UNIVERSIDADE DO ALGARVE

FACULDADE DE CIÊNCIAS E TECNOLOGÍA

POPULATION DYNAMICS AND FISHERIES ASSESSMENT OF THE BIGEYE THRESHER (*Alopias superciliosus*) IN THE ATLANTIC: A COMPARISON BETWEEN NORTH ATLANTIC AND SOUTH ATLANTIC STOCKS.

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DISSERTAÇÃO
DOUTORAMENTO EM CIÊNCIAS DO MAR, DA TERRA E DO AMBIENTE, RAMO DE CIÊNCIAS E TECNOLOGIAS DAS PESCAS
(ESPECIALIDADE DE BIOLOGIA PESQUEIRA)

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2014

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<u>Declaração de autoria de trabalho</u>

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

Joana

ACKNOWLEDGMENTS

Along these years several people have, in different ways, contributed to this thesis. Without them, this work would have been impossible to accomplish. Special thanks are therefore acknowledged to:

My supervisors Prof. Dr. Karim Erzini, Dr. Miguel Neves dos Santos and Dr. Rui Coelho, for all the support, advice and trust they gave me during these years. They were excellent supervisors, always available for answering my questions and providing wise recommendations and excellent ideas on how to improve this work and always in a constructive and encouraging way.

Ao Instituto Português do Mar e da Atmosfera (IPMA, I.P.), bem como ao Instituto que o precedeu (INRB/IPIMAR), nas pessoas dos seus Directores, Professor Doutor Miguel Miranda e Doutor Carlos Costa Monteiro, pela oportunidade que me proporcionaram de realizar este trabalho.

The "Coastal Fisheries Research Group" at CCMAR, University of Algarve, whose members have not only been excellent work colleagues but also true friends. Special thanks goes to Dr. Jorge Gonçalves who I will always see as a mentor, Luís Bentes and Pedro Monteiro, whose advice and support along these years has been fundamental for the development of this thesis. Further thanks are extended to Frederico Oliveira, Pedro Veiga, Carlos Afonso (Camané), Ines Sousa and Mafalda Rangel for providing an excellent work environment and a constant good mood in our office or laboratory at the University of Algarve.

To all my colleagues from IPMA (Tibério, Zé Luis e Lina), thank you for all your support. Special thanks to Dr. Pedro Lino for his continuous assistance over the years and endless patience to solve all my informatic troubles. Obrigada

To Dr.George Burgess for giving me my first job as a biologist. Thank you for your continuous support (and friendship) as I gave my "first steps as a scientist". I will never forget all the valuable lessons I learned by your side.

Aos meu amigos de BMP, Anabela Bensimon, Catarina Ferreira, Diogo Tavares, João Alves, Ligea Primo, Raquel Verissimo e Rui Guedes, Wilson Pinto um grande OBRIGADO. Aprendemos a ser biólogos juntos e muito mais! Muito obrigada pelo vosso apoio continuo e amizade verdadeira.

À minha familia, dizer obrigado não é de todo suficiente! Agradeço aos meus primos Jõao, Patricia e Alexandre, e tios Vitor e Sandra por todo vosso apoio e boa disposição ao longo dos anos, pois é muito mais divertido crescer numa família unida e bem disposta. Ao meu Avô por sempre me ter ajudado ao longo da vida apesar de não compreender muito bem o que os biólogos fazem. À minha querida avozinha, que teria gostado tanto de ver a tua neta ser "*doutora*"... Aos meus sogros, Vitor e Dina, por sempre me terem tratado como uma filha e não como uma nora.

A todos mis titos y primos, porque la distancia geográfica nunca nos ha separado.Gracias por quererme de lejos.

A mi "hermanito" Guille. Sé que, contrariamente a lo que piensa la mayoría, no ha sido muy fácil ser mi hermano chico…Muchas gracias por apesar de todo haberme ayudado siempre y haberme aguantado todos estos años.

Aos meus pais por sempre me terem ajudado a cumprir todos os meus desejos e sonhos. Poucas são as pessoas da minha idade que já cumpriram practicamente todos os seus sonhos, e graças a vocês eu tenho a sorte de ser uma delas. Sem a vossa ajuda não teria conseguido acabar esta tese. Obrigada por sempre porem a minha vida antes da vossa. É tão fácil ser feliz sendo a vossa filha...

Ao meu marido Rui, tenho tanto que agradecer! Obrigada por me apoiares em todos os meus projectos e me fazeres acreditar que consigo fazê-los. Se não fosse pelos teus "empurrões" não acabaría muitos dos mesmos. Obrigada por sempre me incentivares a ser melhor. Obrigada por nunca te cansares de responder às minhas perguntas. Obrigada por termos trabalhado tão bem juntos ao longo de tantos anos. Obrigada por seres o meu melhor amigo. Obrigada por seres tão bom marido. E por fim, obrigada por seres tão bom pai. À minha filhota Leonor que nasceu durante o fim desta tese, obrigada por seres tão boazinha e dares tão boas noites, pois facilitou esta árdua tarefa. Obrigada por fazeres parte da minha vida, a qual já não consigo imaginar sem ti.

SUPPORT

Funding

This work was integrated in the Research Project THRESHER funded by the Portuguese Foundation for Science and Technology (FCT – *Fundação para a Ciência e Tecnologia*) (Project Reference: FCT PTDC/MAR/109915/2009) and Project SELECT-PAL funded by PROMAR (Project Reference: PROMAR 31-03-05-FEP-1).

Joana Fernandez-Carvalho was funded by a PhD grant (Reference: SFRH / BD / 60624 / 2009) from the Portuguese Foundation for Science and Technology (FCT – *Fundação para a Ciência e Tecnologia*).

Institutional support

This work would not be possible without the support from the following Institutions:

Instituto Português do Mar e da Atmosfera (IPMA, I.P.)

Centro de Ciências do Mar do Algarve (CCMAR)

RESUMO

Dinâmica populacional e avaliação das capturas do tubarão raposo olhudo (*Alopias superciliosus*) no Atlântico: comparação entre os mananciais do Atlântico Norte e Sul.

Apesar dos elasmobrânquios (tubarões e raias) tradicionalmente não terem um valor económico elevado, recentemente tornaram-se recursos pesqueiros importantes. De facto, actualmente, os elasmobrânquios são alvo tanto de exploração directa como de pesca acesória dirigidas a outras especies de teleósteos. No entanto, este aumento na sua captura não tem sido acompanhado por um aumento no conhecimento da biologia e ecologia destas especies, informação que é imprescindível para uma boa gestão e consequente conservação das espécies. Os elamobrânquios em geral são muito susceptíveis à pressão pesqueira devido ao seu lento crescimento e reducido potencial reproductivo. Assim sendo, a sua sobrexploração pode ocorrer mesmo com níveis de mortalidade por pesca relativamente baixos. A gestão e conservação dos tubarões pelagicos oceânicos é particularmente complicada devido à sua natureza migratória, pois atravessam tanto águas nacionais como internacionais.

O tubarão raposo olhudo, *Alopias superciliosus*, é um tubarão pelágico com uma distribuição global em águas tropicais e temperadas, habitando maioritariamente o ambiente epipelágico, com algumas incursões em águas mais costeiras. Esta espécie pertence à ordem dos Lamniformes, e como tal, a sua estratégia reproductiva consiste em viviparidade aplacentaria com oofagia, sendo típico desta especie produzir apenas duas crias por ciclo reproductivo, o que significa uma fecundidade muito reduzida. Apesar do tubarão raposo olhudo ser capturado com frequência como pesca acesória do palangre de superfície dirigida ao espadarte, pouca informação existe sobre o ciclo de vida desta especie, especialmente para o Atlântico. No entanto, devido à sua alta vulnerabilidade, a Organização Internacional para a Conservação do Atum do Atlântico (ICCAT) e a União Internacional para Conservação da Natureza (IUCN), entre outras, têem vindo a salientar a necessidade urgente de obter informação biológica sobre esta espécie. Assim, de modo a preencher esta lacuna no conhecimento do tubarão raposo olhudo, o presente estudo focou aspectos relativos à pesca, biologia, ciclos de vida, distribuição e ecologia desta espécie no Oceano Atlântico.

Foi analizada a mortalidade no convés dos tubarões pelágicos capturados como pesca acessória da pescaría portuguesa de palangre de superfície dirigido ao espadarte. Uma das principais conclusões obtidas foi que o tubarão raposo olhudo possui uma das taxas mais elevadas de mortalidade no convés, sendo esta cerca de 50%. Assim sendo, as regulamentações actuais que obrigam a rejeição desta especie não são inteiramente eficazes pois cerca de metade dos exemplares capturados estão a ser rejeitados ao mar já mortos. Desta forma, é necessário considerar medidas de gestão alternativas, como modificações tecnológicas na arte de pesca ou fecho espacial e/ou sazonal de zonas importantes para os juvenis, de modo a diminuir a pesca acessória desta espécie tão vulnerável. Para tal, o impacto da utilização de diversas combinações de diferentes características de anzois e tipo de isco sobre as capturas acidentais e dirigidas da pescaria portuguesa de palangre de superfície foi avaliado. No entanto, não foram encontrados efeitos significativos nas capturas de tubarão raposo olhudo em nenhum dos tratamentos. Assim, o uso de anzóis circulares ou isco de cavala (em vez de anzol tipo J e isco de lula) não parece ser uma medida de gestão eficaz para a redução da captura acidental desta espécie.

De modo a determinar a estrutura de tamanhos da espécie e possíveis zonas de reprodução no Oceano Atlântico, foi elaborado pela primeira vez um estudo de colaboração internacional em larga escala que incluiu dados de frotas de 6 países (Japão, Portugal, Espanha, Taiwan, Uruguay e USA). A região do Atlântico identificada como mais significativamente diferente foi o Atlântico norte tropical (perto da região do arquipélago de Cabo Verde), sendo caracterizada pela ocorrência de exemplares mais pequenos e a proporção de juvenis ser mais alta do que em outras zonas. Foram propostas três áreas de berçário do tubarão raposo olhudo para o Atlântico, especificamente no nordeste tropical e equatorial perto do continente Africano, no noroeste tropical perto do mar Caribe e da Flórida, e no sudoeste Atlântico perto da elevação do Rio Grande (*Rio Grande Rise*). Um modelo foi ainda desenvolvido para calcular as razões de rácios (*odds-ratios*) de capturar mais juvenis nas várias combinações entre regiões e estações do ano, sendo estes resultados usados para proporcinar aconselhamento sobre mitigação da pesca acesória nestes habitats críticos para a espécie.

Parâmetros de ciclos de vida (idade e crescimento e reprodução) do tubarão raposo olhudo foram calculados para o Atlântico, uma vez que estes são indispensáveis para o estudo da dinâmica populacional da espécie. Assim, foram calculados os parâmetros de crescimento da espécie através da leitura de 546 vértebras recolhidas entre 2007 e 2009. A composiçao de tamanhos da amostra incluía exemplares de 102 cm de comprimento furcal (CF) até 265 cm CF, com idades estimadas de 0 a 25 anos de idade para os dois sexos. Cinco modelos de crescimento foram testados e comparados através do critério de informação de Akaike (AIC) e Basiano (BIC). O modelo de crescimento de von Bertalanffy (VBGF) com 3 parâmetros re-parametrizado para estimar L_0 foi o que produziu os melhores resultados tendo estimado os seguintes parâmetros: L_{inf} = 284 cm CF, k = 0.06/yr and L_0 = 109 cm CF para as fêmeas; L_{inf} = 246 cm CF, k = 0.09/yr and L_0 = 108 cm CF para os machos. Os parâmetros de crescimento foram comparados entre o Atlântico norte e sul, com as diferenças obtidas sugerindo taxas de crescimento mais lentas para o hemisferio sul, especialmente para as fêmeas. Os coeficientes de crescimento (k) obtidos no presente estudo representam os coeficientes mais baixos alguma vez obtidos para esta espécie e dentro da família Alopiidae, evidenciando o crescimento extremamente lento do tubarão raposo olhudo e a sua consequente susceptibilidade à sobrepesca. Ogivas de maturação foram calculadas utilizando uma amostra de 642 exemplares, estimando tamanhos médios de maturação de 208.6 cm CF para fêmeas (79% do tamanho máximo observado) e 159.2 cm CF para os machos (61% do tamanho maximo observado). Adicionalmente, um modelo de regressão segmentada foi utilizado para os machos, estimando dois pontos de inflexão (PI_1: 122.5cm CF, PI_2: 173.3cm CF) que identificam as transições entre três estados de maturação dos tubarões (imaturo, em maturação e maturo).

Telemetria por satélite foi usada para estudar a utilização do habitat e as migrações verticais do tubarão raposo olhudo. Foi possivel observar que esta espécie apresenta migrações nictemerais verticais diárias ocupando aguas profundas durante o dia e migrando para a superfície durante a noite. Foi ainda verificado que apesar de apresentarem um padrão de migração vertical semelhante, juvenis e adultos ocupam intervalos de profundidades diferentes, sendo que a classe modal durante o dia correspondeu a 330-360m (18% do dia) para os juvenis enquanto que os adultos apresentaram uma distribução bimodal com um pico aos 240-270m (14.1%) e outro aos 390-420m (16.9%). Para o periodo da noite, a classe modal dos juvenis foi de 30-60 m (49.9 %) sendo a dos adultos 60-90 m (29.8%). Foi ainda observado o mergulho mais profundo para esta espécie alguma vez registado (954.5 m). Com a informação obtida foi possível calcular a sobreposição entre a espécie e a arte de pesca de modo a poder analisar mais eficazmente o impacto da pescaría nos diferentes estados de maturação (juvenis e adultos). Verificou-se que tal sobreposição ocorre exclusivamente durante a noite, sendo esta mais alta para nos juvenis (56.4-60.2%) do que para os adultos (25.4-33.6%).

Esta tese foi realizada no âmbito do maior e mais abranjente projecto alguma vez realizado para esta espécie. Toda a informação obtida durante esta tese foi apresentada ao Comité Científico de Investigação e Estatística da ICCAT (SCRS), a organização responsável pela gestão da pescaría de palangre de superfície, tendo sido usada directamente para aconselhamento científico através da elaboração de modelos de dinâmica populacional, modelos demográficos, e avaliações de risco ecológico (Ecological Risk Assessment), melhorando assim a gestão e conservação desta espécie tão vulnerável no Atlântico.

Palavras-chave: Tubarões pelágicos, redução de captura acidental por pesca, ciclo de vida, distribução por tamanhos, distribuição espacial, utilização de habitat.

ABSTRACT

Population dynamics and fisheries assessment of the bigeye thresher (*Alopias superciliosus*) in the Atlantic: a comparison between north Atlantic and south Atlantic stocks.

The bigeye thresher shark, *Alopias supercilious* is an oceanic pelagic shark, occasionally caught as bycatch in pelagic longline fisheries targeting tunas and swordfish in the Atlantic Ocean. It is particularly vulnerable to fishing pressure, with overexploitation occurring even at low levels of fishing, due to their slow growth, extremely low fecundity and migratory nature crossing both national and international waters. The present study focused on several aspects of the biology and fisheries of this species, including fisheries impact, gear modification for bycatch mitigation, life history, distribution patterns and habitat utilization. The bigeye thresher was amongst the shark species with the highest hooking mortality rates (around 50%) by the Portuguese pelagic longline fleet. When testing possible gear modification to reduce the bycatch, the use of circle hooks or mackerel bait (instead of J-style hook and squid bait) does not seem to be an effective mitigation measure. Life history parameters, specifically age, growth and size at maturity were estimated, with the observed growth coefficients (*k* values) being the lowest ever presented for the species and within the Alopiidae family. Three nursery areas were proposed along the Atlantic Ocean, specifically in the tropical northeast Atlantic and equatorial waters closer to the African continent, in the tropical northwestern Atlantic in areas closer to the Caribbean Sea and Florida, and in the southwest Atlantic closer to the Rio Grande Rise. Finally, satellite telemetry was used to study habitat use and vertical migrations of this species, and when compared to the depth of operation of the longline fishing gear resulted that most of the overlaps between habitat and gear deployment occur during the night and seem to affect more the juveniles. The results presented in this thesis are being integrated into demographic models and being used for stock assessment and ecological risk assessment analysis for pelagic elasmobranchs. Furthermore, the new information can be used to evaluate the impact of recent recommendations prohibiting the retention of some vulnerable elasmobranch species, and assist fishery managers to adopt more informed and efficient conservation measures for this species in the Atlantic.

Keywords: Pelagic sharks; bycatch mitigation; life history; size distribution; spatial distribution, habitat use.

CONTENTS

CHAPTER I. GENERAL INTRODUCTION

I.1. General introduction to the Chondrichthyan fishes

Chondrichthyan fishes (sharks, rays, skates and chimeras) are probably some of the most successful of all fishes, having survived and evolved for the last 400 million years, including surviving through major mass extinction episodes (Compagno 2001). This group seems to have first appeared during the Devonian, with the earliest unquestionable evidence in the fossil record dating from this period [409 – 363 million years ago (mya)], while the modern Chondrichthyans living today derived from the forms present in the Mesozoic Period (245 – 65 mya) (Grogan and Lund 2004).

Chondrichthyans are characterized by an internal skeleton formed by flexible cartilage, without the formation of true bone in their skeletons, fins or scales. Other characteristic that further separate the Chondrichthyans from other fishes are the presence of claspers in males (sexual organs used to inseminate females) that are formed by the mineralization of the endoskeleton tissue along the pelvic fins (Grogan and Lund 2004). It is accepted that the class Chondrichthyes is a monophyletic group (Compagno et al. 2005) that is divided into two sister taxa: the subclass Elasmobranchii that groups sharks, rays and skates, and the subclass Holocephali that groups the chimaeras. Within this group, the Elasmobranchs are recognized from their multiple (5 to 7) paired gill openings on the sides of the head, while the Holocephalans have a soft gill cover with just a single opening on each side of the head that protects the 4 pairs of gill openings (Compagno et al. 2005). There are currently *circa* 1180 Chondrichthyan species described worldwide (White and Last 2012), including approximately 480 species of sharks, 650 batoids (skates and rays) and 50 chimaeras.

Chondrichthyan fishes occupy a wide range of habitat types, including freshwater rivers and lake systems, inshore estuaries and lagoons, coastal waters, the open sea, and the deep ocean. Although sharks are generally thought of being wide-ranging, only a few (including some commercially important species) are capable of making oceanic migrations. Overall, some 5% of Chondrichthyan species are oceanic (found offshore and migrating across ocean basins), 50% occur in shelf waters down to 200 m depth, 35% are found in deeper waters from 200 to 2000 m, 5% occur in fresh water, and 5% have been recorded in several of these habitats (Camhi et al. 1998).

I.2. The exploitation of Chondrichthyans with emphasis on the pelagic sharks

In recent years elasmobranch fishes have become relatively important fishing resources, with a substantial increase in fishing effort worldwide (Vannuccini 1999, Barker and Schluessel 2005). However, elasmobranchs have not traditionally been highly priced products. The exception used to be the fins of some species that are marketed at very high prices in oriental markets for shark fin soup (Bonfil 1994, Clarke et al. 2007), even though more recently there has been a drop in the price of fins as the market appears to have shifted away from an elite towards the average consumer in China and southeast Asia (IOTC 2014). The exploitation of elasmobranch resources has been attributed in part to fisheries specifically targeting elasmobranchs (e.g. Campbell et al. 1992, Castillo-Geniz et al. 1998, Francis 1998, Hurley 1998, McVean et al. 2006, Cartamil et al. 2011) but perhaps more importantly to the bycatch of fisheries targeting other species (e.g. Stevens 1992; Buencuerpo et al. 1998, McKinnell and Seki 1998, Francis et al. 2001, Beerkircher et al. 2003, Coelho et al. 2003, Megalofonou et al. 2005, Coelho and Erzini 2008, Belcher and Jennings 2011, Coelho et al. 2012a). Game fishing also has some impact on elasmobranch fishes, especially on some large pelagic species (e.g. Stevens 1984, Pepperell 1992, Campana et al. 2006, Lynch et al. 2010).

Even though elasmobranchs are currently impacted by commercial and recreational fisheries, there is still limited information about most of these species life cycles, biological parameters, movement patterns and habitat utilization, and in the general impact of fisheries on their populations. Elasmobranch fishes have typically K-strategy life cycles, characterized by slow growth rates and reduced progeny, with maturity occurring late in their life cycle (Smith et al. 1998, Stevens et al. 2000, Cortés 2000, Coelho and Erzini 2002, 2006, Cortés 2007). This low fecundity and relatively high survival rate of newborns suggests that there is a strong relationship between the number of mature females in the population and the new recruits for the next cohort, meaning that the success of the future generation is mainly dependant on the present mature population abundance (Ellis et al. 2005).

