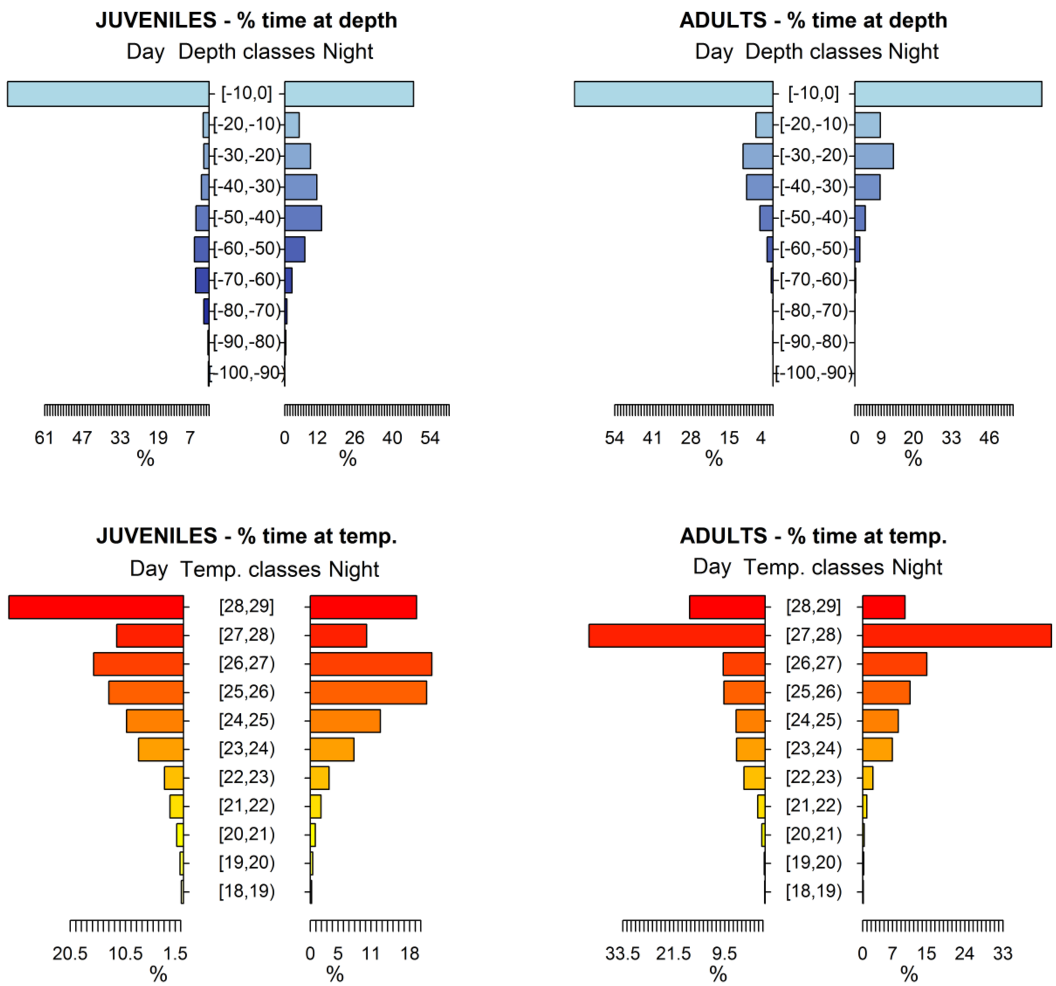

Figure 3.6 - Habitat utilization for juvenile and adult smooth hammerhead sharks, *Sphyrna zygaena*, for daytime and nighttime in terms of depth and temperature. Depth classes are categorized in 10 m intervals and temperature classes in 1 °C intervals.

Overlap between shark habitat and fishing gear depth

The depth of hooks varied according to the length of the float lines. The average hook depth of the pelagic longline fishery was 41 m and 48 m, when using 12 m and 16 m float lines, respectively, with those differences statistically significant (Permutation test: observed differences = 6.68; p-value < 0.01).

The 90% percentile depth distribution of the hooks was 24.8-63.1 m and 29.4-70.3 m for the 12 m and 16 m float lines, respectively. The analysis of the spatial overlap between hook depth distribution and *S. zygaena* vertical habitat shows that sharks are generally more susceptible to interactions with the longline fishing gear during nighttime. Also, the overlap was particularly noticeable for the juveniles (Figure 3.7) (Table 3.4).

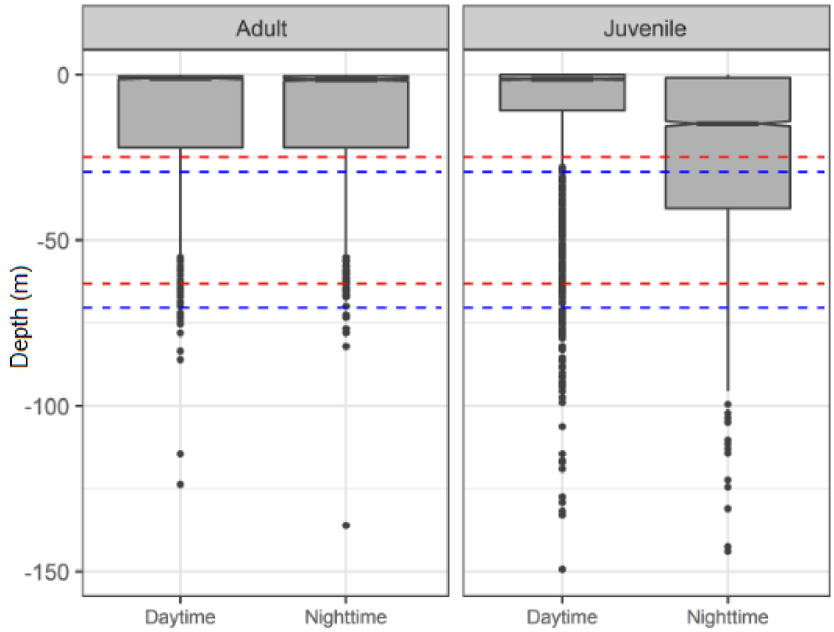

Figure 3.7 - Overlap between the vertical habitat of smooth hammerhead shark, *Sphyrna zygaena*, and the depth of operation of shallow water pelagic longlines targeting swordfish, separated by maturity stage (adult and juvenile), during daytime and nighttime. Horizontal dashed lines represent the 90% percentile depth distribution of the hooks for the 12 m (red lines) and 16 m (blue lines) float lines.

Table 3.4 - Overlap, in percentage of time (%), between the vertical habitat of smooth hammerhead shark, *Sphyrna zygaena*, and the depth of operation of shallow water pelagic longlines targeting swordfish.

Float line length	Daytime		Nighttime	
	Juveniles	Adults	Juveniles	Adults
12 m	16.4	21.5	41.2	21.7
16 m	18.6	16.1	37.1	14.2

Discussion

Understanding habitat preferences and vulnerability of smooth hammerhead sharks to fisheries is crucial to ensure successful species conservation strategies and effective management measures. The present work represents the most continuous recording of the movements and habitat use of smooth hammerhead sharks in the Atlantic Ocean to date. In this study, we were able to tag and track both juvenile and adult sharks, hence the differences between maturity stages were analyzed and reported for the first time.

Our findings showed that smooth hammerhead sharks moved in multiple directions, suggesting that they do not follow clear movement patterns in the intertropical Atlantic Ocean. The sharks did not appear to be reliant on any specific area; instead, they moved over large areas and travelled long distances. Two juvenile females were observed making excursions into inshore waters towards Cape Verde coast. Inshore waters are linked to provision of shelter and food (Olson *et al*., 1994; Beck *et al*., 2001; Queiroz *et al*., 2012), and therefore increasing survival for young sharks (Knip *et al*., 2010). Thus, these migrations may be related with shelter seeking from predators and foraging behavior. In addition, one adult female displayed the longest migration ever recorded for the smooth hammerhead shark (total distance travelled of 6610 km), which confirms the highly migratory nature of this species. Previous studies reported broad-scale horizontal movements for *S. zygaena* (News - SWFSC, 2015; Clarke et al., 2015), however this sharks' track represents the first trans-equatorial migration ever recorded and documented for this species. This movement might be driven by feeding events, since the shark moved towards the Benguela Marine Ecosystem, one of the most productive systems in the oceans, which attracts many top predators including smooth hammerhead sharks (Petersen *et al*. 2007). Moreover, this migration may also be associated with the water temperature. The specimen moved progressively into cooler waters, similarly to what has already been documented for the smooth hammerhead, which are thought to undergo seasonal migrations towards cooler waters in the summer and warmer waters in the winter (Bester, 2008; Diemer *et al*., 2011). With these results, it is interesting to highlight that the sharks did not travel to waters of the western Atlantic. This evidence may indicate the existence of separate western and eastern stocks in the Atlantic, contrary to the current north-south division used for all pelagic sharks by ICCAT (ICCAT, 2006-2016).