While the total worldwide marine fishes landings seem to have reached a plateau in the late 1980’s, elasmobranch catches increased progressively since the 1950’s until the early 2000’s, followed by a decreasing trend for the more recent years (Figure I.1). However, and even though the marine fish catches seem to have remained relatively stable since the late 1980’s, fisheries have shifted in these last decades from catching mainly long lived high trophic level species, towards catching more short lived, low trophic level invertebrates and small planktivorous pelagic fishes (Pauly et al. 1998, Pauly and Palomares 2005). This effect, originally called “fishing down the marine food web” by Pauly et al. (1998), shows that the marine ecosystems top predators (such as the sharks) are the first to suffer from overfishing and significant population declines.

Up until the 1980’s, elasmobranch fisheries were generally unimportant small fisheries, with a generally low commercial value. Traditionally, these elasmobranch fisheries of the past were multi-species fisheries that caught several species of elasmobranchs depending on the region and season of the year. There was little interest in these fisheries, mainly due to their relatively small scale and low commercial value. Bonfil (1994) reported that cartilaginous fishes were a minor group which contributed with an average of 0.8% of the total world fishery landings between 1947 and 1985, while bony fishes such as clupeoids, gadoids and scombroids, accounted for 24.6%, 13.9% and 6.5%, respectively. In the last decades, however, the declining catches per unit effort (CPUE) and rising prices of traditional consumed fishes, along with the market of shark fins for the oriental markets, have made the previously underutilized elasmobranchs increasingly important resources (Castro et al. 1999).

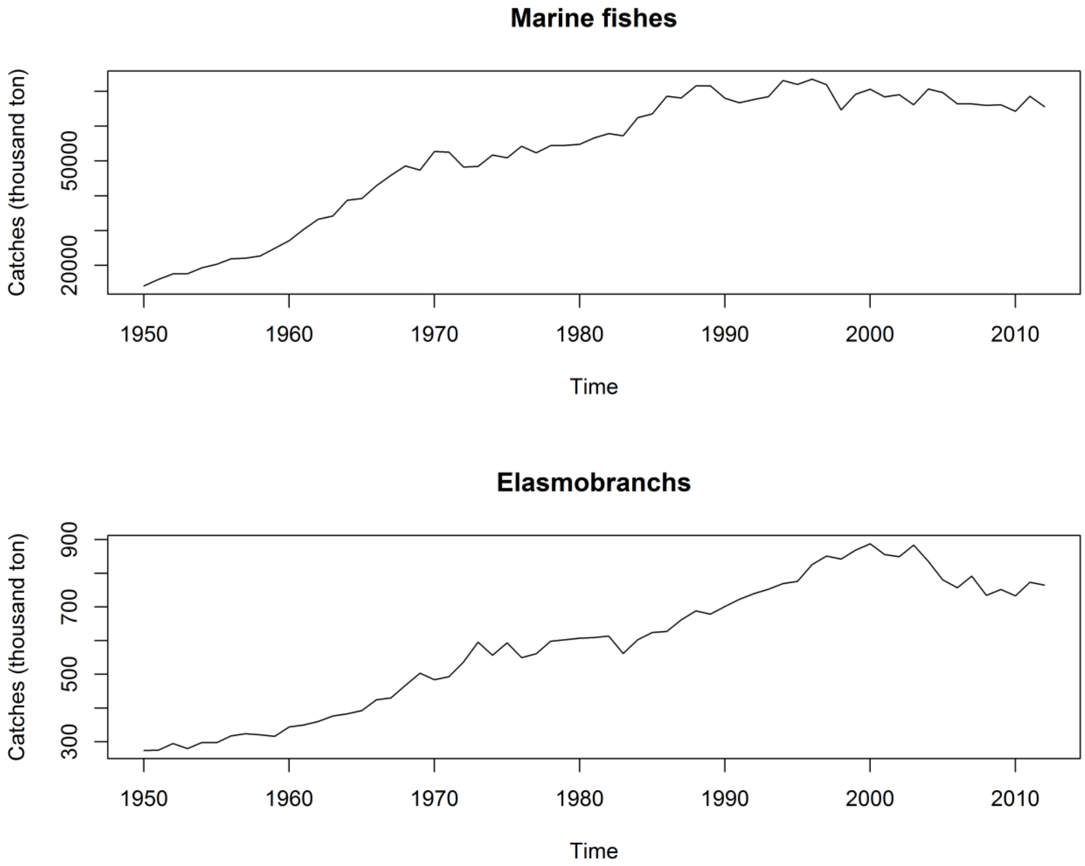

Figure I.1: Global capture of marine fishes (top) and elasmobranchs (bottom) from 1950 to 2012. Data from FAO FIGIS data collection (FAO 2014)

The history of elasmobranch fisheries worldwide indicates, however, that these resources are usually not sustainable. Most elasmobranch targeted fisheries have been characterized by "*boom and burst*" scenarios, where an initial rapid increase of the exploitation and catches is followed by a rapid decline in catch rates and eventually a complete collapse of the fishery (Stevens et al. 2000). Bonfil (1994) and Shotton (1999) provided reviews of world elasmobranch fisheries and included examples of situations where commercial catches have been declining, such as in the northeast Atlantic and Japan, and examples of situations of high concern such as in India. Baum et al. (2003) stated that the northwest Atlantic populations of large pelagic sharks including the scalloped hammerhead, *Sphyrna lewini*, and the threshers *Alopias vulpinus* and *A. superciliosus*, have declined by more than 75% over the last 15 years, and even though the values presented in Baum et al. (2003) seem to have been severely overestimated

(Burgess et al. 2005), there is consensus that there are currently causes for concern. However, and even though overexploitation and population collapses is the most common scenario in elasmobranch fisheries, Walker (1998) demonstrated that some elasmobranch stocks like the blue shark (*Prionace glauca*) can be harvested sustainably and provide for stable fisheries when carefully managed.

Within the industrial oceanic fisheries such as longlines, driftnets and purse seines, the pelagic longlines are responsible for most of the captures of oceanic sharks at a global level, usually as by-catch of fishing operations that target swordfish and tunas (Aires-da-Silva et al. 2008). Oceanic sharks and rays face additional threats associated with low conservation priority and lack of management because they occur within the range of many largely unregulated gillnet and longline fisheries in their epipelagic habitat (Dulvy et al. 2008, Amorim et al. 2009). Consequently, three-quarters of these species are classified as *threatened* or n*ear threatened* by the International Union for Conservation of Nature (IUCN) Red List Criteria (Dulvy et al. 2008).

About 2.5% (26 to 31 species) of the existing elasmobranchs species are classified as oceanic, meaning that most part of their lives is spent in the open ocean far from continental landmasses (Compagno 2008, Pikitch et al. 2008). Compared with coastal waters, oceanic waters are generally less productive and present less diversity. Nevertheless, hot spots of high productivity and biodiversity generally related to seamounts or eddies can be found (Pikitch et al. 2008). As these areas can shift due to oceanographic conditions or vary seasonally, oceanic large predators such as tunas, billfishes and sharks need to migrate long distances (Block et al. 2001).

Although fewer species of sharks inhabit the open ocean than coastal waters, they occupy an important place in the ecosystem as apex predators, strongly influencing the food web structure (Pikitch et al. 2008). Apex predators are extremely important for the entire ecosystems balance, by regulating not only their direct main preys, but also lower trophic level non-prey species through the trophic linkages (i.e. “top-down” control) (Schindler et al. 2002). The effects of the removal of such predators from the marine ecosystems are difficult to foresee, but may be ecologically and economically significant, and may persist over long time periods (Stevens et al. 2000). Therefore, as the removal of pelagic sharks can deeply impact the ecosystem and undermine the sustainability of the fisheries, there is a critical need for increased understanding of the biology, current status, and ecological role of oceanic sharks (Pikitch et al. 2008). However, although oceanic sharks are among the most heavily impacted by fishing, they remain among the least studied and least managed of the elasmobranchs, mostly due to the difficult access as they live far from land and in international waters. Although advances have been made in the understanding of the biology, status and trends of some pelagic shark species in the past decade, some of the least productive species, like the threshers sharks, remain understudied, making their research crucial and urgent (Pikitch et al. 2008).

I.3. The pelagic longline fisheries in the Atlantic

Pelagic longline and purse seine are the primary methods of commercially capturing large pelagic fishes such as tunas, swordfish, istiophorid billfishes and pelagic sharks, which in the Atlanitc are managed by ICCAT (International Commission for the Conservation of Atlantic Tunas). Although purse-seine is the major fishing gear in ICCAT fisheries that capture tunas, pelagic longline is the main gear responsible for most pelagic shark captures (Figure I.2). The ICCAT fisheries catch is dominated by tuna species, although the category “major tuna species” as defined by ICCAT also includes swordfish and some marlins (major tuna species in ICCAT category: *Thunnus albacares*, *Thunnus obesus*, *Thunnus alalunga*, *Thunnus thynnus*, *Katsuwonus pelamis*, *Xiphias gladius*, *Istiophorus albicans*, *Makaira nigricans*, *Tetrapturus albidus*). This category accounted in 2013 for approximately 470,000t, out of an overall catch of 647,000t, while the major sharks (*Prionace glauca*, *Isurus oxyrinchus* and *Lamna nasus*) accounted for approximately 62,500t (Figure I.2).

The most extensive form of pelagic longline seems to have originated in Japan in the early 19th century with the introduction of the internal combustion engine (Watson and Kerstetter 2006). This and other developments in technology enabled the expansion of the fishing grounds in the beginning of the 20th century (Watson and Kerstetter 2006). As a result, the globalization of the longline fisheries began in the 1950s and 1960s driven both by the Japanese tuna market (and the subsequent swordfish market) and the introduction of the freezing technology and international transportation (Watson and Kerstetter 2006). Finally, in the 1970s the use of polyamide monofilament line (instead of multifilament nylon) and baited hooks with chemical light sticks, further developed the fishery commercially worldwide (Watson and Kerstetter 2006). Currently, Japan, Korea and the Republic of China (Taiwan) are the main industrial fleets operating in the Pacific Ocean, while Spain is one of the major nations operating in the Atlantic along with Japan, the United States, Portugal and Canada (Watson and Kerstetter 2006).

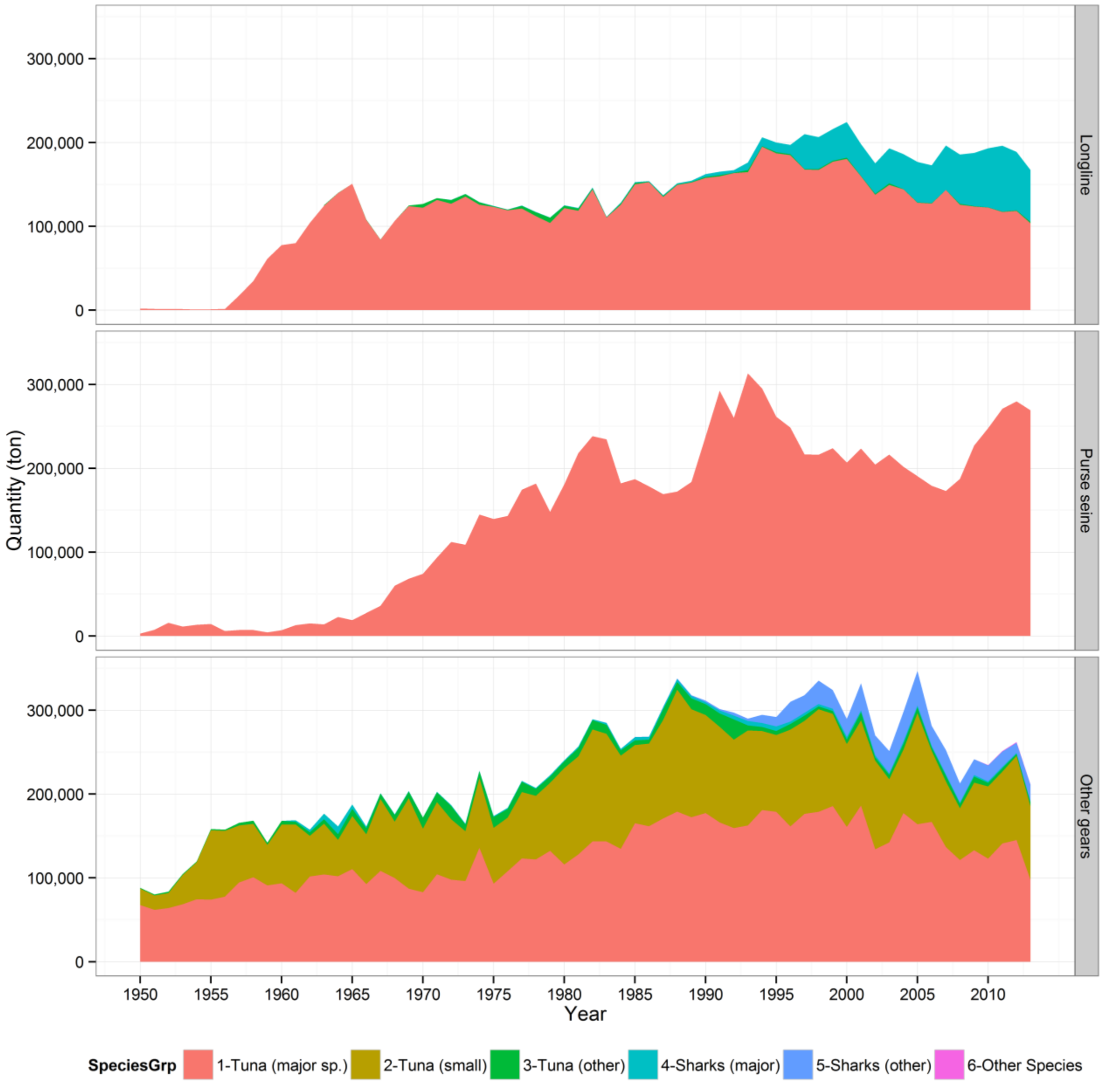

Figure I.2: Nominal catches of tuna and tuna-like species reported in ICCAT (International Commission for the Conservation of Atlantic Tunas) fisheries between 1950-2013 for the major fishing gears: longline, purse seine and other gears. Data from ICCAT Task1 (nominal catch information) database (ICCAT 2014).

Pelagic longline gear is composed by three basic components: the mainline, the branch line and the baited hook (Figure I.3). Different deployment strategies and materials and configurations of these components can be used depending on the target species. For example, when targeting highly migratory species, the gear is suspended below the surface using buoys and float lines at aproximately 100-300 m if targeting tunas (e.g. Japanese fleet) and less than 60 m while targeting swordfish (e.g. Portuguese fleet) (Watson and Kerstetter 2006, Santos et al. 2013a). Additionally, longlines that are set in deeper waters to target tunas typically fish during the day, while shallower longlines targeting swordfish usually fish during the night.

Due to the growing demand for swordfish by the international markets, in 1986 Portuguese ship owners adapted their fishing vessels to catch this species. In 1997 Total Allowable Catches (TAC) and corresponding quotas were implemented and the criteria for the licensing of Portuguese vessels for fishing swordfish was established (Portaria nº 1221 - A/97 de 5 de Dezembro). The Portuguese surface longline fishery is multi-species and as such other species besides swordfish are often caught, including tunas, marlins and pelagic sharks. Among the pelagic sharks, the blue shark (*Prionace glauca*) and shortfin mako (*Isurus oxyrinchus*) are the most important species (Coelho et al. 2012a). Although pelagic sharks (mainly blue shark) were discarded (and not recorded in the logbooks) in the early years of the Portuguese pelagic longline fishery, recently, due to the international growing interest for these species, vessels occasionally direct their fishing effort to shark species along with swordfish. Specifically, the blue and the shortfin mako sharks together can account for more than 50% of the total Portuguese oceanic longline fishery catch, and can represent more than 95% of the total elasmobranch catch (Coelho et al. 2012a).

The Portuguese pelagic longline fishery targeting swordfish has remained almost unchanged since the 1980s (Santos et al. 2012). Nevertheless, some changes have been incorporated in the last decade: i) fishermen shifted from the traditional gear (described by Rey and Alot 1984) to the automatic or “American-style”, using mainlines and branch lines of monofilament, and light attractors (initially light sticks and now flashlights) and ii) the use of of multifilament steel in the terminal tackle of the branch lines (wire leaders), in specific areas and seasons when pelagic sharks are the target species (i.e. taking advantage of higher abundance of these resources).

In the Portuguese pelagic longline targeting swordfish the mainline can have tens of kilometers of length. The most common material used for the branch lines and the mainline (3.6 mm) is polyamide (nylon) monofilament since it is lighter, less visible and has less drag. However, in some cases, a wire leader can be used in the terminal section of the branch lines. As such, two main configurations are used by the Portuguese fleet depending on the operating area and season. One that uses two monofilament sections in the branchline, with a swivel placed immediately after the snap of the mainline, which is attached to a nylon monofilament with 2.0 to 2.5 mm diameter (Santos et al. 2013a). In the middle of the branch line a swivel with a lead of 60-80 g may be attached and a luminescent device is connected to it. Another swivel is then attached to the hook by a nylon monofilament of approximately 2 m with a diameter of 1.8 to 2.2 mm (Figure I.3). In the second configuration, the branch line has three sections, with the last one made of wire. Though historically J-style hooks have been used, the shape and size of the hooks is affected by catch and bycatch concerns. Depending on the target species and/or area, variations can be found between vessels in terms of type, length and dimension of branch line and mainline, bait type, hook type, hook number and hook configuration between floats (Santos et al. 2013a).

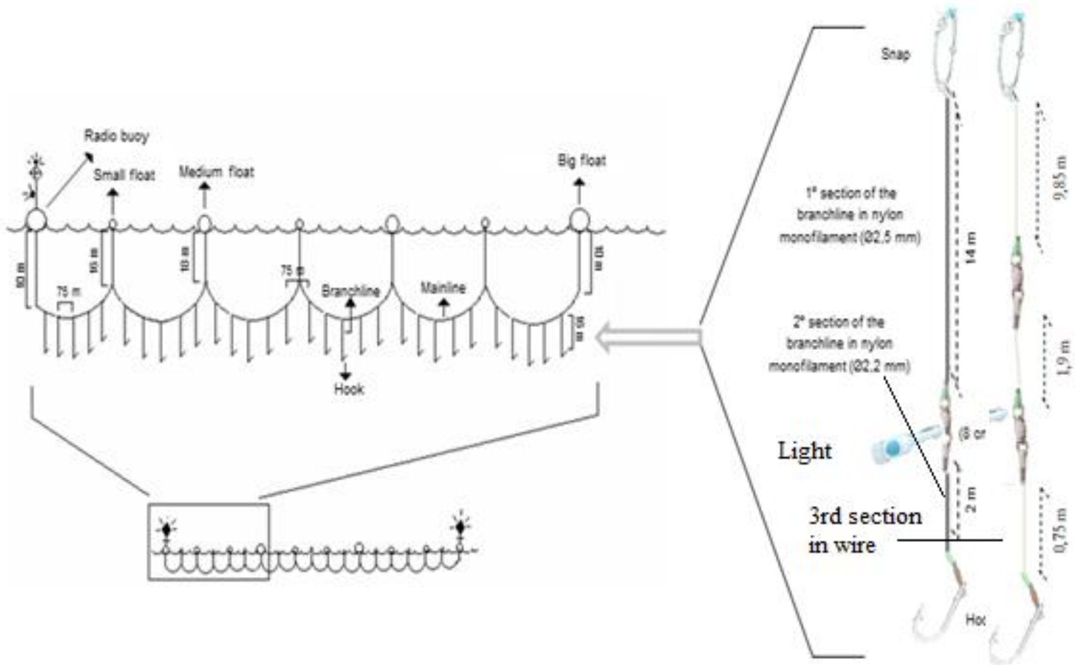

Figure I.3: Schematic drawing of the two main configurations used by the Portuguese swordfish pelagic longline fishing gear (Source: adapted from Santos et al. 2013a)

Gear setting can last between 5 to 7 hours, depending on the number of hooks deployed and/or velocity of the vessel. Longlines targeting swordfish preferably set their gear at sunset due to the adaptation to phototropism of this species. Once released, the gear drifts for a few hours (6 to 7 hours) until it is hauled, normally at sunrise lasting between 7 to 10 hours, depending on the catches and constraints that might arise. The most used baits are squid (*Illex spp*.) and mackerel (*Scomber spp*.) that can be hooked through the head or the lower body.