Similar to what was reported by Francis *et al*. (2016), tag data revealed the smooth hammerhead sharks swam mostly at surface waters (0-50 m) above 23 °C, with no evidence of a clear diel activity pattern. Sporadically, short dives below 100 m were recorded. Deep diving behavior has been suggested to be related with foraging ecology for other pelagic sharks like blue shark, scalloped hammerhead, bigeye thresher and oceanic whitetip (Stevens *et al*., 2010; Hoffmayer *et al*., 2013; Coelho *et al*., 2015; Howey *et al*., 2016). In swordfish, deep dives have also been described as feeding excursions targeting mesopelagic organisms in the deep scattering layer (Carey *et al*., 1990; Dewar *et al*., 2011). In addition, as determined from a swimming behavior study by Klimley *et al*. (2002), this type of movement may also be linked to orientation, since chemical and magnetic information is used to guide migrations. Although preferring shallow waters, differences in the vertical habitat utilization were found when comparing maturity stages, with the juveniles staying in deeper colder waters than the adults during nighttime. Consequently, maturity stage differences resulted in differences in the ways juveniles and adults are impacted by the pelagic longline fisheries.

Our analysis of the overlap between the species vertical habitat utilization and the depth of operation of shallow setting longline fishing gear indicated it was more marked during nighttime (when the fishery operates) especially for the juveniles (~40% of overlap time), which is consistent with the distributional patterns observed for the smooth hammerhead shark. Thereby, juveniles are potentially more impacted than the adults by this particular fishery targeting mostly swordfish. However, it is worth noting that the fact that hooks were baited (typically with squid or mackerel) was not considered in this analysis. Baits have attractant characteristics that may condition the behavioral responses of the fishes. A previous study by Coelho *et al*. (2015) analyzed the overlap of fishing gear and habitat distribution of the bigeye thresher shark (*Alopias superciliosus*), and similar to what was observed in our study, the percentage of overlap time was greater for juveniles during nighttime (~60% of overlap time). Again, these results agree with those of Cortés *et al*. (2015), who observed that smooth hammerhead was less vulnerable to pelagic longline fleets when compared to other pelagic sharks, including the bigeye thresher, mainly due to a lower overlap between the species habitat and fishing gear utilization.

From the 8 tags deployed, only one failed to transmit, meaning the overall PSAT reporting rate was 88%. Four tags detached before their scheduled pop-up date, representing a premature release rate of 58%. However, this rate is lower in comparison with the average rate of 66% premature release reported by Hammerschlag *et al*. (2011). The causes of tag failure in data transmission and early tag detachment are still not well understood (Musyl *et al*., 2011). Battery failure, antenna damage, death of the tagged animal, biofouling or mechanical failure of the release mechanism have been reported as possible reasons of tag failure and early detachment (Hays *et al*., 2007; Musyl *et al*., 2011). In addition, the success rate of PSATs also seems to be related with social behaviors of the tagged fish. Smooth hammerhead sharks have been observed swimming in schools (Bass *et al*., 1975; Bester, 2008; Diemer *et al*., 2011), hence the touch of another animals swimming very close may trigger an early release or damage the PSAT.

It is important to mention that geolocation estimates have some limitations, since they are calculated from the ambient light-level irradiance which is influenced by variable natural conditions such as water clarity (Musyl *et al*., 2001). Shark diving behavior has also been described as an important factor while creating accurate estimates. Previous studies have documented some difficulties when using satellite technology to estimate geo-locations for deep-diving species (Musyl *et al*., 2003; Coelho *et al*., 2015), as light attenuation with depth prevented the light-sensor on PSATs from correctly recording sunrise and sunset. However, the smooth hammerhead showed a preference for shallow waters both during the day and night, allowing us to use with higher confidence the recorded data for the horizontal spatial analysis.

In conclusion, our study confirmed the smooth hammerhead is a highly migratory species, making long migrations across the Atlantic Ocean. This species did not exhibit diel vertical movement behavior, spending most of its time at surface waters. Nevertheless, we found differences in the vertical habitat utilization during nighttime when comparing adults and juveniles, resulting in distinct percentage of overlap between the vertical habitat of the species and the fishing gear distribution. Moreover, since the overlap percentage is higher for juveniles, we believe these are more vulnerable to shallow setting longline fisheries targeting swordfish. Thus, aiming the adoption of more effective conservation and management measures, it is suggested that future research on the smooth hammerhead shark should seek to identify hotspot areas for the species and particularly for juveniles. Furthermore, long-term monitoring is required to better understand spatial distribution and habitat utilization patterns, namely in terms of sex-related differences.

The results presented in this study are a major contribution to increase the current knowledge on the smooth hammerhead ecology, habitat use in the pelagic environment, overlap and potential impacts with pelagic longline fishing gear. However, the sample size of seven transmitting tagged sharks is insufficient for deducing general conclusions. Nonetheless, this information can be used to provide sustainable management tools such as mitigation measures to avoid sharks captures, as well as to serve as input for Ecological Risk Assessments for pelagic sharks caught in Atlantic pelagic longline fisheries.

References

[Rec. 10-08] Recommendation by ICCAT on hammerhead sharks (family Sphyrnidae) caught in association with fisheries managed by ICCAT.

Abascal FJ, Mejuto J, Quintans M, García-Cortés B, Ramos-Cartelle A. Tracking of the broadbill swordfish, *Xiphias gladius*, in the central and eastern North Atlantic. Fisheries Research. 2015; 162:20-8.

Abascal FJ, Quintans M, Ramos-Cartelle A, Mejuto J. Movements and environmental preferences of the shortfin mako, *Isurus oxyrinchus*, in the southeastern Pacific Ocean. Marine Biology. 2011; 158:1175-84.

Bass AJ, DAubrey JD, Kistnasamy N. Sharks of the east coast of Southern Africa. III. The families Carcharhinidae (excluding *Mustelus* and *Carcharhinus*) and Sphyrnidae. Durban, Republic of South Africa: Oceanographic Research Institute; 1975; 38:45-47.

Beck MW, Heck Jr KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates: a better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. Bioscience. 2001; 51:633-41.

Bessudo S, Soler GA, Klimley AP, Ketchum JT, Hearn A, Arauz R. Residency of the scalloped hammerhead shark (*Sphyrna lewini*) at Malpelo Island and evidence of migration to other islands in the Eastern Tropical Pacific. Environmental Biology of Fishes. 2011; 91:165-76.

Bester, C. Smooth Hammerhead. Florida Museum of Natural History. 2008. Available from: https://www.floridamuseum.ufl.edu/fish/discover/species-profiles/sphyrna-zygaena

Biavati G. RAtmosphere: standard atmospheric profiles. R package version 1.1. 2014. Available from: https://CRAN.R-project.org/package=RAtmosphere.

Buencuerpo V, Rios S, Morón J. Pelagic sharks associated with the swordfish, *Xiphias gladius*, fishery in the eastern North Atlantic Ocean and the Strait of Gibraltar. Fishery Bulletin. 1998; 96:667-85.

Camhi MD, Valenti SV, Fordham SV, Fowler SL, Gibson C (comp. and ed.). The conservation status of pelagic sharks and rays: report of the IUCN Shark Specialist Group Pelagic Shark Red List Workshop, Tubney House, University of Oxford, UK, 19-23 February 2007. Newbury: IUCN Species Survival Commissions Shark Specialist Group; 2009.

Carey FG, Scharold JV, Kalmijn AJ. Movements of blue sharks (*Prionace glauca*) in depth and course. Marine Biology. 1990; 106:329-42.

Casper BM, Domingo A, Gaibor N, Heupel MR, Kotas E, Lamónaca AF, Pérez Jimenez JC, Simpfendorfer C, Smith WD, Stevens JD, Soldo A. *Sphyrna zygaena*: The IUCN Red List of Threatened Species 2005. 2005:e.T39388A10193797.
Available from: http://dx.doi.org/10.2305/IUCN.UK.2005.RLTS.T39388A10193797.en.

Clarke SC, Coelho R, Francis MP, Kai M, Kohin S, Liu K, Simpendorfer C, Tovar-Availa J, Rigby C, Smart JJ. Report of the Pacific Shark Life History Expert Panel Workshop. Western and Central Pacific Fisheries Commission. 2015.

Coelho R, Fernandez-Carvalho J, Amorim S, Santos MN. Age and growth of the smooth hammerhead shark, *Sphyrna zygaena*, in the Eastern Equatorial Atlantic Ocean, using vertebral sections. Aquatic Living Resources. 2011; 24:351–7.

Coelho R, Fernandez-Carvalho J, Santos MN. Habitat use and diel vertical migration of bigeye thresher shark: Overlap with pelagic longline fishing gear. Marine Environmental Research. 2015; 112:91-9.

Compagno LJ. FAO species catalogue: sharks of the world: an annotated and illustrated catalogue of shark species known to date. Food and Agriculture Organization of the United Nations; 1984.

Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Proposal to include Hammerhead Sharks in Appendix II. Sixteenth meeting of the Conference of Parties. 2013. Available from: https://www.cites.org/sites/default/files/eng/cop/16/prop/E-CoP16-Prop-43.pdf

Cortés E, Arocha F, Beerkircher L, Carvalho F, Domingo A, Heupel M, Holtzhausen H, Santos MN, Ribera M, Simpfendorfer C. Ecological risk assessment of pelagic sharks caught in Atlantic pelagic longline fisheries. Aquatic Living Resources. 2010; 23:25-34.