I.4. The studied species, bigeye thresher (*Alopias superciliosus*)

Taxonomy, distribution and ecology

Within the order Lamniformes, the Alopiidae family has one genus and three species of large, active, and strong-swimming sharks, commonly called thresher sharks or sea foxes due to their scythelike tails (Compagno 1984). The bigeye thresher shark, *Alopias superciliosus* Lowe, 1841, is easily distinguished by its large eyes and lateral grooves, indented forehead, long whiplike upper caudal lobe and its purplish grey coloration in the *dorso* and light cream ventrally (Bigelow and Schroede 1948) (Figure I.4).

Figure I.4: The bigeye thresher shark, *Alopias superciliosus* (Drawing by: João T. Tavares/Gobius).

The bigeye thresher is distributed circumglobally in the Atlantic (and Mediterranean), Pacific and Indian Oceans, ranging from tropical to temperate seas, occurring mostly in oceanic epipelagic waters and at times in more coastal waters (Figure I.5) (Stillwell and Casey 1976, Compagno 2001, Nakano et al. 2003, Weng and Block 2004, Smith et al. 2008a, Cao et al. 2011). When compared with the other two Alopiidae, the bigeye thresher is found in the deepest waters, making forays into the mesopelagic zone to at least 500 m and although it usually inhabits warm temperate to tropical seas, it can tolerate cold water temperatures down to 6ºC and remain there for longer periods of time than many other pelagic sharks (Compagno 1984, 2001, Nakano et al. 2003, Smith et al. 2008a, *vidé* Chapter VI).

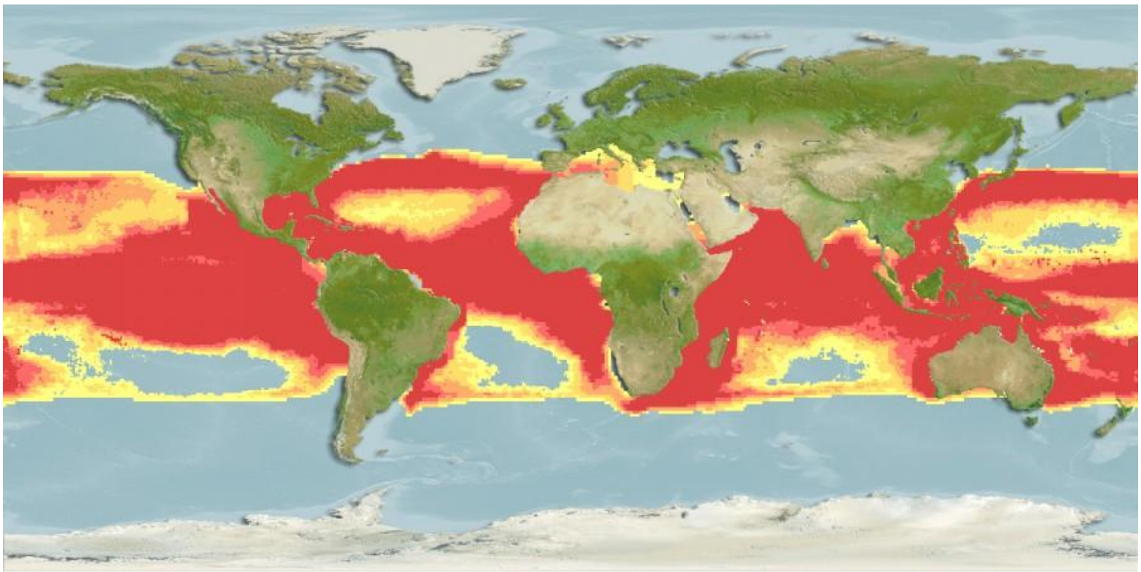

Figure I.5: Global distribution map for the bigeye thresher, *Alopias superciliosus*. The color scale represents the relative probabilities of occurrence, with red and yellow representing higher and lower probabilities of occurrence, respectively. Map generated from Fishbase (Froese and Pauly 2012) using AquaMaps, a presence-only species distribution model (Ready et al. 2010).

In the eastern Pacific, through the use of pop-up satellite archival tags and acoustic telemetry, patterns of diel vertical migration have been observed for this species, with the studied sharks staying at 200 to 500 m depth during the day and at 80 to 130 m at night (Weng and Block 2004, Nakano et al. 2003). This species is also known to travel long distances from off North Carolina south to Cuba, with the longest straight line migration reported at 2,767 km, from waters off New York to the Eastern Gulf of Mexico (Kohler et al. 1998, Weng and Block 2004).

Biology

The bigeye thresher, like all Lamniform sharks (family Alopiidae and family Lamnidae), presents aplacental viviparity with embryonic oophagy as reproductive mode. In this mode, the fertilized ova are packed in egg capsules (blastodisc capsules) in the nidamental gland individually, before moving to the uterus where development takes place (Snelson et al. 2008). During the encapsulated or prehatching phase, embryos are nourished by the yolk sac, hatching from the capsule once it is depleted (Snelson et al. 2008). In the following phase (posthatching phase) after hatching from the capsule, the embryos feed on unfertilized yolked ova that the mother keeps producing in the process called oophagy (Snelson et al. 2008). Unlike most pelagic sharks, the litter size of the bigeye thresher is small, and though litters of one, three and four have been observed, this species typically presents only two young per litter (Bass et al. 1975, Moreno and Morón 1992, Liu et al. 1999, Compagno 2001). Regarding size at birth, the largest recorded embryo was 137 cm total length (TL) (Chen et al. 1997) while the smallest free-swimming neonate was 130 cm TL (Bigelow and Schroeder 1948). Estimates of size of birth for this species range from 100 to 140 cm TL (Bass et al. 1975, Gilmore 1983, Moreno and Morón 1992, Chen et al. 1997, Compagno 2001) though some smaller estimates of 60 to 75 cm TL have been presented by earlier authors using smaller sample sizes (Nakamura 1935, Bigelow and Schroeder 1948, Cadenat 1956).

In the Alopiidae family no evidence of seasonality in the reproductive cycle has been found, making the determination of the length of the gestation cycle, which has been estimated to be 12 months for the three species difficult (Compagno 2001, Snelson et al. 2008). Similarly, the reproductive cycle has not been specifically defined for this family, with adult females bearing embryos along the year with apparently no reproductive seasonality or resting period (Gruber and Compagno 1981, Chen et al. 1997, Liu et al. 1999). On the other hand, some seasonal periods of parturition have been suggested for the bigeye thresher, like the summer, fall and winter in the Florida Straits (Gilmore 1993) and from autumn to winter in the Strait of Gibraltar (Moreno and Morón 1992). In addition, many small juveniles and females with full-term litters have been observed in Cuban waters (Snelson et al. 2008). Sex and size segregation has been observed for this species off the US west coast where gillnet catches north off Oregon were mostly adult males while south of Monterey Bay and in the Southern California Bight immature females comprised most of the bigeye thresher catch (Smith et al. 2008a). Some new information related to the species reproduction is provided in Chapter IV.

Like other threshers, the bigeye feeds on small-medium size schooling fish and pelagic cephalopods, often using the long caudal fin to stun and disorient prey near the surface, which often results in sharks being tailhooked on longlines (Preti et al. 2008, Smith et al. 2008a). More specifically, bigeye thresher diet includes hake, squid, scombrids, alepisaurids, clupeids, istiophorids, and other elasmobranchs (Bass et al. 1975, Stillwell and Casey 1976, Gruber and Compagno 1981). The specialized eyes of the bigeye thresher can roll into upward-directed sockets, allowing it to predate from below (Smith et al. 2008a). In addition, the presence of a *rete* system may allow them to maintain body heat in cold water, facilitating foraging opportunities (Carey et al. 1985, Preti et al. 2008).

Within the *Alopias* genus, the bigeye thresher seems to grow more slowly (k= 0.09; Liu et al. 1998), mature later (*female*: 332-341 cm TL, *male*: 270-288 cm TL; Chen et al. 1997) and reach a smaller maximum size (461 cm TL) than the common thresher but larger than the pelagic thresher (Smith et al. 2008a). Life history information for this species is scarce, with the few studies available being mostly from the Pacific Ocean (Chen et al. 1997, Liu et al. 1998) or from the Atlantic but with a small sample size (Stillwell and Casey 1976, Moreno and Morón 1992). Some new information related to the species growth is provided in Chapter V. In addition, while most pelagic sharks are in the midrange of shark productivity, the bigeye thresher sharks rank among the least productive species when using demographic models, presenting the lowest rates of annual increase even within the genus (Cortés 2008, Dulvy et al. 2008, Smith et al. 2008b).

Threats

Understanding the worldwide fisheries impacts on thresher sharks is difficult, mainly because many fishing nations do not keep detailed landings statistics for this species, which are often grouped with other sharks (Smith et al. 2008a). Specifically, the bigeye thresher is an important component of oceanic and offshore coastal shark fisheries both as target and bycatch, due to their high quality meat and fins that are sold for human consumption in the oriental markets (Compagno 2001, Smith 2008a). Commercial fishing areas where thresher sharks are known to be caught and landed incidentally include the US Coasts (Pacific, Atlantic, and Gulf of Mexico), the Caribbean, Uruguay, northeast Atlantic, Iberian Peninsula and Mediterranean Sea, South Africa, northwest and central Indian Ocean, Taiwan, north central Pacific, western tropical Pacific, New Zealand and southern Australia, Pacific Coast of Mexico and Gulf of California and Guatemala, Panama, Colombia and Ecuador (Moreno and Morón 1992, Last and Stevens 1994, Liu et al. 1998, Shotton 1999, Smith et al. 2008a, Amorim et al. 2009). Furthermore, its epipelagic habitat includes many unregulated gillnet and longline fisheries making this species particularly vulnerable to fisheries exploitation (Amorim et al. 2009). Even though the bigeye thresher can be captured by a variety of fishing gears, most captures take place as bycatch in pelagic longlines targeting tunas and swordfish. In the Atlantic Ocean, the management of the oceanic tuna and tuna-like species (including pelagic sharks) is a mandate of ICCAT, which maintains the catch records from those fisheries and carries out stock assessments and other research initiatives for determining their vulnerability status.

Within the ICCAT scientific work, an Ecological Risk Assessment (ERA) was carried out for priority species of pelagic sharks in the Atlantic in 2008 (Cortés et al. 2010), with that analysis being updated with more recent information in 2012 (Cortés et al. 2012). With both analyses, it was demonstrated that most pelagic sharks have exceptionally limited biological productivity and high susceptibility to pelagic longline gear and as such, can be overfished even at very low levels of fishing mortality, with the bigeye thresher in particular shown to be at high risk of overexploitation (ranked 4th in 11 species).

The Shark Specialist Group from the International Union for the Conservation of Nature (SSG/IUCN) considered all the members of the genus *Alopias* as “Vulnerable” globally (according to the IUCN Red List Criteria) because of their declining populations due to the combination of slow life history characteristics and high levels of largely unmanaged and unreported mortality in target and bycatch fisheries (Amorim et al. 2009). Specifically, this species was considered especially vulnerable to fisheries exploitation, even within the *Alopias* genus, due to its exceptionally low potential of population increase and least resilience to fisheries of the genus (Amorim et al. 2009). Due to the report of reduction in thresher CPUE in pelagic longlines in the northwest Atlantic and eastern Pacific, the species was listed as “Endangered” in the northwest Atlantic and western central Atlantic and “Near Threatened” in the southwest Atlantic (Amorim et al. 2009). The need for reliable, species-specific catch and discard data for thresher sharks was also highlighted by the SSG/IUCN, with special requirement for data collection for the bigeye thresher throughout its range, especially in the south Atlantic (Amorim et al. 2009).

Conservation actions

Several levels of protection are currently in place in the Atlantic for the bigeye thresher. In the fisheries managed by ICCAT, which are the oceanic fisheries targeting tuna and tuna-like species, and include pelagic longlines, purse seines, tuna traps, bait boats, and drift gillnets, it is forbidden to retain, store or sell any part of bigeye thresher sharks, with the prompt release back to the sea of accidentally caught sharks of this species and record of this information following the ICCAT data requirements being mandatory (ICCAT Recommendation 09-07). In the Atlantic coast of the US, the bigeye thresher is included under the Fishery Management Plan for Atlantic tunas, swordfish and shark, being its possession prohibited. Similar no-retention management actions are also in place for other oceans, specifically for the Indian Ocean, where the Indian Ocean Tuna Commission (IOTC) responsible for the management of tuna and tuna-like fisheries, has also prohibited the retention of thresher sharks, and requires the immediate release of any specimen accidentally caught (IOTC Resolution 12/09).

I.5. General objectives of the study

The present study was designed as a means to fill critical voids in the knowledge of the Atlantic bigeye thresher shark, a species commonly caught as by-catch in pelagic longline fisheries. Not only is this species extremely vulnerable to fisheries but it is also very poorly known, and therefore there was an urgent need to study both the species life history parameters and the impacts of pelagic longline fisheries on the species from a trans-boundary and inter-hemispheric perspective. This would allow more thorough scientific advice aiming a more efficient fisheries management and the species conservation. The specific objectives of the present study were to:

1) Provide a general introduction to the Chondrichthyan fishes, their biology and susceptibility to fishing mortality, with a particular emphasis on the oceanic sharks and especially the bigeye thresher shark (Chapter I);

2) Study the impacts of the Portuguese pelagic longline fishing on the bigeye thresher shark and potential mitigation measures::

   2.1) Determine the hooking mortality of the bigeye threshers captured in the Portuguese longline fishery in the Atlantic Ocean (Chapter II);

   2.2) Test different hook styles and bait types as a possible mitigation measure for reducing the bycatch of this vulnerable species (Chapter III);

3) Determine life history parameters of the north and south Atlantic populations of the bigeye thresher, establishing comparisons between them:

   3.1) Study the distributional patterns in terms of size and sex in different regions across the Atlantic, estimate the size-at–maturity, and identify possible critical habitats such as nursery areas in the Atlantic (Chapter IV);

3.2) Estimate age and growth parameters for the two hemispheres (Atlantic), and determine the best technique for enhancing growth bands in the vertebra of this species aiming age reading (Chapter V);

4) Characterize habitat preferences in terms of depth and temperature, and related movements along the Atlantic Ocean using satellite tagging (Chapter VI)

Each of the following chapters (specifically chapters II to VI) of this thesis has been written in a paper-style format, suitable and appropriate to be published in a scientific journal. Accordingly, each of these chapters constitutes a complete study and can be read independently of the others. The publication status of the particular chapter is given at the beginning of the section on the footnote. Tables and figures appear in the text inside each chapter, but all eferences have been compiled in a final section.

SECTION 1:

FISHERIES

(photos by IPMA)

CHAPTER II. OVERVIEW OF HOOKING MORTALITIES FOR SHARKS CAPTURED BY PELAGIC LONGLINES IN THE ATLANTIC OCEAN[1]

II.1. Introduction

In the Atlantic Ocean, several pelagic elasmobranch species are commonly caught as bycatch in pelagic swordfish longline fisheries (e.g., Buencuerpo et al. 1998; Petersen et al. 2009). The natural mortality rates of these species are usually low, so increased fishing mortality may have severe consequences for their populations (Dulvy et al. 2008), with declines occurring even at relatively low levels of fishing mortality (Smith et al. 1998; Stevens et al. 2000). As many bycatch species are discarded by these fisheries, information on hooking (also known as "at-haulback") fishing mortality is important for the evaluation of the impacts of these fisheries on the species captured and the pelagic ecosystem.

Previous studies have focused on elasmobranch fishing mortality. However, most were carried out for coastal trawl fisheries [e.g., spurdog (*Squalus acanthias*) by Mandelman and Farrington (2007); small-spotted catshark (*Scyliorhinus canicula*) by Rodríguez-Cabello et al. (2005); and Rajidae skates by Enever et al. (2009)]. In terms of longlines, Morgan and Burgess (2007) and Morgan and Carlson (2010) analysed hooking mortality of coastal sharks caught in the U.S. bottom longline fishery, while Afonso et al. (2011) analysed fishing gear modifications that could reduce elasmobranch mortality in bottom and pelagic longlines in Brazil. For pelagic elasmobranchs captured in longline fisheries, previous studies addressing hooking mortality have focused mainly on the blue shark (*Prionace glauca*). Campana et al. (2009) carried out a comprehensive study of blue shark caught in the northwest Atlantic (Canadian fishery), including both the short-term hooking mortality recorded at haulback and the post-release long-term mortality recorded by satellite telemetry. Also in the northwest Atlantic, Diaz and Serafy (2005) analysed factors that could affect the numbers of blue sharks in good enough condition for live release, using data from the U.S. Atlantic pelagic fishery observer program. In the Pacific Ocean, Moyes et al.

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[1] ***Based on the manuscript***: Coelho R, Fernandez-Carvalho J, Lino PG, Santos MN. 2012. An overview of the hooking mortality of elasmobranchs caught in a swordfish pelagic longline fishery in the Atlantic Ocean. Aquat. Living Resour. 25, 311–319.

(2006) predicted post-release survival of blue sharks, Musyl et al. (2011) analysed the post-release survival of five pelagic elasmobranch species, and Walsh et al. (2009) analysed mortality of several shark species for the Hawaii-based longline fishery, including deep and shallow water sets.

Knowledge on hooking mortality can be used to evaluate conservation and management measures, including the prohibition to retain particular vulnerable species, such as those recently implemented by some tuna Regional Fisheries Management Organizations (tRFMOs). These include the recent management recommendations by the International Commission for the Conservation of Atlantic Tunas (ICCAT), which implemented mandatory discards of the bigeye thresher *Alopias superciliosus* (ICCAT Rec. 2009/07), oceanic whitetip *Carcharhinus longimanus* (ICCAT Rec. 2010/07), hammerheads (ICCAT Rec. 2010/08) and silky shark *Carcharhinus falciformis* (ICCAT Rec. 2011/08). However, both the at-haulback/hooking mortality and the long-term post-release survivorship remain largely unknown for these species, so the impact of such measures also remains unknown.

Hooking mortality estimations are also important as they can be incorporated into stock assessment studies. Cortés et al. (2010) conducted an Ecological Risk Assessment (ERA) for eleven pelagic elasmobranch species in the Atlantic Ocean, and determined their relative productivity/susceptibility in order to rank and compare the vulnerability of the species caught in the fishery. More recently, Arrizabalaga et al. (2011) carried out an ERA analysis that included all bycatch groups captured in pelagic longline tuna fisheries in the Atlantic Ocean. One parameter that can be used and included in such types of assessment (in the susceptibility component of the analysis) is the probability of survival after capture, which can be partially inferred from the proportions of species-specific hooking mortality.

The aim of this paper is to explore hooking mortality (recorded at haulback, during fishing gear retrieval) in a pelagic longline fishery targeting swordfish in the Atlantic Ocean and by-catching pelagic sharks. The main objective of the study was to present species-specific proportions of hooking mortality, while a secondary objective was to explore relationships between the hooking mortality and some possible explanatory variables, such as specimen size, sex and region of operation of the fishery.

II.2. Material and Methods

Data for this study were collected by IPMA, I.P. (Portuguese Marine and Atmospheric Institute) fishery observers' onboard Portuguese longliners targeting swordfish along the Atlantic Ocean. Data were collected between August 2008 and December 2011. During this period, information was collected during 18 fishing trips of five different fishing vessels. This produced information from a total of 834 longline sets, corresponding to 1,078,199 hooks deployed.

Geographically the fishery covers a wide area of the Atlantic Ocean in both hemispheres. The study area was divided into four areas of fleet operation for the fleet: the temperate northeast Atlantic, tropical northeast Atlantic, equatorial, and southern Atlantic regions (Figure II.1). Many characteristics of the vessels of the fleet are similar between regions. For example, the targeted species is mainly swordfish and, to a lesser extent, tropical tunas, with fishing conducted at depths of 20-50 m below the surface, with gear deployment beginning at around 17:00 h and haulback starting the next day from about 06:00 h. The traditional hooks used by the fishery are stainless steel J-style hooks, and the baits are usually either squid (*Illex* spp.) or mackerel (*Scomber* spp.). Both monofilament and wire branch lines are used, but only one type is used per fishing set. However, some differences do exist within the fleet, which is why the study area was divided into the four regions mentioned above. For example, the vessels that operate in the northeast Atlantic temperate region (closer to mainland Portugal and the Azores archipelago) tend to be smaller in size and mostly do not have freezing capacity (the catch is usually refrigerated); therefore, they make shorter trips of a few days to weeks. In contrast, the vessels that operate mainly in the more distant regions of the equatorial and southern Atlantic are usually larger vessels with freezing capacity that tend to make longer trips of up to four months in duration.