Cortés E, Domingo A, Miller P, Forselledo R, Mas F, Arocha F, Campana S, Coelho R, Da Silva C, Hazin F, Holtzhausen H. Expanded ecological risk assessment of pelagic sharks caught in Atlantic pelagic longline fisheries. Collect Vol. Sci. Pap. ICCAT. 2015; 71:2637-88.

Dewar H, Prince ED, Musyl MK, Brill RW, Sepulveda C, Luo J, Foley D, Orbesen ES, Domeier ML, Nasby-Lucas NI, Snodgrass D, Laurs RM, Hoolihan JP, Block BA, Mcnaught LM. Movements and behaviors of swordfish in the Atlantic and Pacific Oceans examined using pop-up satellite archival tags. Fisheries Oceanography. 2011; 20: 219-41.

Diemer KM, Mann BQ, Hussey NE. Distribution and movement of scalloped hammerhead Sphryna lewini and smooth hammerhead Sphyrna zygaena sharks along the east coast of southern Africa. African Journal of Marine Science. 2011; 33:229-38.

Domeier ML, Kiefer D, Nasby-Lucas N, Wagschal A, O'Brien F. Tracking Pacific bluefin tuna (*Thunnus thynnus orientalis*) in the northeastern Pacific with an automated algorithm that estimates latitude by matching sea-surface-temperature data from satellites with temperature data from tags on fish. Fishery Bulletin. 2005; 103:292-306.

Fay MP, Shaw PA. Exact and Asymptotic Weighted Logrank Tests for Interval Censored Data: the interval R Package. Journal of Statistical Software. 2010; 36:1–34. Available from: https://CRAN.R-project.org/package=perm.

Francis MP. Distribution, habitat and movement of juvenile smooth hammerhead sharks (*Sphyrna zygaena*) in northern New Zealand. New Zealand Journal of Marine and Freshwater Research. 2016; 50:506-25.

Hammerschlag N, Gallagher AJ, Lazarre DM. A review of shark satellite tagging studies. Journal of Experimental Marine Biology and Ecology. 2011; 398:1-8.

Hays GC, Bradshaw CJ, James MC, Lovell P, Sims DW. Why do Argos satellite tags deployed on marine animals stop transmitting? Journal of Experimental Marine Biology and Ecology. 2007; 349:52-60.

Heithaus MR, Wirsing AJ, Dill LM, Heithaus LI. Long-term movements of tiger sharks satellite-tagged in Shark Bay, Western Australia. Marine Biology. 2007; 151:1455-61.

Hilborn R, Branch TA, Ernst B, Magnusson A, Minte-Vera CV, Scheuerell MD, Valero JL. State of the world's fisheries. Annual review of Environment and Resources. 2003; 28:359-99.

Hoffmayer ER, Franks JS, Driggers WB, Howey PW. Diel vertical movements of a scalloped hammerhead, *Sphyrna lewini*, in the northern Gulf of Mexico. Bulletin of Marine Science. 2013; 89:551-7.

Howey LA, Tolentino ER, Papastamatiou YP, Brooks EJ, Abercrombie DL, Watanabe YY, Williams S, Brooks A, Chapman DD, Jordan LK. Into the deep: the functionality of mesopelagic excursions by an oceanic apex predator. Ecology and Evolution. 2016; 6:5290-304.

Howey-Jordan LA, Brooks EJ, Abercrombie DL, Jordan LK, Brooks A, Williams S, Gospodarczyk E, Chapman DD. Complex movements, philopatry and expanded depth range of a severely threatened pelagic shark, the oceanic whitetip (*Carcharhinus longimanus*) in the western North Atlantic. PloS one. 2013; 8(2):e56588.

ICCAT. ICCAT Manual. International Commission for the Conservation of Atlantic Tuna. In: ICCAT Publications [on-line]. Updated 2016. 2006-2016.
Available from: http://www.iccat.int/en/ICCATManual.asp.

Jorgensen SJ, Klimley AP, Muhlia-Melo AF. Scalloped hammerhead shark *Sphyrna lewini*, utilizes deep-water, hypoxic zone in the Gulf of California. Journal of Fish Biology. 2009; 74:1682-7.

Ketchum J, Hearn A, Shillinger G, Espinoza E, Peñaherrera C, Klimley P. Shark movements and the design of protected pelagic environments within and beyond the Galapagos Marine Reserve. Proceedings of the Galapagos Science Symposium, Puerto Ayora. 2009; 127-130.

Klimley AP, Beavers SC, Curtis TH, Jorgensen SJ. Movements and swimming behavior of three species of sharks in La Jolla Canyon, California. Environmental Biology of Fishes. 2002; 63:117-35.

Knip DM, Heupel MR, Simpfendorfer CA. Sharks in nearshore environments: models, importance, and consequences. Marine Ecology Progress Series. 2010; 402:1-11.

Lam CH, Nielsen A, Sibert JR. Improving light and temperature based geolocation by unscented Kalman filtering. Fisheries Research. 2008; 91:15-25.

Lemon J. Plotrix: a package in the red light district of R. R-news. 2006; 6:8-12.

Levene H. Robust tests for equality of variances. Contributions to Probability and Statistics. 1960; 1:278-92.

Lilliefors HW. On the Kolmogorov-Smirnov test for normality with mean and variance unknown. Journal of the American Statistical Association. 1967; 62:399-402.

Manly BFJ. Randomization, bootstrap and Monte Carlo methods in biology. 3rd ed. New York: Chapman & Hall/CRC; 2007.

Musick JA, Burgess G, Cailliet G, Camhi M, Fordham S. Management of sharks and their relatives (Elasmobranchii). Fisheries. 2000; 25:9-13.

Musyl MK, Brill RW, Boggs CH, Curran DS, Kazama TK, Seki MP. Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys, and seamounts near the main Hawaiian Islands from archival tagging data. Fisheries Oceanography. 2003; 12:152-69.

Musyl MK, Brill RW, Curran DS, Gunn JS, Hartog JR, Hill RD, Welch DW, Eveson JP, Boggs CH, Brainard RE. Ability of Archival Tags to Provide Estimates of Geographical Position Based on Light Intensity. In: Electronic Tagging and Tracking in Marine Fisheries Reviews: Methods and Technologies in Fish Biology and Fisheries. J.R. Sibert & J.L. Nielsen (eds) Dordrecht: Kluwer Academic Press. 2001; 343–68.

Musyl MK, Domeier ML, Nasby-Lucas N, Brill RW, McNaughton LM, Swimmer JY, Lutcavage MS, Wilson SG, Galuardi B, Liddle JB. Performance of pop-up satellite archival tags. Marine Ecology Progress Series. 2011; 433:1-28.

Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH. Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science. 2007; 315:1846-50.

News - SWFSC [Internet]. Swfsc.noaa.gov. 2015. Available from: https://swfsc.noaa.gov/news.aspx?ParentMenuId=39&id=20903

Nielsen A, Sibert JR, Ancheta J, Galuardi B, Lam CH. ukfsst: Kalman filter tracking including sea surface temperature. R package version 0.3. 2012.

Olson DB, Hitchcock GL, Mariano AJ, Ashjian CJ, Peng G, Nero RW, Podestá GP. Life on the edge: marine life and fronts. Oceanography. 1994; 7:52-60.

Petersen S, Nel D, Omardien A. Towards an Ecosystem Approach to Longline Fisheries in the Benguela: an assessment of impacts on seabirds, sea turtles and sharks. WWF Report Series - 2007/Marine/001. 2007.

Petersen SL, Honig MB, Ryan PG, Underhill LG, Compagno LJ. Pelagic shark bycatch in the tuna-and swordfish-directed longline fishery off southern Africa. African Journal of Marine Science. 2009; 31:215-25.

Poisson F, Crespo FA, Ellis JR, Chavance P, Pascal B, Santos MN, Séret B, Korta M, Coelho R, Ariz J, Murua H. Technical mitigation measures for sharks and rays in fisheries for tuna and tuna-like species: turning possibility into reality. Aquatic Living Resources. 2016; 29:402.

Queiroz N, Humphries NE, Mucientes G, Hammerschlag N, Lima FP, Scales KL, Miller PI, Sousa LL, Seabra R, Sims DW. Ocean-wide tracking of pelagic sharks reveals extent of overlap with longline fishing hotspots. Proceedings of the National Academy of Sciences. 2016; 113:1582-7.

Queiroz N, Humphries NE, Noble LR, Santos AM, Sims DW. Spatial dynamics and expanded vertical niche of blue sharks in oceanographic fronts reveal habitat targets for conservation. PLoS One. 2012 Feb 29 ;7:e32374.

R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria 2016. Available from: http://www.R-project.org/.

Rosa D, Coelho R, Fernandez-Carvalho J, Santos MN. Age and growth of the smooth hammerhead, *Sphyrna zygaena*, in the Atlantic Ocean: comparison with other hammerhead species. Marine Biology Research. 2017; 13:300-13.