For every elasmobranch specimen caught, the onboard fishery observers recorded the taxon (usually to the species level, except for manta, devil and eagle rays, which were identified to the family level), specimen size (FL - fork length for sharks and DL - disk length for the manta, devil and eagle rays, both measured to the nearest lower cm) and condition at haulback (alive or dead at time of fishing gear retrieval). For each fishing set, information on the date, geographical coordinates (latitude and longitude) and number of hooks used was recorded. The condition of the sharks at fishing gear retrieval (alive or dead) was categorized based on any responsiveness from the sharks indicating that specimens were alive.

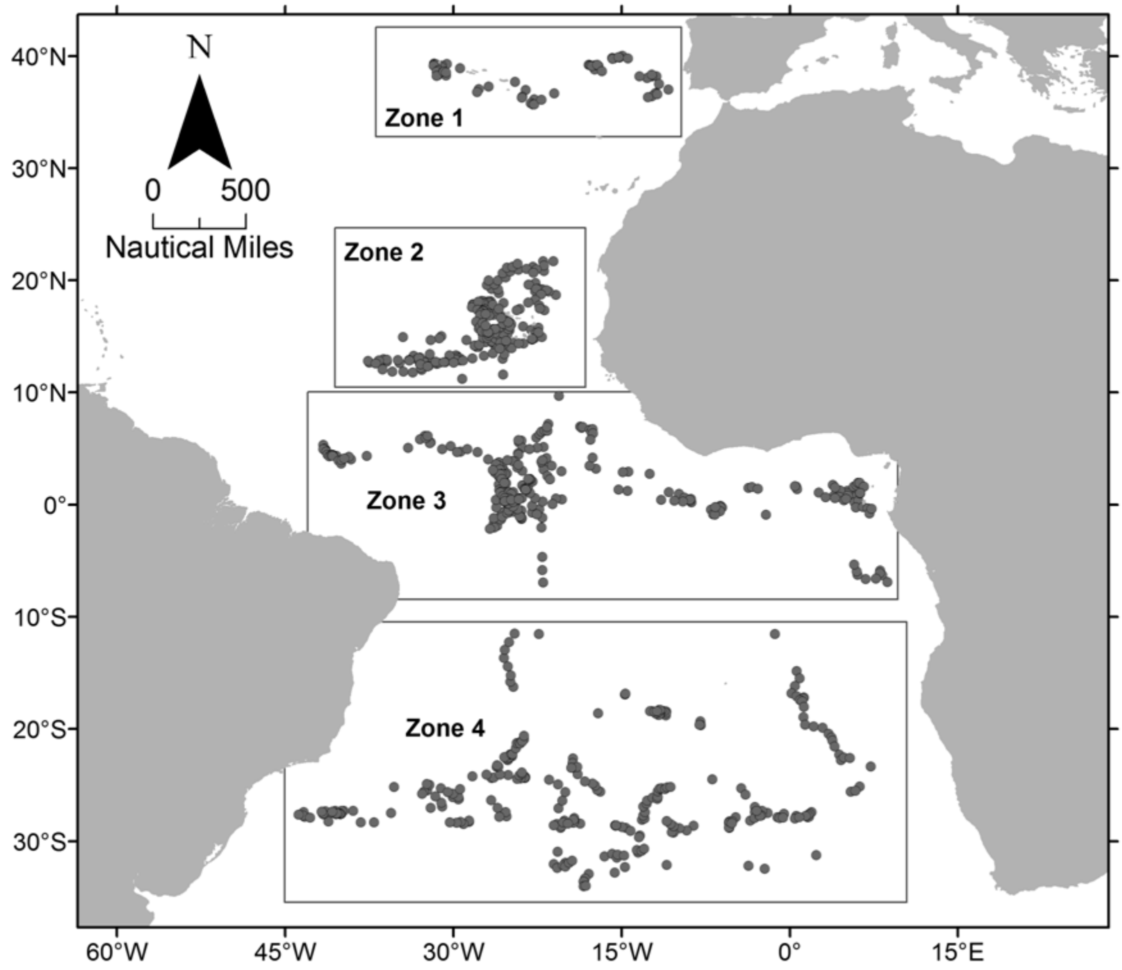

Figure II.1: Location of the longline fishing sets analysed in this study in the Atlantic Ocean, showing the four areas of operation of the Portuguese longline fleet that were considered for the analysis: Zone 1: temperate NE Atlantic; Zone 2: tropical NE Atlantic: Zone 3: equatorial; Zone 4: southern Atlantic.

Species-specific quantities of live and dead specimens were recorded at the time of capture, and their respective percentages calculated. These percentages were calculated for both sexes combined, but also by sex for the most abundant species, namely the blue shark (*Prionace glauca*), crocodile shark (*Pseudocarcharias kamoharai*), shortfin mako (*Isurus oxyrinchus*) and bigeye thresher (*Alopias superciliosus*). These four species were selected because of their larger sample sizes (> 1000 specimens).

The size distributions of these four most abundant species were compared between regions and sexes. For the comparison between regions, Kruskal-Wallis (KW) tests were used, while the comparison between sexes was carried out with Mann-Whitney and 2-sample Kolmogorov-Smirnov (K-S) tests. Non-parametric were used rather than parametric ones because the data was not normally distributed (as shown by Lilliefors tests) and the variances were heterogeneous between groups (as shown by Levene tests).

The relationship between hooking mortality and specimen size was assessed for the four species. Multivariate generalized linear models (GLM) with binomial error structure and a logit link function (logistic models) were applied to the mortality data using specimen size (FL, in cm), sex and region as the explanatory variables. The event of interest considered in these models was the specimen mortality (coded with 1), while live specimens at haulback were coded with 0. The significance of the explanatory variables was determined with Wald statistics and likelihood ratio tests, comparing nested models. The linearity of the continuous explanatory variable (in this case the specimen size) with the linear predictor was assessed with generalized additive model (GAM) plots. After fitting the models for each species, the odds-ratios with the respective 95% confidence intervals were calculated. For the categorical variables, the odds-ratios were calculated with reference to a baseline level for each variable: in this case region 1 (northeast temperate) for the region variable, and females for the sex. For the continuous variable, the odds-ratios were calculated in terms of changes in the mortality rates for a 10 cm increase in specimen FL.

All statistical analyses were carried out with the "R Project for Statistical Computing" version 2.14.0 (R Development Core Team 2011). Most analysis carried out are available under the core R program, except the contingency table analysis that was carried out using the “gmodels” library (Warnes et al. 2011), and the GAM plots that were created with “gam” library (Hastie 2011).

II.3. Results

During this study, data on a total of 36,067 specimens from 21 different taxa were recorded (Table II.1). The blue shark was the most commonly captured species, representing 84% of the total elasmobranch catch, followed by the crocodile shark (5%), shortfin mako (4%) and bigeye thresher (3%) (Figure II.2). The average CPUE for the main target species of the fishery (swordfish) was 12.8 specimens (n) per 1000 hooks while, considering the commonest shark by-catch species, it was 27.9 n/1000 hooks for the blue, 1.5 n/1000 hooks for the crocodile, and 1.3 n/1000 hooks for the shortfin mako (Figure II.2). Of the 36,067 specimens that were caught during the study period, information on hooking mortality was recorded for most: 35,502 specimens, representing 98.4% of the sample (Table II.1).

The length of the mainline and number of hooks used per set varied among vessels and fishing sets according to each particular vessel's operating capacity and the specific sea conditions during the fishing operations. On average, for the whole fleet combined, 1293 hooks were used per set (SD = 187); although, considering the four separate regions, there was a tendency for an increase in effort for the more distant areas. Specifically, the mean effort per set was 924 (SD = 79), 1216 (SD = 105), 1334 (SD = 106) and 1385 (SD = 195) hooks deployed per set for regions 1, 2, 3 and 4, respectively.

In terms of the condition of the animals at time of haulback, it was possible to determine significant species-specific differences (Table II.1, Figure II.2). Species such as the blue and crocodile sharks had relatively low percentages of dead specimens at haulback (around 15%), while for the smooth hammerhead, silky shark and bigeye thresher, the percentages of dead specimens at haulback were generally higher than 50% (Figure II.2). In particular, the smooth hammerhead had a very high hooking mortality rate, with 71% of the specimens caught being dead at haulback. In contrast, all the batoids (pelagic stingray, manta, devil and eagle rays) had very low percentages of dead specimens at haulback (≤ 2%).

The size distributions of the four most frequently captured species varied significantly between regions (Figure II.3), as shown by Kruskal-Wallis tests (blue shark: KW = 8206.5, $df = 3$, p-value < 0.01; crocodile shark: KW = 57.9, $df = 2$, $p < 0.01$; shortfin mako: KW = 53.9, $df = 3$, $p < 0.01$; bigeye thresher: KW = 140.7, $df = 3$, $p < 0.01$).

Table II.1: Descriptive statistics of elasmobranchs caught and analysed for this study. Both the scientific names and the FAO 3 letter codes are given. Sample size refers to the number of specimens caught and sampled of each species. Hook mortality refers to the species-specific hooking mortality (% dead). Size data is given in fork length (FL, cm) for sharks, and disk length (DL, cm) for the manta, devil and eagle rays, with values of the minimum (Min), maximum (Max), mean size (Mean) and standard deviation (SD).

FAO Code	Taxon	Common name	Sample size (N)	Hook mortality (% dead)	Size (FL/DL)			
					Min	Max	Mean	SD
BSH	*Prionace glauca*	Blue shark	30168	14.3	40	315	197.1	34.5
PSK	*Pseudocarcharias kamoharai*	Crocodile shark	1621	13.3	38	117	83.5	9.3
SMA	*Isurus oxyrinchus*	Shortfin mako	1414	35.6	66	305	168.8	35.4
BTH	*Alopias superciliosus*	Bigeye thresher	1061	50.6	80	265	167.0	29.5
PLS	*Pteroplatytrygon violacea*	Pelagic stingray	396	1.0	30	103	46.9	15.0
SPZ	*Sphyrna zygaena*	Smooth hammerhead	372	71.0	136	275	197.5	24.9
FAL	*Carcharhinus falciformis*	Silky shark	310	55.8	61	242	130.1	43.2
OCS	*Carcharhinus longimanus*	Oceanic whitetip shark	281	34.2	63	227	128.0	33.7
LMA	*Isurus paucus*	Longfin mako	168	30.7	68	266	145.5	43.1
MAN	Mobulidae	Mantas and devil rays	145	1.4	55	240	104.8	90.2
GAC	*Galeocerdo cuvier*	Tiger shark	36	2.9	134	300	197.5	41.3
GAG	*Galeorhinus galeus*	Tope shark	25	0.0	80	175	95.2	19.7
SPL	*Sphyrna lewini*	Scalloped hammerhead	21	57.1	160	240	194.9	19.3
EAG	Myliobatidae	Eagle rays	19	0.0	30	50	41.7	10.4
CCA	*Carcharhinus altimus*	Bignose shark	11	60.0	78	110	95.3	8.9
POR	*Lamna nasus*	Porbeagle	10	30.0	129	236	192.1	33.8
ALV	*Alopias vulpinus*	Thresher	3	66.7	200	220	212.3	10.8
SPM	*Sphyrna mokarran*	Great hammerhead	3	0.0	165	251	217.3	45.9
GNC	*Ginglymostoma cirratum*	Nurse shark	1	0.0				
GUP	*Centrophorus granulosus*	Gulper shark	1	100.0	72	72	72.0	
ISB	*Isistius brasiliensis*	Cookie cutter shark	1	0.0	48	48	48.0	

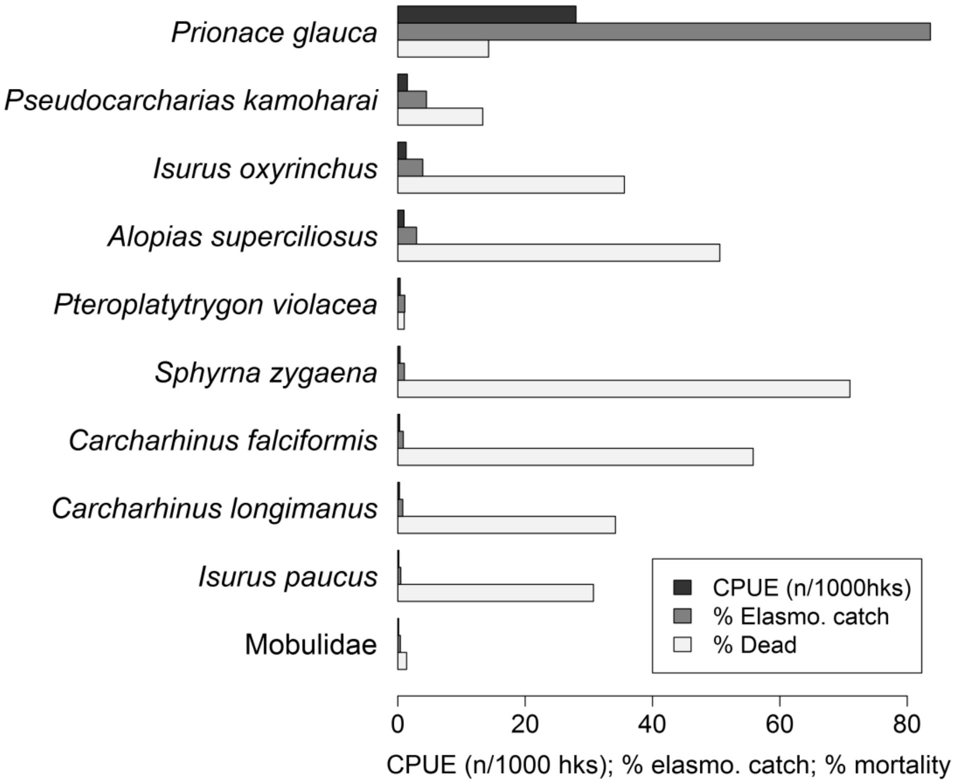

Figure II.2: Species-specific CPUEs (n/1000 hooks), percentages of each species within the total elasmobranch catch, and species-specific percentages of dead specimens at haulback. Only taxa with large sample sizes (n > 100) are plotted.

For three of the four species there were significant differences in the size distribution between sexes (Figure II.4). Specifically, the size distribution was significantly different between male and female blue sharks (2-sample K-S test: D = 0.099, $p < 0.01$), with the median size of males smaller than that of females (Mann-Whitney test: W = 109 392 283, $p < 0.01$). For the bigeye thresher, the size distribution between sexes was also significantly different (2-sample K-S test: D = 0.23, $p < 0.01$) but the median size of males was significantly larger than that of females (Mann–Whitney test: bigeye thresher: W = 73496, $p < 0.01$).

For the blue and shortfin mako sharks there was a general trend of decreasing mortality with increasing specimen size, with relatively linear trends (Figure II.5). For the crocodile shark and bigeye thresher, however, the effects of specimen size did not seem to influence the hooking mortality rates, as relatively similar rates were observed for all sizes (Figure II.5). In terms of the multivariate logistic models, the significant variables in each model varied depending on the species. Specimen size was significant for the blue and shortfin mako sharks, region was significant for the blue, shortfin mako and crocodile sharks, and sex was significant for the blue and crocodile sharks (Table II.2). For the bigeye thresher, none of the variables considered were significant, meaning that there were no differences in the mortality rates depending on specimen size, region or specimen sex (Table II.2).

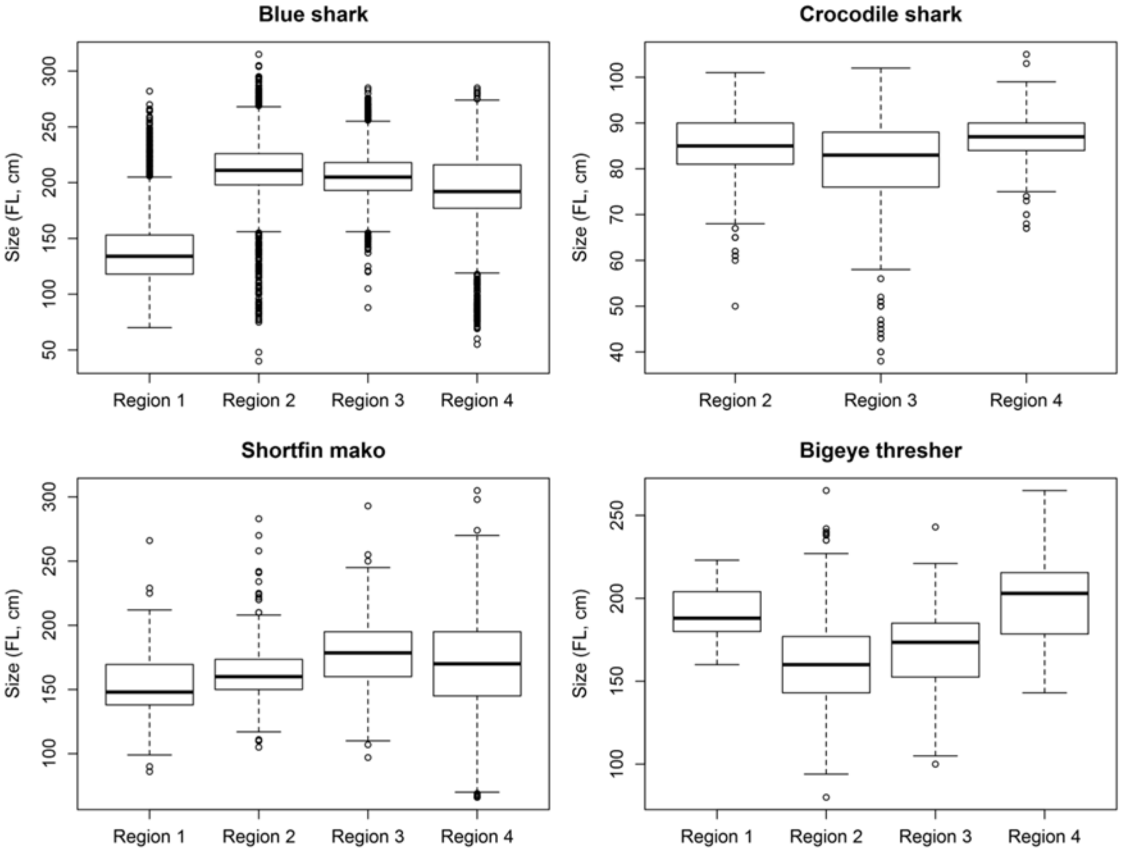

Figure II.3: Size distribution of the four most frequently captured elasmobranch species (n > 1000) per region in the study area. In each boxplot, the central line represents the median, the box represents the 0.25 and 0.75 quartiles, the whiskers represent the non-outlier range, and the dots represent the outliers.

Multivariate model interpretation using odds-ratios for the blue shark showed that hooking mortality decreased by 14% for an increase of 10 cm in size (FL), with the 95% confidence interval between 13% and 15% (Table II.3). Likewise, the effects of size on the shortfin mako also showed a negative trend, with hooking mortality decreasing by 6.2% for an increase of 10 cm FL, with the 95% confidence interval between 3% and 9% (Table II.3).

Table II.2: Deviance table for the effects of specimen size, region and sex on the hooking mortality rates of the four most frequently captured elasmobranch species. BSH - *Prionace glauca*; PSK - *Pseudocarcharias kamoharai*; SMA - *Isurus oxyrinchus*; BTH - *Alopias superciliosus*. The table presents the degrees of freedom needed to estimate parameters for each variable (df), the deviance explained by each variable, and the residual degrees of freedom and deviance after including each parameter. The significance of including each variable in the analysis is given by the p-value of the Chi-square test.

Variable	df	Deviance	Resid. *df*	Resid. Dev.	*p*-value
P. glauca					
Null			28329	23294	
Size	1	869.89	28328	22424	< 0.01
Region	3	308.47	28325	22116	< 0.01
Sex	1	24.08	28324	22092	< 0.01
P. kamoharai					
Null			954	953	
Size	1	0.04	953	953	0.84
Region	2	37.81	951	915	< 0.01
Sex	1	13.60	950	902	< 0.01
I. oxyrinchus					
Null			1324	1728	
Size	1	12.90	1323	1715	< 0.01
Region	3	31.01	1320	1684	< 0.01
Sex	1	0.09	1319	1684	0.76
A. superciliosus					
Null			874	1212	
Size	1	0.00	873	1212	0.95
Region	3	4.90	870	1207	0.18
Sex	1	1.03	869	1206	0.31

Table II.3: Multivariate logistic GLMs for the hooking mortality of the most frequently captured elasmobranch species. BSH - *Prionace glauca*; PSK - *Pseudocarcharias kamoharai*; SMA - *Isurus oxyrinchus*. Only the significant variables in each model were calculated and are presented, with the respective standard error (SE) and statistical significance (Wald statistic and respective p-value). The odds-ratios are calculated for an increase of 10 cm FL (continuous variable), and for each level of the categorical variables with reference to the baseline category. The 95% confidence intervals of the odds-ratios are given. Note that a model for the BTH (*Alopias superciliosus*) is not presented, as differences in the hooking were not significant for any of the variables.

Parameter	Logistic GLM				Odds-Ratios		
	Estimate	SE	Wald Stat.	*p*-value	Estimate	Lower 95%	Upper 95%
P. glauca							
Intercept	0.65	0.10	6.61	< 0.01			
Size	-0.01	0.00	-22.82	< 0.01	0.86	0.85	0.87
Region2	0.04	0.07	0.48	0.63	1.04	0.90	1.20
Region3	0.32	0.07	4.31	< 0.01	1.37	1.19	1.58
Region4	0.70	0.06	11.09	< 0.01	2.01	1.78	2.28
SexM	0.17	0.04	4.90	< 0.01	1.19	1.11	1.28
P. kamoharai							
Intercept	-2.68	0.21	-13.05	< 0.01			
Region3	1.04	0.20	5.06	< 0.01	2.82	1.89	4.21
Region4	0.61	0.25	2.45	0.01	1.84	1.13	2.99
SexM	0.45	0.17	2.63	0.01	1.57	1.12	2.20
I. oxyrinchus							
Intercept	0.58	0.39	1.49	0.14			
Size	-0.01	0.00	-3.91	< 0.01	0.94	0.91	0.97
Region2	-0.67	0.33	-2.05	0.04	0.51	0.27	0.97
Region3	-0.12	0.34	-0.37	0.71	0.88	0.46	1.70
Region4	0.13	0.31	0.43	0.66	1.14	0.62	2.10

Region had an effect on blue and crocodile sharks as the mortality rates in the equatorial and southern Atlantic areas were higher than those in the northeastern Atlantic, while the opposite effect was observed for the shortfin mako, with lower mortality rates in the southern regions (Table II.3). Finally, in this multivariate modeling approach, the effects of sex were significant for blue and crocodile sharks, with the males of both species having higher odds of dying than females in both cases (Table II.3).

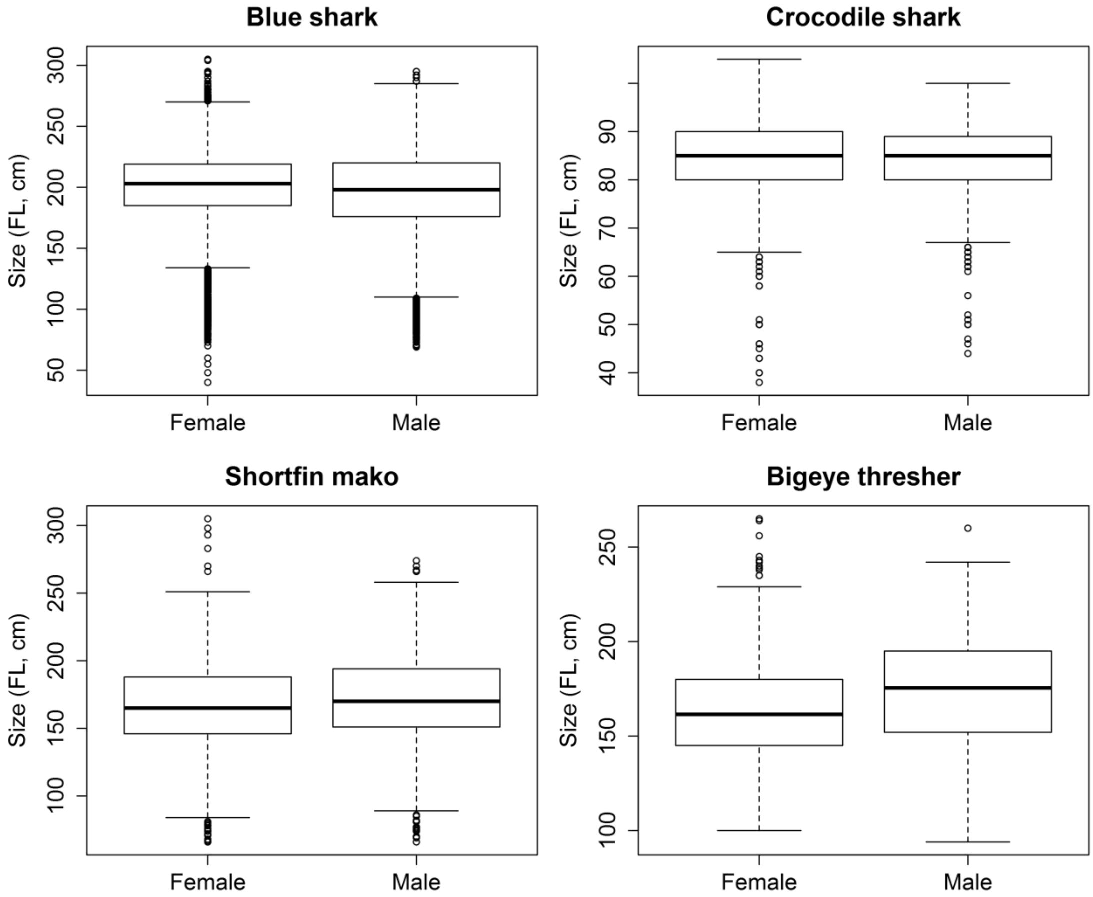

Figure II.4: Size distribution of males and females for the four most frequently captured elasmobranch species (n > 1000). In each boxplot, the central line represents the median, the box represents the 0.25 and 0.75 quartiles, the whiskers represent the non-outlier range, and the dots represent the outliers.

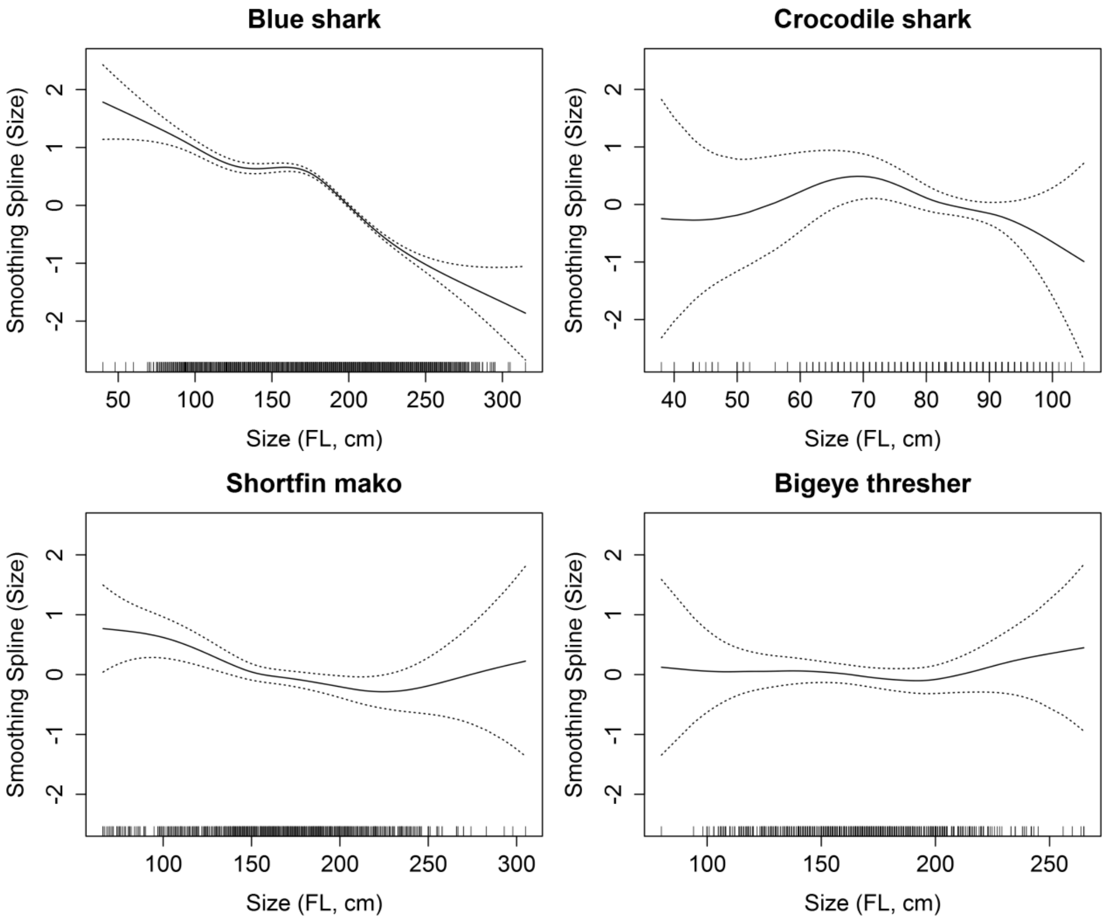

Figure II.5: Generalized additive models (GAM) plots with the effects of specimen size (FL, cm) on hooking mortality. The analysis is presented for the four most frequently captured elasmobranch species (n > 1000).

II.4. Discussion

During this study it was possible to determine that the hooking mortality percentages of pelagic elasmobranchs caught in pelagic longline fisheries are species-specific, and that management options therefore need to consider those specificities. The batoids, including the pelagic stingray, manta, devil and eagle rays tend to have very low percentages of dead specimens at haulback, with most batoids therefore being discarded alive. Some shark species, such as blue and crocodile sharks, also have relatively low percentages of dead specimens, with hooking mortalities generally lower than 15%. In contrast, species such as the smooth hammerhead, silky shark and bigeye thresher had higher hooking mortality rates, usually with more than 50% of specimens captured (and discarded) dead. The smooth hammerhead seems to be a particularly vulnerable species in this respect, as 71% of the specimens are captured already dead.

A recent study by Campana et al. (2009) on blue sharks captured by the Canadian longline fishery in the northwest Atlantic Ocean, concluded that short-term hooking mortality was in the 12-13% range (measured by fishery observers), which is a little lower than the 14.3% estimated in our study. However, these authors also calculated hooking mortality from scientifically examined specimens, and hypothesized that the fishery observer values could have been underestimated, so that actual hooking mortality for blue sharks in the Canadian fishery could be around 20%. If a similar potential underestimation of shark condition by fishery observers is also occurring in the Portuguese fishery, then it is expected that, at least for the blue shark, our assessment of hooking mortality may be underestimated. Additionally, we only considered the short-term hooking mortality that resulted from the actual fishing process. Some specimens may be discarded alive but with severe trauma that may result in long-term post-release mortality, not accounted for in this study. To measure such effects, the deployment of satellite telemetry tags would be needed, as they allow sharks' vertical and horizontal movements to be tracked for weeks or months after they are released. Therefore, the values presented in this paper should be regarded as the minimum mortality values for each taxon caused by the fishing process, and these values may be increased by long-term post-release mortality.

Another factor that needs to be taken into account in hooking mortality studies is the type of hook used by the fishery. The Portuguese swordfish longline fishery traditionally uses J-style hooks, and the values reported in our study therefore refer to that specific type of hook. Other fisheries may use other types of hooks (e.g., circle hooks, tuna hooks, or a combination of different types). For some species, including the blue shark, J-style hooks have already been shown to cause higher hooking mortality rates than circle hooks (Carruthers et al. 2009); however, for the elasmobranch species that are most frequently discarded (e.g., bigeye thresher, crocodile shark, pelagic stingray and manta rays) Coelho et al. (2012b) showed that the hook style (J-style vs. circle hooks) was unrelated to hooking mortality.

The logistic models used in our study seem to be adequate for evaluating the contribution of potential explanatory variables (e.g., sex, region and specimen size) to the mortality odds-ratios, even though the explanatory abilities of the final models are relatively low. For this study, we explored only those three possible explanatory variables, but others could be considered to further explain these hooking mortality rates. One potentially important variable that was not recorded during our study and that may significantly affect hooking mortality is the time that each specimen spent on the longline after capture (period between being hooked and being retrieved by the vessel crew). To analyse the contribution of such a variable, it would be necessary to deploy hook timers, as did Morgan and Carlson (2010) for the US bottom longline fishery. These authors concluded that the time the sharks spent on the bottom longline contributed significantly to explaining part of the hooking mortality, with positive relationships established for sandbar (*Carcharhinus plumbeus*), blacktip (*Carcharhinus limbatus*) and blacknose sharks (*Carcharhinus acronotus*). Before that study, Morgan and Burgess (2007), studying the bottom longline fishery, and Diaz and Serafy (2005), studying the pelagic longline fishery, had already shown positive relationships between fishing gear soak time and hooking mortality.

In our study, it was interesting to note that for the blue shark and shortfin mako there were decreasing odds of hooking mortality with increasing specimen size, meaning that the odds of a specimen surviving after being hooked were higher for larger specimens. At least for the blue shark, some previous studies had reached similar conclusions, including Campana et al. (2009) and Diaz and Serafy (2005).

The sex of the specimens and region of operation of the fishery also showed significant differences between the observed vs. expected proportions of dead vs. alive specimens for some of the species analysed. In blue shark, the odds of a male blue shark dying while hooked were higher than the odds for a female. However, in this case, it is possible that there could have been a confounding effect between sex and size, as significant differences were detected in the size distributions of male and female blue sharks. In the crocodile shark, in contrast, while males also showed significantly higher odds-ratios of dying compared with the females, no significant differences were detected in the size distribution between sexes.

Several conservation and fisheries management options have been put forward, which include the mandatory release and prohibition of retention of particular vulnerable bycatch species. It is important to assess the impact of such measures by analysing what component of the bycatch are being captured and discarded dead. Current ICCAT management recommendations request mandatory discards of all bigeye threshers, hammerheads, oceanic whitetips and silky sharks. According to the results presented in this paper, it is possible to infer that, on average, at least 34% of the oceanic whitetip, 51% of the bigeye threshers, 56% of the silky sharks and 71% of the smooth hammerheads are being captured and discarded dead, meaning that even though the specimens are not retained, fishing mortality is still taking place at very high levels. Discarding practices need therefore to be assessed at a species-specific level. In the particular case of this fishery, such measures seem to be largely inefficient for some of the species (e.g., smooth hammerhead), but seem to be more efficient, for example, for the oceanic whitetip, where a higher proportion of the specimens captured and discarded alive.

This paper presents important new information on the impacts of this longline fishery on pelagic elasmobranch populations. These results can now be incorporated into future stock assessment models, including ecological risk assessment analysis. They also provide some insights on the efficiency of the recent ICCAT recommendations for mandatory discards of some elasmobranch species.

II.5. Acknowledgments

Data and samples were collected within the scope of the EU Data Collection Framework, Project SELECT-PAL (PROMAR 31-03-05-FEP-1) and Project THRESHER (FCT PTDC/MAR/109915/2009). The authors are grateful to the fishery observers S. Amorim, S. Goes, J. Regala, I. Ribeiro, F. Leitão and M. Cerqueira for collecting the onboard data, and to the crews of the fishing vessels for assisting the observers during data collection. J. Fernandez-Carvalho received a grant from FCT (Ref: BD 60624 /2009). R. Coelho was supported by a grant from FCT (Ref: BPD 40523 / 2007), co-funded by “POCI-2010, Programa Operacional Ciência e Inovação 2010” and “FSE, Fundo Social Europeu”.

CHAPTER III. TESTING THE EFFECTS OF HOOK STYLES AND BAIT TYPES ON FISH CATCHES IN A PELAGIC LONGLINE FISHERY IN THE NORTHEAST ATLANTIC[2]

III.1. Introduction

Over the last decades the unintentional capture of non-targeted species, known as "bycatch", has become a major issue in global fisheries management and conservation, with special concern for the accidental capture of vulnerable marine megafauna such as marine mammals, sea birds and sea turtles (Soykan et al. 2008). Although, pelagic longlines are considered more selective when compared to other fishing gears like trawls or gillnets (Gilman et al. 2006), there is considerable concern over the ecological effects of pelagic longline fishing, which is carried out throughout tropical and temperate regions of the world's oceans (Gilman et al. 2012, Lewison et al. 2004). Pelagic longlines consist of a series of baited hooks attached to a mainline that is suspended from floating buoys, that are deployed in daily operations to catch large tuna (*Thunnus* spp.) and billfishes (Istiophoridae and Xiiphidae). Since the late 1990's there has been an increasing retention of sharks in pelagic longline fisheries, mostly due to changes in the markets and restrictions on the catches of traditional target species. Currently the industry is making use of a wider range of shark products, such as fins, meat, liver and skin. As a result, some changes in the traditional fishing gear configuration have been observed, namely the use of multifilament wire leaders. Such fishing gear configuration is used in particular areas and/or seasons where the abundance of sharks is high, such as in the tropical northeastern Atlantic region.

In order to mitigate the incidental capture of sea turtles (and other vulnerable bycatch species) in fisheries, several measures have been proposed or implemented over the last years in different fleets worldwide. Some of the most common strategies to reduce this bycatch involve gear modifications such as changes in hook style and/or bait type, although time/area closures, limitation of fishing effort and fishery bans have been proposed as well. Particular attention has been given to the use of circle hooks, a hook with the point turned perpendicularly back towards the shank, as a means to reduce

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[2] ***Based on the manuscript***: Fernandez-Carvalho J, Coelho R, Santos MN, Amorim S. *In press*. Effects of hook and bait in a tropical northeast Atlantic pelagic longline fishery: Part II – target, bycatch and discard fishes. Fish. Res.

bycatch and mortality (see reviews by Read 2007, Serafy et al. 2012, Wallace et al. 2010). However, several authors have mentioned that the efficiency of such gear modifications is not only taxon-specific, but also depends on the specificities of the fleets and fisheries (e.g. Gilman et al. 2008, Read 2007), and as such thorough experimental studies should be developed and implemented to test the efficiency of such gear modifications in each particular fishery (Gilman et al. 2012).

The Portuguese pelagic longline fishery targeting swordfish in the Atlantic Ocean began in the 1970s, with only minor changes being incorporated in the last decade. Namely, in the late 1990s fisherman transitioned to the “modern gear” using mainlines and branch lines of monofilament, and lightsticks or flashlights while the gear is left fishing during the night (Watson and Kerstetter 2006). Currently, “J hooks baited with squid” is the more common combination used by the fishery, though when pelagic sharks are a major component of the catch multifilament wire leaders and mackerel bait might be used instead.

Often bycatch mitigation studies have focused on the ability of particular measures to reduce mortality of the species of concern, such as marine turtles accidentally caught by pelagic longlines (Cambiè et al. 2012, Santos et al. 2012, 2013b, Stokes et al. 2012). However, a more holistic approach is emerging with the broadening of studies to include the effects of such mitigation measures on the catches of target and non-target species, and on the economical aspects of the fisheries (Coelho et al. 2012b, Curran and Bigelow 2011, Foster et al. 2012, Graves et al. 2012). To the author’s best knowledge, the present study is the first carried out in the tropical north-eastern Atlantic area, which in recent years became a major fishing ground for the European pelagic longline fleets (i.e. Spanish and Portuguese). The study was designed to test the influence of different hook styles and bait type combinations on the catches of target and non-target fish species in the Portuguese pelagic longline fishery operating in the tropical north-eastern Atlantic. It complements a previous paper that used the same experimental design and the same geographical region but was focused on the sea turtles (Coelho et al. In press). Specifically, the effects of two circle hooks were compared to the traditional J-style hook, and the effect of using mackerel was compared to using the traditional squid. The study reports the catch composition, and addresses the issues of catch rates and hooking mortality on target, non-target and fish discards from this fishery. Moreover, it includes analyses of the financial impact (value per unit of effort) for the different hook style and bait type combinations tested.