Stevens JD, Bonfil R, Dulvy NK, Walker PA. The effects of fishing on sharks, rays, and chimaeras (Chondrichthyans), and the implications for marine ecosystems. ICES Journal of Marine Science. 2000; 57:476-94.

Stevens JD, Bradford RW, West GJ. Satellite tagging of blue sharks (*Prionace glauca*) and other pelagic sharks off eastern Australia: depth behaviour, temperature experience and movements. Marine Biology. 2010; 157:575-91.

Teets DA. Predicting sunrise and sunset times. The College Mathematics Journal. 2003; 34:317-21.

Wickham H. ggplot2: elegant graphics for data analysis. 1st ed. New York: Springer. 2009. Available from: https://CRAN.R-project.org/package=ggplot2.

Wilson SG, Lutcavage ME, Brill RW, Genovese MP, Cooper AB, Everly AW. Movements of bluefin tuna (*Thunnus thynnus*) in the northwestern Atlantic Ocean recorded by pop-up satellite archival tags. Marine Biology. 2005; 146:409-23.

CHAPTER 4: FINAL CONSIDERATIONS

This dissertation aimed to fill gaps in knowledge for the smooth hammerhead shark, namely related with the species distribution patterns and habitat use in the Atlantic Ocean. For that purpose, detailed fishery observer data including catch and effort (used to calculate CPUEs), as well as biological data (i.e., size and sex distribution) were analyzed to determine large-scale distribution patters. Additionally, data from satellite telemetry and Temperature and Depth Recorders (TDRs) were analyzed to determine movement patters, depth related habitat, and estimate overlaps between habitat and pelagic longline fishing operations.

Our results confirmed the wide occurrence of the smooth hammerhead in the Atlantic Ocean. Higher abundances (using CPUEs as a proxy) were found closer inshore within the Tropical North and Equatorial regions. Those trends may be related with the species' preference for warmer waters and the possible existence of nursery and feeding grounds within the Tropical and equatorial regions of the Atlantic Ocean. The size distribution revealed that the larger sharks tend to occur in the open ocean habitat, while the smaller sized specimens prefer more coastal areas. This distribution pattern may be associated with changes in the migratory behavior of the smooth hammerhead shark through life history cycle, and with the habitat characteristics. Our results show that the overall sex ratio is biased towards males (1.4 : 1), which suggests differential selection of habitats in the Atlantic Ocean between sexes, whether for social, thermal or forage-related reasons. In addition, a more detailed CPUE and size distribution analysis was carried out in order to examine differences between regions, years and quarters of the year. The sample was composed mostly of specimens captured in the Equatorial and Tropical North regions of the Atlantic Ocean, therefore only the specimens caught in these areas were considered for the analysis. Differences in CPUE and size distributions were detected both spatially and temporally. We highlight the increase in the mean CPUE along with a decrease in the mean specimen size in the Equatorial region from 2012 onwards. Intense fishing pressure and the capture of larger specimens over the years may be possible explanations for the decrease in the mean specimen size.

Furthermore, given the paucity of information on habitat use of the smooth hammerhead shark, eight specimens were tagged with Pop-up Satellite Archival Tags (PSATs) in the inter-tropical region of the Northeast Atlantic Ocean. We would like to point out the record of the longest migration ever documented for the smooth hammerhead shark (> 6600 km), which corroborates previous conclusions about its highly migratory nature. This particularly large migration crossed the equatorial line, from North to South, hence opening the question on the population structure of this species in the Atlantic. At present, 2 populations are considered (North and South, separated by 5ºN), but in light of those new results this may need revision. Also, our results showed no supporting evidence of diel vertical movement behavior and confirmed that the smooth hammerhead inhabits preferentially shallow warm waters. However, differences in the vertical habitat utilization were found when comparing adults and juveniles, with the juveniles staying in deeper colder waters during the night. Consequently, these differences result in distinct impacts of the pelagic longline fisheries on juveniles and adults. Particularly, the overlap between the species vertical habitat utilization and the depth of operation of shallow setting longline fishing gear is more marked for the juveniles during nighttime.

The results presented here are valuable contributions to improve the knowledge and our understanding of the smooth hammerhead shark and raise questions about the future sustainability of the species. However, the results are preliminary and their interpretations are inevitably tentative. Besides, it is important to note the study limitations. Specifically, the data used were fishery-dependent and were obtained from only a fraction of the Portuguese pelagic longline fleet. Moreover, the light-based fish geolocations estimated by PSATs may not be completely accurate. Also, the majority of the PSATs deployed suffered from early detachment and, to some extent, data transmission failure. Thus, future work is required to properly understand the spatio-temporal variations in distribution and habitat use of the smooth hammerhead in the Atlantic Ocean.