III.2. Material and Methods

III.2.1. *Experimental design and data collection*

A total of 202 experimental longline fishing sets, corresponding to 254,520 deployed hooks (42,420 with each hook/bait combination), were carried out in the tropical northeast Atlantic (Figure III.1), between August 2008 and December 2011. The experimental fishing was carried out by a commercial Portuguese longline vessel hired to carry out the experiments, following the general practices of the European longline fleet in this area. Therefore, most of the fishing experiments occurred between October and January, as this is the period when the longline fleet is most active in the area. Gear deployment started at around 17:00 hr and haulback the next day from about 06:00 hr, with the gear fishing mostly at depths between 20-50 m. The fishing gear consisted of a standard monofilament polyamide mainline of 3.6 mm diameter (~55 nm long), with five branch lines between floats. Each branch line had two sections connected by a 5 cm swivel (60 g): the first section of approximately 11 m long, consisting of two monofilaments portions of 9 m long (ø 2.5 mm) and 2.2 m (ø 2.2 mm), connected by a swivel; the second section, corresponding to the terminal tackle, consisting of a 0.75 m long multifilament wire leader (ø 1.4 mm) with a hook. A battery-powered flashlight (green light) was attached to each leader.

Three different stainless steel hook styles (produced by WON YANG) were used in each longline set. The control of the experiment corresponded to the traditional J hook typically used by the fleet (EC-9/0-R), and the treatments corresponded to: G style hook, a non-offset circle hook (H17/0-M-S); and Gt style hook, a 10º offset circle hook (H17/0-M-R). The characteristics and a photograph of the different hooks are summarized in Figure III.2. Hook styles were alternated section by section of the longline, with each section containing between 70-80 hooks, to minimize the potential for confounding effects specific to a set (e.g. location, water temperature, turtle density, or other factors). Moreover, the hook style of the first section in the water changed every set following a fixed scheme (i.e., J:G:GT:J:G:GT, and so on).

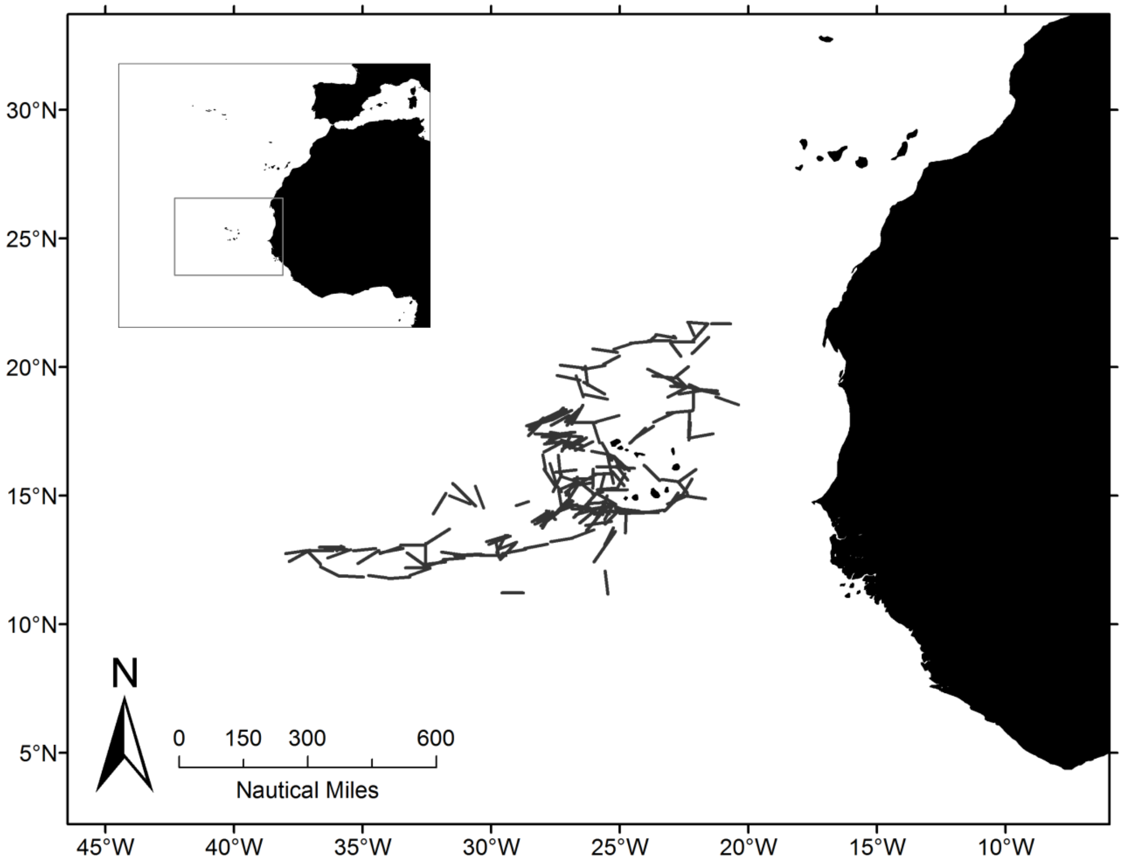

Figure III.1 Location of the experimental pelagic longline sets carried out during this study in the tropical northeast Atlantic.

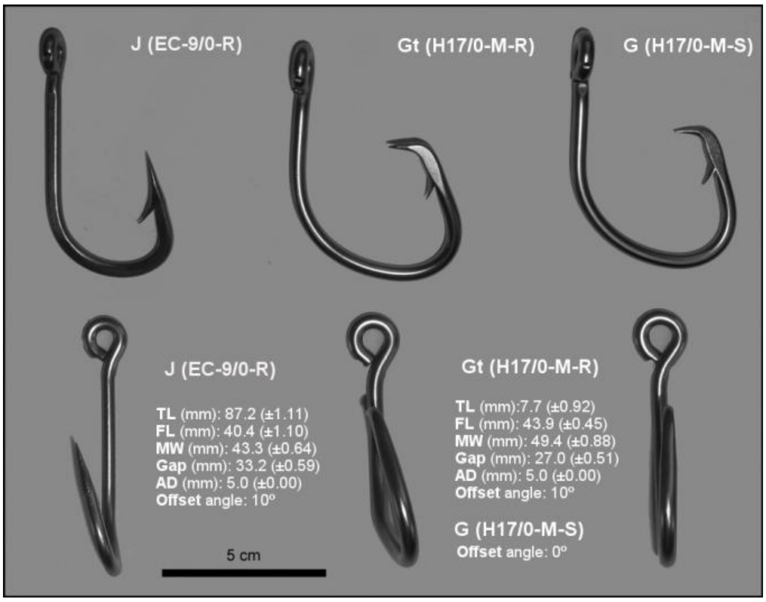

Figure III.2: Photograph of the three hook styles used during this study (J-hook with 10° offset; Gt circle hook with 10° offset; and G circle hook without offset), and their respective measurements. Standard deviation is indicated between parentheses. TL= Total length; FL= Front length; MW= Maximum width; AD= Arm diameter.

Two different bait types were used in the experiment, namely mackerel (*Scomber* spp.) and squid (*Illex* spp.). However, only one bait was used in each set to avoid possible interaction effects, as suggested by Watson et al. (2005). Standardized bait sizes was used in all longline sets (squid 27.8±0.97 cm and mackerel 35.1±1.19 cm).

All operational and biological data were collected by onboard fishery observers. For each set, information on location, date, and number of hooks of each style and bait type used was recorded. In addition, for every fish captured, the species, fork length (FL) to the nearest cm, hook style and bait type used for capture, condition at-haulback (alive /dead), specimen's fate (retained /discarded) and its condition if discarded (alive /dead) was recorded.

Three categories were established for the captured fish species: target, bycatch and discards. In the study area the fleet is currently using mainly multifilament wire leaders, and therefore we considered that the main target species were swordfish (*Xiphias gladius*), blue shark (*Prionace glauca*) and shortfin mako (*Isurus oxyrinchus*), whereas species that are usually considered minor target species in the pelagic longline fishery, such as bigeye tuna (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*), were classified as bycatch. Likewise, other billfishes and other large pelagic sharks, such as the longfin mako (*Isurus paucus*), were also considered bycatch. Finally, all the species that were accidentally caught but not retained were considered discards and included mostly species of teleosts and elasmobranchs with low commercial value, and large elasmobranch species whose retention is currently forbidden by ICCAT, the International Commission for the Conservation of Atlantic Tunas (e.g. bigeye thresher (*Alopias superciliosus*), hammerhead sharks (*Sphyrna* spp.), oceanic whitetip (*Carcharhinus longimanus*) and silky shark (*Carcharhinus falciformis*).

III.2.2.*Data analysis*

For the target and bycatch species, the catch per unit of effort (CPUE) was estimated in weight (kg) per 1000 hooks, using conversion equations, as the retained catches were processed and frozen onboard and weighing was difficult. For swordfish and tunas these were calculated using the ICCAT conversion equations. However, in the case of remaining species, conversion equations from the Portuguese Institute for the Sea and Atmosphere (IPMA, unpubl. data) were used. For the discarded species, however, the bycatch per unit of effort (BPUE) was estimated using the number of specimens (n/1000 hooks) instead of biomass, as those specimens were usually discarded before being hauled onboard. Both CPUEs and BPUEs were calculated for each species and each fishing set, including the sets with zero catches, and for each hook/bait combination. Mean CPUEs and BPUEs, and their respective standard deviations were calculated for each combination using those values. The VPUE, defined as the total retained catch value per unit effort, was also calculated for each hook style and bait type combination. This value was calculated as the value in Euros per 1000 hooks, using as a reference the values in the Vigo (Spain) market during December 2010 for frozen products (first sale).

Kolmogorov-Smirnov tests with Lilliefors correction (Lilliefors 1969) were used for testing the CPUEs and VPUEs for normality, while Levene tests were used for testing the homogeneity of variances. Due to the lack of normality and homogeneity of variances, the differences between hook styles and bait types were tested with non-parametric Kruskal-Wallis and Mann-Whitney tests, respectively. Further, randomization tests were also used to test if the observed differences between different hook-styles and bait types were significant or if they were occurring due to randomness in the sampling (Manly 2007). For this, a Monte Carlo approach was used with the data randomized and resampled 9,999 times to build the expected distribution of the differences under a random distribution, which was then compared and used to determine the significance of the differences observed in the sample.

Generalized Linear Models (GLMs) for the response variables CPUE and BPUE were also applied using bait type and hook style as explanatory variables, with models built for the swordfish (main target species), blue shark (most captured species) and bigeye thresher (most captured discard species). Because of the continuous nature of the CPUE and BPUE data, and the existence of some fishing sets with zero catches, a Tweedie distribution with a log link function was used, as previously used by some other authors (e.g. Coelho et al. 2012b). The baseline reference levels for the explanatory variables were those commonly used by the fleet, namely J style hooks baited with squid, and the other levels of the variables were compared against this combination. Given that the log link function was used, the odds ratios for model interpretation were calculated as the exponential values of the estimated parameters.

For the three targeted species (swordfish, blue shark and shortfin mako) and the two most abundant bycatch species (bigeye tuna and yellowfin tuna), the mean FL and respective standard deviations were calculated for every hook/bait combination. The size distribution was compared between the three hook styles and the two bait types with non-parametric Kruskal-Wallis and Mann-Whitney tests, respectively. For the four more frequently captured species that are commonly discarded, the proportions of alive and dead individuals at time of fishing gear retrieval (at-haulback) was calculated for every hook/bait combination. These proportions were analysed with contingency tables and tested with Chi-square proportion tests.

Data analysis for this paper was carried out using the R Project for Statistical Computing version 3.0.0 (R Core Team 2013). Most analyses used functions available in the core R program, and exceptions were the Levene test to compare homogeneity of variances using library “car” (Fox and Weisberg 2011), the GLM fitting using the Tweedie distribution using functions available in library “tweedie” (Dunn 2010), the permutation tests that were carried out using library “perm” (Fay and Shaw 2010), and some plots that were built using ggplot2 (Wickham 2009).

III.3. Results

III.3.1. *Description of the catches*

A total of 16 taxa were retained in the experiments, with the swordfish, the blue shark and the shortfin mako representing 8.7%, 84.9% and 2.3% of the total weight, respectively (Table III.1). From the remaining 13 bycatch taxa, the tropical tunas were the most captured species, with bigeye and yellowfin tuna representing 1.4% and 1.2% of the total weight, respectively. In addition, 16 taxa were captured and discarded, specifically five species of teleosts and 11 of elasmobranchs. The discarded species with highest catch rates in number were the bigeye thresher shark, followed by the crocodile shark (*Pseudocarcharias kamoharai*) (Table III.2).

The frequency of occurrence varied greatly among species, with the blue shark (present in 100% of the sets) being the most frequently-caught species, followed closely by swordfish (97.1%), shortfin mako (61.9%) and at a much lower frequency by bigeye tuna (32.2%) and yellowfin tuna (13.4%).

III.3.2.*Effects of hook and bait on retained catch*

The effects of the hook style and bait type in the catch rates was taxon specific, with the swordfish being the only species whose catches had significant differences when comparing both bait types and hook styles (Table III.1). The combination of J-style hook baited with squid showed the highest CPUE for the swordfish (486.8 kg/1000 hooks), with significantly lower values obtained with other hook/bait combinations (Table III.1, Figure III.3). For the yellowfin tuna and the escolar (*Lepidocybium flavobrunneum*) only the bait type had a significant effect with catches decreasing when using mackerel instead of squid. On the other hand, the catches of the white marlin (*Kajikia albida*) were significantly lower when using squid instead of mackerel. With regards to the elasmobranchs, the hook style had a significant effect in the catch rates of the longfin mako (*Isurus paucus*), with lower catches obtained with circle (Gt-style) hooks (Table III.1). When considering the overall bycatch rate, only squid bait had a significant effect, providing the highest catch rates. In terms of the overall VPUE of the total retained catch, no significant differences were detected between either bait type or hook style (Table III.1).

Table III.1. Mean CPUE (kg/1000 hooks) and VPUE (€/1000 hooks) with respective standard deviation between parentheses, for the various hook-bait combinations. P-values from non-parametric tests refer to Mann-Whitney tests to compare bait types and Kruskal-Wallis tests to compare hook styles (*: sig. at the 10% level; **: sig. at the 5% level; ***: sig. at the 1% level).

Species	Squid			Mackerel			Non-parametric tests (*p-values*)		Permutation tests (*p-values*)	
	J	G	Gt	J	G	Gt	Bait	Hook	Bait	Hook
P. glauca	3131.4 (± 2166.3)	3345.3 (± 2349.9)	3007.1 (± 1824.2)	3242.6 (± 2158.6)	3358.6 (± 2197.2)	3167.1 (± 1885.8)	0.49	0.39	0.60	0.43
X. gladius	486.8 (± 446.8)	319.3 (± 467.5)	366.1 (± 345.7)	285.7 (± 282.5)	242.9 (± 351.5)	271.5 (± 355.1)	<0.01***	<0.01***	<0.01***	0.02**
I. oxyrinchus	82.8 (± 157.2)	80.4 (± 145.4)	89.3 (± 174.1)	91.4 (± 205.0)	76.3 (± 168.8)	97.1 (± 229.7)	0.52	0.87	0.72	0.70
Total targeted fishes	3701.0 (± 2353.0)	3745.1 (± 2638.3)	3462.6 (± 1879.7)	3619.8 (± 2247.5)	3677.9 (± 2407.3)	3535.7 (± 1907.0)	0.92	0.77	0.86	0.60
T. albacares	81.2 (± 342.3)	63.0 (± 236.9)	55.7 (± 240.1)	33.2 (± 148.0)	20.5 (± 84.2)	28.9 (± 149.0)	0.54	0.86	0.04**	0.73
T. obesus	62.5 (± 176.4)	57.9 (± 297.3)	46.1 (± 168.8)	54.1 (± 150.4)	42.1 (± 134.1)	49.6 (± 150.3)	0.36	0.33	0.65	0.85
M. nigricans	26.8 (± 125.9)	16.9 (± 139.7)	23.0 (± 119.6)	18.5 (± 75.5)	20.2 (± 92.7)	22.5 (± 100.1)	0.22	0.54	0.88	0.92
L. flavobrunneum	13.2 (± 44.2)	17.1 (± 57.0)	16.8 (±50.8)	7.4 (± 25.0)	5.8 (± 22.1)	12.4 (± 38.7)	0.43	0.96	0.03**	0.59
I. paucus	9.2 (± 46.6)	11.4 (± 60.2)	4.8 (± 34.9)	16.5 (± 68.1)	12.7 (± 69.3)	3.82 (± 27.1)	0.55	0.03**	0.61	0.21
C. hippurus	8.2 (± 25.8)	7.4 (± 19.3)	5.3 (± 18.0)	6.6 (± 16.9)	4.0 (± 14.0)	4.9 (± 16.8)	0.40	0.24	0.24	0.43
K. albida	2.3 (± 14.8)	2.1 (± 14.9)	0	4.9 (± 22.7)	2.1 (± 12.7)	4.8 (± 26.0)	0.06*	0.31	0.08*	0.65
I. platypterus	3.5 (± 25.6)	0.4 (± 3.6)	0	0	0.4 (± 4.3)	0.6 (± 5.6)	0.82	0.65	0.41	0.36
T. alalunga	1.7 (± 13.5)	1.3 (± 13.0)	0	0	0.9 (± 9.3)	0	0.32	0.37	0.42	0.48
R. pretiosus	0.6 (± 5.5)	1.1 (± 8.1)	0	0.3 (± 2.8)	0.7 (± 5.0)	0.6 (± 4.9)	0.74	0.71	0.88	0.50
Sphyraena sp.	0	0.7 (± 7.3)	0	0	0.9 (± 8.6)	0.6 (± 4.6)	0.32	0.37	0.59	0.28
A. solandri	0.3 (± 3.1)	0	0	0.2 (± 1.7)	0	0.4 (± 4.2)	1.00	0.17	0.75	0.58
K. pelamis	0	0.3 (± 2.7)	0	0	0.3 (± 2.7)	0	1.00	0.13	1.00	0.33
Total bycatch	209.8 (± 450.8)	179.8 (± 400.3)	151.9 (± 334.1)	141.8 (± 238.6)	110.6 (± 209.1)	129.3 (± 224.1)	0.68	0.40	0.04**	0.48
Total retained catch	3910.8 (± 2462.1)	3925 (± 2719.8)	3614.5 (± 1904.7)	3761.7 (± 2251.5)	3788.6 (± 2419)	3665.1 (± 1981.6)	0.77	0.70	0.64	0.55
VPUE of retained catch	7182.7 (± 4338.8)	6718.5 (± 4957.0)	6393.4 (± 3179.4)	6339.7 (± 3519.1)	6224.8 (± 4103.7)	6181.5 (± 3263.4)	0.14	0.72	0.10	0.46

Table III.2. Mean BPUE (n/1000 hooks) of discarded species for the various hook-bait combinations. Standard deviation is indicated between parentheses. P-values from non-parametric tests refer to Mann-Whitney tests to compare baits and Kruskal-Wallis tests to compare hooks (*: sig. at the 10% level; **: sig. at the 5% level; ***: sig. at the 1% level).