Since our study was restricted to the fishing areas of the Portuguese longline fleet, and the possibility of occurrence of *S. zygaena* in areas not covered in this study cannot be excluded, future analyses should cover a wider geographical range. Due to the low relative bycatch of this species in most tuna and tuna-like fisheries, aiming to more easily and faster collect and gather additional information, it would be essential to involve a higher number of research teams and fisheries data collection entities on future studies. Furthermore, models that standardize CPUE data should be applied so that the effect of fishery-dependent factors that bias CPUE as an index of abundance is removed. Despite all its limitations, satellite telemetry proved to be a useful tool for studying the spatial ecology of the smooth hammerhead shark. The challenge, therefore, is to start undertaking long-term monitoring of this species and increase the sample size. Aiming for the adoption of more effective conservation and management measures, we suggest that future research should seek to identify hotspot areas for the smooth hammerhead and explore behavioral patterns concerning different maturation states and sexes. On the other hand, electronic tagging can provide very relevant information on post release mortality for the smooth hammerhead, since there is currently a prohibition of retention but no studies are ongoing on the possible effectiveness of such conservation measure.

In conclusion, our results provide an important upgrade of the current information available for the smooth hammerhead in the Atlantic Ocean and can now be used in upcoming evaluations, such as Ecological Risk Assessments, to better inform future management decisions and implement more efficient conservation strategies for the species.

APPENDIX A

Mean annual reported catch of Hammerhead shark species by the fleets of various countries

		Catches (tonnes)		
Species	**Flag/country**	**Mean**	**1987-2010**	**2011-2016**
Sphyrna tiburo	U.S.A.	2.6	3.2	0.0
Sphyrna mokarran	Chinese Taipei	0.0	0.0	0.0
	EU.España	0.0	0.0	0.0
	EU.France	0.0	0.0	0.1
	Nigeria	0.7	0.3	2.3
	Sta. Lucia	0.3	0.1	0.8
	U.S.A.	1.2	1.1	1.6
Sphyrna lewini	Brazil	25.5	31.8	0.0
	Chinese Taipei	0.0	0.0	0.0
	Côte d'Ivoire	5.0	6.0	1.1
	EU.España	0.3	0.3	0.0
	EU.France	0.2	0.0	1.2
	EU.United Kingdom	0.4	0.5	0.0
	Korea Rep.	0.0	0.0	0.0
	Maroc	0.0	0.0	0.2
	Mexico	0.3	0.4	0.0
	U.S.A.	23.8	25.1	18.6
	Venezuela	0.4	0.2	1.0
Sphyrna zygaena	Barbados	0.1	0.0	0.3
	Benin	0.9	1.1	0.0
	Cape Verde	0.0	0.0	0.0
	Chinese Taipei	0.0	0.0	0.1
	Côte d'Ivoire	15.7	17.3	9.3
	EU.España	2.8	3.5	0.0
	EU.France	0.4	0.0	1.8
	EU.Italy	0.0	0.0	0.0
	EU.Malta	0.0	0.0	0.0

Appendix A (continued)

Species	Flag/country	Catches (tonnes)		
		Mean	1987-2010	2011-2016
Sphyrna zygaena	EU.Portugal	2.8	3.4	0.3
	EU.United Kingdom	0.0	0.0	0.0
	Guyana	10.8	13.5	0.0
	Korea Rep.	0.3	0.1	1.2
	Maroc	10.3	0.0	51.3
	Mexico	0.1	0.1	0.0
	Russian Federation	0.0	0.0	0.0
	Senegal	15.7	0.3	77.2
	South Africa	0.0	0.0	0.0
	U.S.A.	0.2	0.2	0.2
	UK.Bermuda	0.0	0.0	0.0
Sphyrna spp	Brazil	48.5	50.3	41.5
	Chinese Taipei	0.2	0.1	0.5
	Côte d'Ivoire	10.9	13.7	0.0
	EU.España	152.8	191.0	0.0
	EU.France	0.0	0.0	0.0
	EU.Italy	0.3	0.0	1.3
	EU.Portugal	7.0	8.8	0.1
	Gabon	5.4	6.7	0.0
	Ghana	62.0	0.0	309.8
	Guyana	0.1	0.2	0.0
	Mexico	0.1	0.0	0.5
	Namibia	4.6	5.6	0.6
	Senegal	159.8	171.5	112.7
	South Africa	0.0	0.0	0.0
	Sta. Lucia	0.1	0.0	0.4
	Trinidad and Tobago	34.0	6.8	142.7
	U.S.A.	49.2	60.0	5.7
	Uruguay	7.3	9.1	0.0
	Venezuela	0.8	0.0	0.1