Species	Squid			Mackerel			Non-parametric tests (*p-values*)		Permutation tests (*p-values*)	
	J	G	Gt	J	G	Gt	Bait	Hook	Bait	Hook
A. ferox	0.11 (± 0.70)	0.16 (± 0.96)	0.04 (± 0.47)	0.09 (± 0.57)	0.04 (± 0.47)	0.25 (± 1.34)	0.79	0.83	0.79	0.83
M. mola	0.18 (± 1.10)	0.04 (± 0.47)	0.02 (± 0.23)	0.30 (± 1.53)	0.04 (± 0.47)	0.02 (± 0.23)	0.56	0.04**	0.66	<0.01***
T. asper	0.04 (± 0.47)	0	0.04 (± 0.47)	0.18 (± 0.87)	0	0.11 (± 0.70)	0.06*	0.06*	0.15	0.07*
B. brama	0	0.04 (± 0.47)	0.02 (± 0.23)	0	0.04 (± 0.47)	0.04 (± 0.47)	1.00	0.37	1.00	0.55
G. serpens	0	0	0	0.04 (± 0.33)	0	0	0.16	0.13	0.53	0.32
Total teleosts discards	0.35 (±1.36)	0.25 (±1.16)	0.18 (±0.99)	0.63 (±1.84)	0.14 (±0.81)	0.45 (±1.57)	0.12	0.04 **	0.25	0.08*
A. superciliosus	3.30 (± 6.03)	3.55 (± 7.70)	3.44 (± 5.42)	3.79 (± 6.32)	2.85 (± 4.89)	2.52 (± 4.21)	0.96	0.56	0.41	0.62
P. kamoharai	1.98 (± 4.44)	2.38 (± 5.34)	2.87 (± 5.65)	2.47 (± 5.13)	2.68 (± 4.78)	3.30 (± 7.66)	0.37	0.61	0.35	0.31
S. zygaena	1.01 (± 2.82)	1.22 (± 3.58)	0.82 (± 2.61)	0.89 (± 2.44)	0.40 (± 1.39)	0.49 (± 1.72)	0.22	0.33	0.03**	0.51
C. longimanus	0.58 (± 2.48)	0.25 (± 1.38)	1.46 (± 8.20)	0.44 (± 2.68)	0.37 (± 1.67)	0.58 (± 2.16)	0.52	0.04	0.37	0.13
Myliobatidae	0.04 (± 0.47)	0.23 (± 1.23)	0.14 (± 0.87)	0.28 (± 1.22)	0.21 (± 0.95)	0.18 (± 0.87)	0.10	0.88	0.29	0.79
C. falciformis	0.16 (± 1.17)	0.18 (± 1.15)	0.11 (± 0.70)	0.21 (± 1.17)	0	0.16 (± 0.96)	0.79	0.54	0.81	0.64
G. cuvier	0.07 (± 0.52)	0.33 (± 3.31)	0.18 (± 1.45)	0.09 (± 0.57)	0	0.04 (± 0.33)	0.75	0.23	0.35	1.00
G. galeus	0.11 (± 0.85)	0.02 (± 0.23)	0.28 (± 1.27)	0.04 (± 0.47)	0.07 (± 0.52)	0.14 (± 1.00)	0.28	0.16	0.50	0.07
P. violacea	0.23 (± 1.23)	0	0	0.21 (± 1.30)	0	0	1.00	<0.01***	0.91	<0.01***
S. lewini	0.02 (± 0.23)	0.07 (± 0.71)	0.02 (± 0.23)	0.02 (± 0.23)	0	0.02 (± 0.23)	0.65	0.82	0.72	1.00
G. cirratum	0.02 (± 0.23)	0.02 (± 0.23)	0	0	0	0	0.16	0.61	0.52	1.00
Total elasmob. discards	7.56 (±7.79)	8.29 (±12.2)	9.35 (±12.3)	8.48 (±9.19)	6.60 (±6.80)	7.47 (±8.91)	0.36	0.34	0.26	0.63
Total discards	7.92 (±7.94)	8.55 (±12.4)	9.54 (±12.3)	9.12 (±9.27)	6.74 (±6.97)	7.92 (±8.97)	0.54	0.17	0.34	0.53

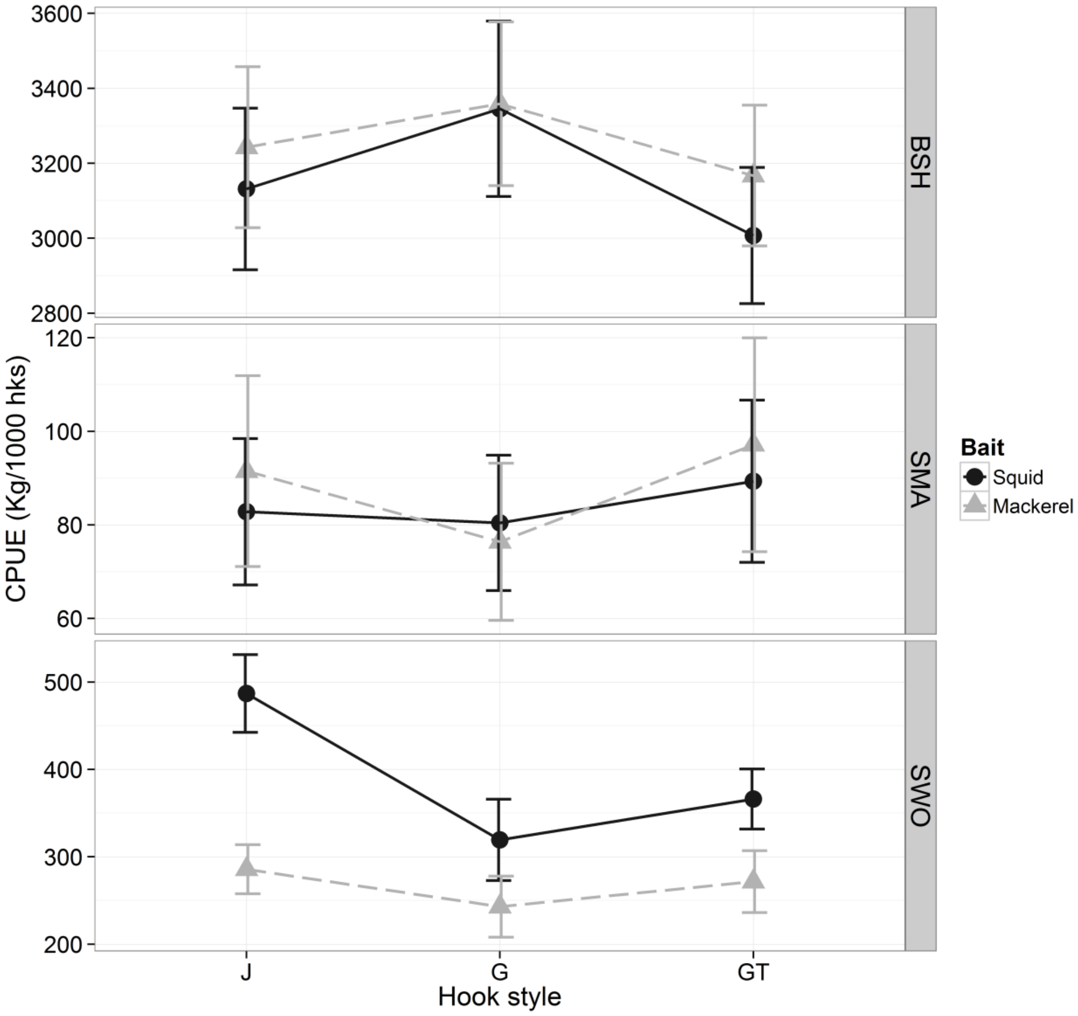

Figure III.3. Catch per unit of effort (CPUE, kg/1000 hooks) with the various hook style and bait type combinations tested in this study, for the three targeted species, namely the swordfish (SWO), blue shark (BSH) and shortfin mako (SMA). The point values refer to the means and the error bars refer to the standard errors

When modeling the swordfish catch rates, both factors (hook-style and bait type) were significant, although the bait seemed to have a stronger influence in the CPUE than the hook style (Table III.3). No significant differences were found between the two offset hooks (J and Gt), but the catch rates with G hooks were significantly lower than with J-style by a factor of 0.73 (95% CI between 0.58 and 0.92), which represents an expected reduction of 27% in the catch rates when changing from J-style to G (95% confidence intervals varying between 7.5% and 41.7%). Regarding the bait type, mackerel presented lower swordfish catches than squid by a factor of 0.69 (95% CI between 0.57 and 0.83), corresponding to a reduction of 31% if using mackerel instead of squid, with 95% confidence intervals varying between 17% and 43.2%. Conversely, no significant effects between hook style and bait type were found when modeling the blue shark catch rates (Table III.3), even though the catches with circle hooks (G) and mackerel tended to be slightly higher (Figure III.3).

Table III.3. Coefficients for the swordfish (*X. gladius*) and blue shark (*P. glauca*) GLM with the odds-ratios, considering the variables hook style and bait type. For the models it is presented the estimated parameters, the standard errors (SE), the Wald Statistic and the respective p-values. The point estimate with the lower and upper 95% confidence intervals (CI) is given for the odds-ratios.

	Model				Odds-ratios		
X. gladius	Estimate	SE	Wald stat.	p-value	Estimate	Lower 95%CI	Upper 95% CI
(intercept)	6.122	0.090	-2.620	< 0.01			
Hook-Style_G	-0.309	0.118	-2.620	< 0.01	0.735	0.583	0.925
Hook-Style_Gt	-0.183	0.115	-1.589	0.112	0.832	0.664	1.044
Bait-Type_mackerel	-0.376	0.097	-3.892	< 0.01	0.686	0.568	0.830
P. glauca							
(intercept)	8.052	0.053	151.143	< 0.01			
Hook-Style_G	0.051	0.065	0.782	0.435	1.052	0.9266	1.194
Hook-Style_Gt	-0.032	0.065	-0.488	0.626	0.969	0.852	1.101
Bait-Type_mackerel	0.030	0.053	0.562	0.574	1.030	0.928	1.143

III.3.3.*Size distribution of retained species*

Some differences were found in the mean size of the target species when changing between the hook styles and bait types, even though the effects were species specific (Table III.4). Only the bait type seemed to affect the mean sizes of swordfish and shortfin mako captured, but with opposite effects, as slightly larger swordfish were captured with squid and slightly larger shortfin makos were caught using mackerel. Conversely, only the hook style affected the mean size of bigeye tuna and yellowfin tuna, with J hook capturing larger specimens of both species. On the other hand, both hook style and bait type affected the mean size of captured blue sharks, with J hooks baited with squid capturing slightly larger specimens.

Table III.4. Mean size (FL, in cm) with the respective standard deviation (between parentheses), for the target species (swordfish, *X. gladius*; blue shark, *P. glauca* and shortfin mako, *I. oxyrinchus*) and the two most captured bycatch species (tropical tunas *T. obesus* and *T. albacores*). P-values refer to the Mann-Whitney tests to compare sizes with different baits and Kruskal-Wallis tests to compare sizes with different hooks (*: sig. at the 10% level; **: sig. at the 5% level; ***: sig. at the 1% level).

	Bait type		Hook style			Comparisons (p-values)	
species	Squid	Mackerel	J	G	Gt	Bait	Hook
X. gladius	131.8 (± 29.1)	120.7 (± 24.6)	126.2 (± 27.6)	127.5 (± 27.8)	127.6 (± 28.0)	<0.01***	0.10
P. glauca	214.4 (± 26.9)	208.1 (± 22.5)	211.0 (± 26.0)	210.7 (± 24.3)	210.8 (± 23.8)	<0.01	<0.01***
I. oxyrinchus	158.8 (± 19.6)	165.7 (± 24.9)	161.9 (± 22.6)	162.8 (± 18.5)	161.5 (± 25.5)	<0.01	0.15
T. obesus	118.0 (± 30.5)	121.0 (± 28.2)	129.9 (± 28.7)	114.9 (± 27.8)	115.7 (± 29.1)	0.80	<0.01***
T. albacares	138.9 (± 31.6)	138.5 (± 23.8)	146.1 (± 26.2)	132.9 (± 36.4)	136.4 (± 23.7)	0.95	<0.01***

III.3.4. *Catch rates and mortality of discarded species*

Even though no significant effects of hook style or bait type were found on the catches of the majority of the discarded species, some exceptions were found. With regards to the elasmobranchs, the pelagic stingray was only captured with J-style hooks, while the oceanic whitetip shark (*Carcharhinus longimanus*) and the tope shark (*Galeorhinus galeus*) had higher catch rates with circle Gt hooks, though very low numbers of the later were caught (Table III.2, Figure III.4). However, this difference was not significant when permutation tests were used. Bait type significantly affected the catches of the smooth hammerhead (*Sphyrna zygaena*) with squid bait resulting in higher catch rates. Also significantly higher catch rates of sunfish (*Mola mola*) were obtained with J-style hooks. Furthermore, no significant effects of hook style neither of bait type were found when modeling the bigeye thresher (*Alopias superciliosus*) catches, the most abundant of the discarded species (Table III.5).

Table III.5. Coefficients for the bigeye thresher (*A. superciliosus*) GLM with the odds-ratios, considering the variables hook style and bait type. For the model it is presented the estimated parameters, the standard errors (SE), the Wald Statistic and the respective p-values. The point estimate with the lower and upper 95% confidence intervals (CI) is given for the odds-ratios.

	Model				Odds-ratios		
Parameter	Estimate	SE	Wald stat.	p-value	Estimate	Lower 95%CI	Upper 95% CI
(intercept)	1.325	0.140	9.481	< 0.01			
Hook-Style_G	-0.103	0.176	-0.585	0.559	0.902	0.640	1.273
Hook-Style_Gt	-0.176	0.179	-0.983	0.326	0.839	0.591	1.191
Bait-Type_mackerel	-0.118	0.146	-0.810	0.418	0.889	0.667	1.183

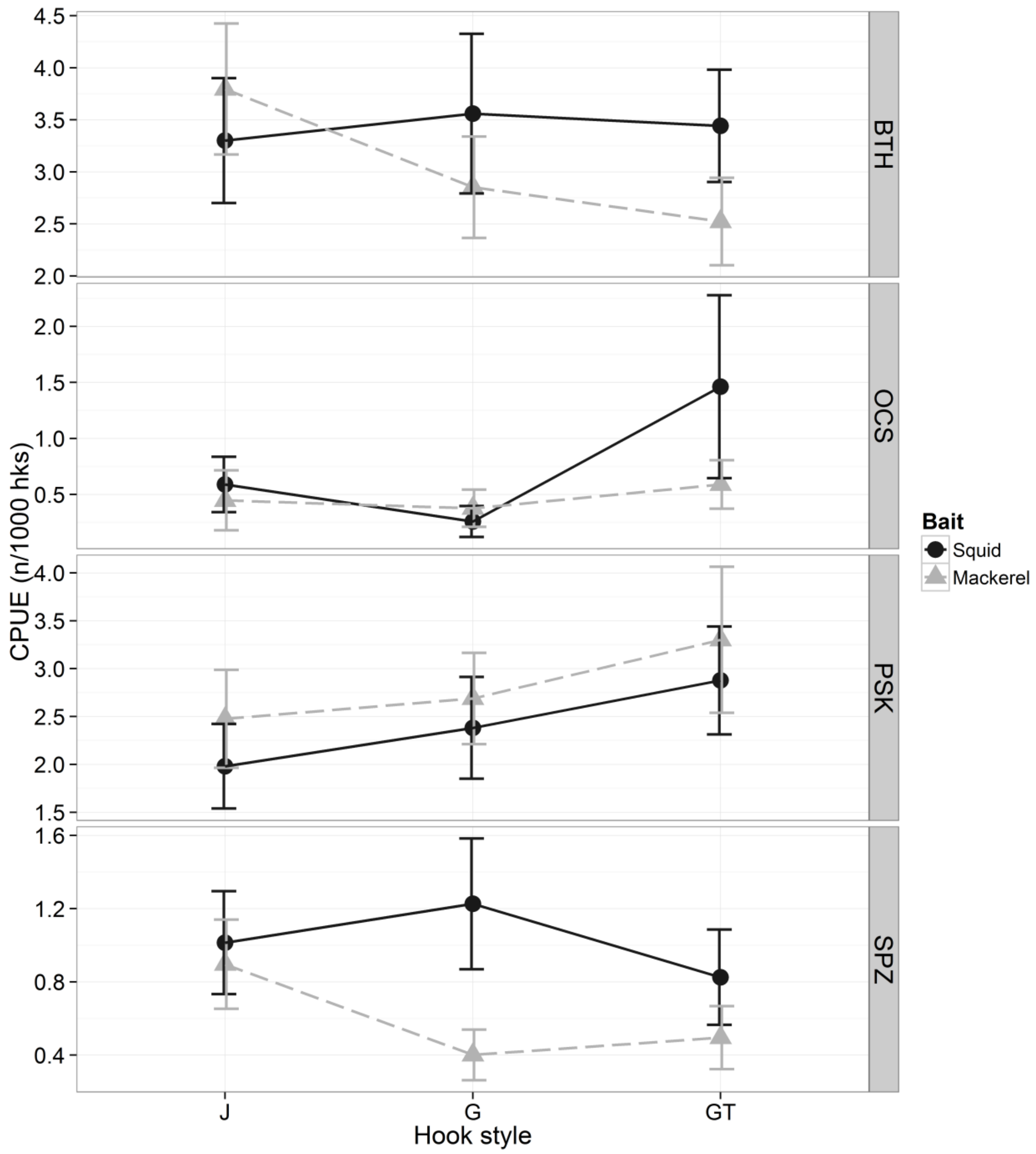

Figure III.4. Catch per unit of effort (CPUE, n/1000 hooks) with the various hook style and bait type combinations tested in this study, for the four most discarded species, namely the bigeye thresher (BTH), oceanic whitetip (OCS), crocodile shark (PSK) and smooth hammerhead (SPZ). The point values refer to the means and the error bars refer to the standard errors.

When comparing at-haulback mortality rates of the four more frequently discarded species, chi-square tests for contingency tables confirmed that no significant differences were occurring between different hook-styles and bait types, except in the case of the bigeye thresher that presented higher mortality when mackerel was used as bait and when circle hooks were used (considering a significance level of 10%) (Table

III.6). Regardless of the hook or bait used, the at-haulback mortality was species-specific, with very different rates between species. The smooth hammerhead presented the highest mortality, which varied from 61 to 64% depending on the hook/bait used, followed by the bigeye thresher with mortality rates varying between 49 to 58%. On the other hand, other elasmobranch species presented much lower at-haulback mortality rates, specifically 11-28% for the oceanic whitetip and 4-8% for the crocodile shark (Table III.6).

Table III.6. Percentage of alive *vs.* dead specimens at-haulback in the four more frequently discarded species: BTH-bigeye thresher shark (A. *superciliosus*), PSK-crocodile shark (*P. kamoharai*), SPZ-smooth hammerhead (*S. zygaena*) and OCS-oceanic whitetip (*C. longimanus*). The statistical comparisons refer to chi-square tests for contingency tables.

Hook/Bait			BTH	PSK	SPZ	OCS
Hook style	J	N	295	190	79	44
		% Dead	49.83	4.74	62.03	22.73
		% Live	50.17	95.26	37.97	77.27
	G	N	272	211	70	27
		% Dead	58.46	8.06	62.86	11.11
		% Live	41.54	91.94	37.14	88.89
	Gt	N	248	263	54	81
		% Dead	49.60	9.13	62.96	28.40
		% Live	50.40	90.87	37.04	71.60
	Comparisons	Chi square	5.55	3.12	0.02	3.38
		p-value	0.06*	0.21	0.99	0.18
Bait	Squid	n	413	339	117	87
		% Dead	48.91	7.08	61.54	20.69
		% Live	51.09	92.92	38.46	79.31
	Mackerel	n	402	325	86	65
		% Dead	56.47	8.00	63.95	27.69
		% Live	43.53	70.46	36.05	72.31
	Comparisons	Chi square	4.67	1.83	0.12	1.01
		p-value	0.03**	0.18	0.73	0.32

III.4. Discussion

To the authors' best knowledge, the present is the first to evaluate the effects of different hook styles and bait types in the species composition, catch rates, size distribution and at-haulback mortality rates of fishes (target, bycatch and discards) in a tropical northeast Atlantic pelagic longline fishery. Coelho et al. (2012b) also compared hook and bait effects on fish catches, including the retained and the discarded species, for the Portuguese pelagic longline fleet operating in a different area, in the Equatorial regio. While in both studies the blue shark and swordfish were the most frequently caught species, the catch rates differed greatly between the two regions. Specifically, Coelho et al. (2012b) reported a much higher CPUE for swordfish and bigeye tuna, while in our study much higher catch rates of blue shark, shortfin mako and other shark species were in general observed.

Other studies comparing hook style and bait type effects have been carried out in other regions of the Atlantic Ocean, such as in the south, equatorial and the northwest regions. In the south Atlantic, Sales et al. (2010) compared 18/0 circle hook with the control 9/0 J-style hook for the south Brazilian pelagic longline fishery and observed significant decreases in the swordfish catches when using circle hooks, similar to what was observed in our study. In contrast, when comparing the same hook styles in northern Brazil, Pacheco et al. (2011) did not find significant differences for swordfish although the swordfish CPUE was slightly lower with circle hooks. In the northwest Atlantic, Foster et al. (2012) compared 18/0–20/0 circle hooks, 10/0 Japanese tuna hooks and standard 9/0 J hooks baited with squid and mackerel, and found that using mackerel bait instead of squid increased catches of swordfish for all hook styles, which is contrary to our findings. On the other hand, when addressing sea turtle bycatch issues in the same region, Watson et al. (2005) concluded that circle hooks baited with mackerel maintained swordfish catches. Also in the northwest Atlantic, Kerstetter and Graves (2006a) compared 9/0 10° offset J hooks with 16/0 0° offset circle hooks for the US coastal pelagic longline fishery, and did not find significant differences between hook styles for most of the species, though in their case circle hooks (as in our study) had lower catches of swordfish. In the Hawaii pelagic longline fishery, however, there was no significant effect of hook design on swordfish standardized catch rates when comparing J, circle and tuna hooks (Gilman et al. 2012).

For the large pelagic sharks, the only significant differences found on our study were the hook style effects on the catches of longfin mako. Although the observed blue shark catch rates tended to be higher when using mackerel, no significant differences were found. Following this trend, Coelho et al. (2012b) also observed significant increases in the catches of blue shark and shortfin mako when using mackerel bait instead of squid. On the other hand, Foster et al. (2012) observed that using mackerel bait instead of squid significantly decreased blue shark catches. Likewise, Watson et al. (2005) reported decreased blue shark catches for mackerel (vs. squid) and increased catches with the use of circle hooks (compared to J-hooks). Similar results were presented by Afonso et al. (2011) with 18/0 circle hooks increasing blue shark CPUEs when compared to 9/0 J hooks, and Sales et al. (2010) who also observed significantly higher catches of blue shark when using circle hooks. In a meta-analysis study, Godin et al. (2012) reported that the combined shark species catchability with circle hooks was slightly higher compared to J-hooks, but statistically not-significant, even though this analysis was highly dependent and sensitive to some specific results included in the meta-analysis.

Although the Cape Verde Archipelago EEZ waters are known for their generally high shark abundance, the fact that our study used wire leaders may account, at least in part, for some of those differences in the catch rates. Although the effects of the leader material on the Portuguese pelagic longline fishery is not yet available, other authors working with other fleets and fisheries have observed higher catches of sharks and blue marlin when using wire leaders, while monofilament leaders seem to catch more bigeye tuna (Ward et al. 2008) and swordfish (Afonso et al. 2012). Mesopelagic species like the bigeye tuna and swordfish have been reported to avoid wire leaders due to their excellent vision, and thus lower catches are obtained when wire leaders are used instead of monofilament (Afonso et al. 2012, Ward et al. 2008). By contrast, for species with sharp teeth like sharks, “bite off” behavior is commonly observed when using monofilament leaders, as the sharks are more able to sever the leader and escape, especially when hooked in the gut rather than in the jaw since in those cases the leader is more exposed to abrasion. As a result, higher catches of sharks may in general be expected when using wire leaders (Ward et al. 2008).

Oceanic pelagic sharks, such as other sharks and rays, typically exhibit low intrinsic rates of population increase due to their slow growth, late maturity and low fecundity, which results in a low capacity to withstand fishing mortality when compared to the earlier-maturity and shorter-lived bony fishes with which they are frequently captured (Dulvy et al. 2008). However, and even though as a group pelagic sharks are considered particularly vulnerable to pelagic longline fisheries, it should be highlighted that there is considerable intrinsic variation in demographic rates among species and populations of pelagic sharks, which renders varying levels of susceptibility to pelagic longline gear between species (Cortés et al. 2010). For example, while the blue shark (*Prionace glauca*) was classified as having an intermediate vulnerability risk of overexploitation (by the pelagic longline fishery) by an ecological risk assessment of pelagic sharks in the Atlantic, the bigeye thresher (*Alopias superciliosus*) was ranked as high-risk by the same assessment (Cortés et al. 2010).

Contrary to the swordfish catches, no significant effects between bait type or hook style were found in the present study for the tropical tunas and the blue marlin, other than the higher catches of yellowfin tuna when using squid, with the J-hooks baited with squid capturing more specimens. In contrast, both Sales et al. (2010) and Pacheco et al. (2011) observed significantly higher catches (higher proportions in the case of Pacheco et al. 2011) of bigeye tuna and albacore when using circle hooks. In the Pacific, standardized catch rates for all tuna species were higher when using circle hooks in the Hawaiian pelagic longline fishery (Gilman et al. 2012). On the other hand, Foster et al. (2012) presented significant decreases when using mackerel bait instead of squid for bigeye tuna and albacore tuna catches for all hook styles.

Thus, and even though there are already several published studies addressing the issue of circle hooks and bait type in pelagic longline fisheries, the discrepancies often found between studies seems to corroborate that the effects of hook and bait modifications appear to vary substantially depending on the species, region, fishery (target species) and fleet. Thus, before implementing possible gear modifications it is crucial to assess such modifications specifically for the fishery and fleet in question (Curran and Bigelow 2011, Gilman et al. 2012, Read 2007, Serafy et al. 2012).

Regarding the size distribution, J hooks captured significantly larger specimens of blue shark, bigeye and yellowfin tuna, even though the actual size differences in value were very low (<10 cm). In contrast, Ward et al. (2009) on Australia and Kerstetter and Graves (2006a) on the northwest Atlantic and Gulf of Mexico both reported that hook style did not seem to affect the size distribution of species captured by pelagic longlines. Regarding bait types, our study showed that the sizes of swordfish, blue shark and shortfin mako differed significantly due to bait types, with smaller blue sharks captured using mackerel bait and smaller shortfin mako captured with squid (again with small differences in size; <13 cm) in particular. For the Equatorial Atlantic, Coelho et al. (2012b) also reported significant bait effects on the sizes of captured blue shark and yellow fin tuna, in both cases with smaller specimens captured when using mackerel bait.

The majority of the discarded species of this fishery were pelagic elasmobranchs which either have very low commercial value (e.g. crocodile shark and pelagic stingray) or are protected by current ICCAT management regulations. The latter case includes the silky (Rec. 2011/07), hammerheads (Rec. 2010/08), bigeye thresher (Rec. 2009/07) and oceanic whitetip (Rec. 2010/07) sharks. Of those currently protected species, only the catches of the smooth hammerhead were affected by the bait type, showing higher catch rates when squid was used. In addition, significant hook effects were detected for the tope shark and the oceanic whitetip shark, which were significantly more captured when circle hooks with offset (Gt) were used, though for the latter this difference was only evident in the non-parametric test and not in the permutation test. Similar findings were presented by Afonso et al. (2011) with circle hooks capturing significantly more oceanic whitetip sharks than J hooks, although the sample size was very small. Conversely, Coelho et al. (2012b) found no differences in catches of this species for either bait type or hook style, while for the silky shark and bigeye thresher the bait type had a significant effect, with mackerel increasing the catches of both species. On the other hand, for the smooth hammerhead, Coelho et al. (2012b) found no hook effects which is similar to our study, although on the other hand the bait type did not affect the catches. Finally, in our study the pelagic stingray was only captured by J hooks, which is similar to Pacheco et al. (2011) that also observed significant higher catches of pelagic stingray with J hooks, but contrary to Coelho et al. (2012b) who for that species only found significant bait effects (with squid increasing the catches) but not hook effects.

When analyzing the vulnerability of the four most discarded species to the fishery, the mortality rates proved to be different between species. Some species such as the crocodile shark and oceanic whitetip presented very low mortality rates while, on the other hand, the bigeye thresher and the smooth hammerhead had mortality rate values higher than 50%, similar to what was observed by Coelho et al. (2012a). Thus, it seems that for the bigeye thresher and the smooth hammerhead current regulations, which mandate their release back to the sea, might not be as effective for their protection as for other species, since the majority of the specimens are captured and discarded already dead. This seems to be particularly problematic if we take into consideration that the bigeye thresher was classified as having the highest vulnerability risk in an ecological risk assessment of pelagic sharks caught in Atlantic pelagic longlines (Cortés et al. 2010). In our study, the only species whose mortality rates were significantly affected by the bait type was the bigeye thresher which showed higher mortality when mackerel was used as bait. In addition, mortalities of these most commonly discarded species were also not affected by the hook style, except for the bigeye thresher that showed a higher mortality rate when the G circle hook was used. Other authors also found that mortality rates seemed in general independent of the hook style used. For example, Coelho et al. (2012b) found no influence of hook style on the mortality rates of the crocodile shark, manta rays or bigeye threshers in the Equatorial Atlantic. Likewise, in the southwestern Atlantic, Afonso et al. (2012) found no significant hook effects on the mortality of any of the species in their study. In the Pacific, Yokota et al. (2006) reported no differences in the mortality of the blue shark when comparing circle with tuna hooks. In Australian waters, Ward et al. (2009) reported equal probabilities of survival between circle and tuna hooks for most species of the fishery, including albacore, yellowfin and bigeye tuna. On the other hand, circle hooks have been sometimes associated with lower mortalities when compared to J hooks. Kerstetter and Graves (2006a) reported that circle hooks reduced at-haulback mortality for a set of bycatch species on the US coastal pelagic longline. On Brazilian pelagic longliners, Afonso et al. (2011) found significantly higher mortalities for blue shark, silky shark and oceanic whitetip when using J hooks (vs. circle hooks). In the Canadian swordfish and tuna longline fishery, Carruthers et al. (2009) presented odds of survival two to five times higher for circle hooks (vs. J hooks) for the pelagic stingray, porbeagle and blue shark. In a meta-analysis study, Godin et al. (2012) reported that circle hooks significantly reduced at-vessel mortality for combined shark species and individually for blue shark. In addition, a few authors have reported lower post release mortalities when using circle hooks due to presenting lower probabilities of deep hooking when compared to J hooks and, as such, preventing the perforation of the internal organs (Campana et al. 2009, Kerstetter and Graves 2006b).

The effects of hook style and bait type on pelagic longline catches have been studied by several authors worldwide in an attempt of find the formula to decrease the capture of vulnerable species (such as turtles and sharks) while maintaining the catches of the target species. In the first part of this work (Coelho et al. In press) the effects of changing hook styles and bait types in terms of the sea turtle catches was addressed, and it was concluded that accidental catches of leatherbacks were significantly reduced when changing from J-style to non offset Gt-style circle hooks, while for the hardshell species both the circle hooks and mackerel bait had significant effects on reducing the bycatches. However, in the present study the only retained species whose catches seemed affected both by the hook style and bait type was the swordfish, with catches decreasing when changing from the traditional J hook baited with squid to the other combinations, which from a management point of view is problematic because swordfish it is the main target species of the fishery. In addition, it may be of concern that some vulnerable sharks such as the oceanic whitetip seem to show higher catches when offset Gt circle hooks were used.

It should be emphasized that in the present study wire leaders were used (as is common practice of the fleet in this region and season), and this factor has been considered by some authors as a possible confounding factor for detecting eventual differences between hook styles for several species, including the sharks (Ward et al. 2008). The high CPUEs presented on this study for most sharks seems to support this, and we could speculate that using monofilament leaders instead of wire leaders might be a more effective measure to reduce the bycatch of vulnerable sharks than changing hook styles and/or bait type, particularly as it would be important to reduce the catches of pelagic sharks such as the shortfin mako and the protected species, as has been recommended by the ICCAT scientific committee. However, a directed study testing leader materials would have to be conducted in order to test this hypothesis for this specific fishery and fleet, including also the effects of the leader material on the targeted (swordfish) and other vulnerable bycatch species (e.g. sea turtles).

It should be highlighted that in terms of VPUE no differences were found for either bait type or hook style, suggesting that such gear modifications would not have major economic impacts for this particular fishery. However, these results should only be regarded as point estimates, as market price fluctuations were not contemplated and bait costs were not considered in the calculation of the VPUE, knowing that mackerel is usually cheaper than squid. Thus, any extrapolation for the fishery should take this into consideration. On the other hand, although the present study showed that the catches of most vulnerable discarded pelagic sharks did not decrease by changing hook style, it was observed in the first part of this study that the catches of sea turtles were significantly reduced by the use of non offset circle hooks and mackerel bait (Coelho et al. In press). Thus, since our results did not indicate that a switch from J-hooks to circle hooks, or from squid to mackerel, would have a significant impact on the overall value of the retained catch, the use of circle hooks baited with mackerel for this particular fleet and region could be beneficial for sea turtle conservation, without affecting the economic viability of the fishery.

III.5. Acknowledgments

This study was carried out within the scope of the SELECT-PAL project (Programa PROMAR Proj. 31-03-05-FEP-1). Thanks are due to the crew of the fishing vessel Príncipe das Marés (PM-1218-C) for their cooperation and commitment during the course of the study. Thanks are also due to the technicians (I. Ribeiro, Francisco Leitão and J. Táta Regala) for collecting the data. During part of this work J. Fernandez-Carvalho was supported by a grant from FCT (Ref: BD 60624/2009). R. Coelho was partially supported by a grant from FCT (Ref: BPD 40523/2007) co-funded by “POCI-2010 Programa Operacional Ciência e Inovação 2010” and “FSE Fundo Social Europeu”.

SECTION 2:

LIFE HISTORY AND POPULATION DYNAMICS

CHAPTER IV. PAN-ATLANTIC DISTRIBUTIONAL AND REPRODUCTIVE ASPECTS OF THE BIGEYE THRESHER (*ALOPIAS SUPERCILIOSUS*) [3]

IV.1. Introduction

The bigeye thresher (*Alopias superciliosus),* is a large epipelagic and mesopelagic species, occurring circumglobally in tropical and subtropical waters of the Atlantic, Indian and Pacific Oceans (Compagno 2001). Together with two other species, it belongs to the Alopiidae family (sea foxes) and Lamniformes order, and is characterized by having a remarkably long caudal fin. Thresher sharks have an aplacental viviparous reproductive mode with oophagy, characterized by the developing embryos being nourished by yolk-filled egg capsules that are continuously produced and deposited in the uteri (Gruber and Compagno 1981, Moreno and Morón 1992, Gilmore 1993, Conrath 2004). Similarly to the common thresher (*Alopias vulpinus*) and pelagic thresher (*Alopias pelagicus*), the litter size of the bigeye thresher is commonly two (rarely four) pups, though they grow more slowly and reach maturity at a later age than the other threshers (Moreno and Morón 1992, Mancini and Amorim 2006, Romero-Caicedo 2007, Smith et al. 2008a). In addition, although the bigeye thresher typically occurs in temperate and tropical waters, they can endure colder water temperatures and linger longer at deeper waters than many other pelagic sharks (Gruber and Compagno 1981, Smith et al. 2008a, See Chapter VI).

Open ocean sharks are one of the least-studied groups of large vertebrates, as the study of wide-ranging and highly migratory fishes that spend most of their lives far from land poses particular difficulties (Pikitch et al. 2008). In the last decade the biological studies and knowledge on life history, genetics, and tagging of these species have been improving. However more research is needed for a better assessment of the impact of fisheries on populations and to facilitate effective management plans for these highly migratory shark species (Camhi et al. 2008a, ICCAT 2013). Due to the shortage of long time series of information (e.g. catches, fishing effort, changes in abundance) on most pelagic shark populations for stock assessment purposes, demographic models are

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[3] ***Based on the manuscript***: Fernandez-Carvalho J, Coelho R, Cortés E, Mejuto J, Domingo A, Yokawa K, Liu KM, García-Cortés B, Forselledo R, Ohshimo S, Ramos-Cartelle AM, Tsai WP, Santos MN. *Submitted*. Pan-Atlantic distributional and reproductive aspects of the bigeye thresher shark (*Alopias superciliosus*). Rev. Fish Biol. Fish.

often chosen to provide initial information and prioritize species for research (Simpfendorfer 2004). Demographic models rely primarily on life history parameters (e.g. age of sexual maturity, maximum reproductive age, instantaneous rate of natural mortality), thus obtaining this type of biologic data should be essential to estimate species vulnerability to the fisheries and also important for stock assessments (Camhi et al. 2008b, Cortés et al. 2010).

Despite being caught as bycatch in pelagic fisheries, little biological information is available for the bigeye thresher in the Atlantic, probably because of the relatively low prevalence observed in surface longline catches (Mejuto and Garcés 1984, Mejuto 1985, Castro et al. 2000, Berrondo et al. 2007, Mejuto et al. 2009), which has been estimated at around 0.2% of the total shark bycatches combined for the Atlantic (Mejuto et al. 2009). The only extensive reproductive study available for the species is from the Pacific Ocean (Chen et al. 1997), although some reproductive parameters have been reported from the Atlantic (Stillwell and Casey 1976, Gruber and Compagno 1981, Moreno and Morón 1992, Gilmore 1993, Amorim et al. 1998) but using limited datasets.

When reviewing the demography of pelagic shark species, several authors ranked the bigeye thresher among the least productive species, highlighting its vulnerability to fisheries impacts (Chen and Yuan 2006, Cortés 2008, Smith et al. 2008b). In addition, an Ecological Risk Assessment (ERA) of pelagic sharks caught in Atlantic pelagic longlines placed the bigeye thresher at high risk, highlighting the urgent need for better basic biological information on this species (Cortés et al. 2010). The International Commission for the Conservation of Atlantic Tunas (ICCAT), responsible for the management of this species in the Atlantic, recently prohibited the retention and commercialization of bigeye thresher sharks caught in the fisheries it manages, recommended the release of live specimens when accidentally captured, and required that both incidental catches and live releases be recorded in accordance with ICCAT data reporting requirements (ICCAT Rec. 2009/07). Despite this, as shown by Coelho et al. (2012a), the hooking mortality of the retained specimens from this species may be high (around 51%) in pelagic surface longline fisheries, and simply releasing the caught specimens may not be the most adequate conservation strategy, as the majority of specimens are captured and discarded already dead. However, it is possible that these high at-haulback mortalities are caused by other factors, such as gear configuration including length and material of branch line, main line, and shortening ratio. The IUCN Shark Specialist Group classifies the bigeye thresher as “Vulnerable in global terms” (according to the IUCN Red List Criteria) and “Endangered” in the northwest Atlantic and western central Atlantic (Amorim et al. 2009).

In order to improve the limited information available for this species in the Atlantic, the main objectives of this study were to provide information on 1) the distributional patterns of the bigeye thresher shark caught by pelagic longlines targeting tunas or swordfish in the Atlantic Ocean, particularly in terms of sizes, sex-ratios and proportions of juveniles and adult specimens and 2) the reproductive aspects, particularly in terms of median size at maturity and litter size. The results can be used to better evaluate the status and manage this species in the Atlantic Ocean.

IV.2. Material and Methods

IV.2.1. *Data collection*

Bigeye thresher shark records and observations were registered within the scope of National or scientific observer programs. The fishery observers from IPMA (*Portuguese Institute for the Ocean and Atmosphere*), NOAA/NMFS (*National Marine Fisheries Service*), DINARA (*Dirección Nacional de Recursos Acuáticos*), NRIFSF (*National Research Institute of Far Seas Fisheries*), Taiwan Fisheries Agency, and scientific projects of IEO (*Instituto Español de Oceanografía*), collected the data onboard Portuguese, US, Uruguayan, Japanese, Taiwanese and Spanish commercial longline vessels targeting tunas or swordfish in the Atlantic Ocean, respectively. Data on bigeye thresher shark sizes by sex was available starting in 1992, 1993, 1997, 2003, 2003 and 2004 for the US, Spanish, Japanese, Portuguese, Uruguayan and Taiwanese fleets, respectively. US and Uruguayan data were available up to 2010, Portuguese, Japanese and Taiwanese data up to 2012, and Spanish up to 2013. The spatial effort distribution for those fleets was expressed as the total number of hooks by 5º x 5º resolution grids using the ICCAT effort distribution (EffDIS) database (Palma and Gallego 2010). Only the years for which bigeye thresher shark data was available for each fleet were considered, noting that the current ICCAT EffDIS database only has data until 2009.

Data were collected along a wide geographical range. For analysis purposes, the two hemispheres were separated based on the 5ºN parallel, as recommended in the ICCAT Manual for shark species (ICCAT 2006-2009). Furthermore, the region was divided into six major areas taking into consideration not only the ICCAT sampling areas for sharks (ICCAT 2006-2009), but also the areas of operation and fishing grounds of these pelagic longline fleets in the Atlantic Ocean. These areas were assigned as follows: Northwest – above 24º N and west of 40ºW; Northeast - above 24ºN and east of 40ºW; Tropical North – between 5º N and 24º N; Equatorial – between 5º N and 5º S; Southwest – below 5º S and west of 20ºW; Southeast – below 5º S and east of 20ºW (Figure IV.1).

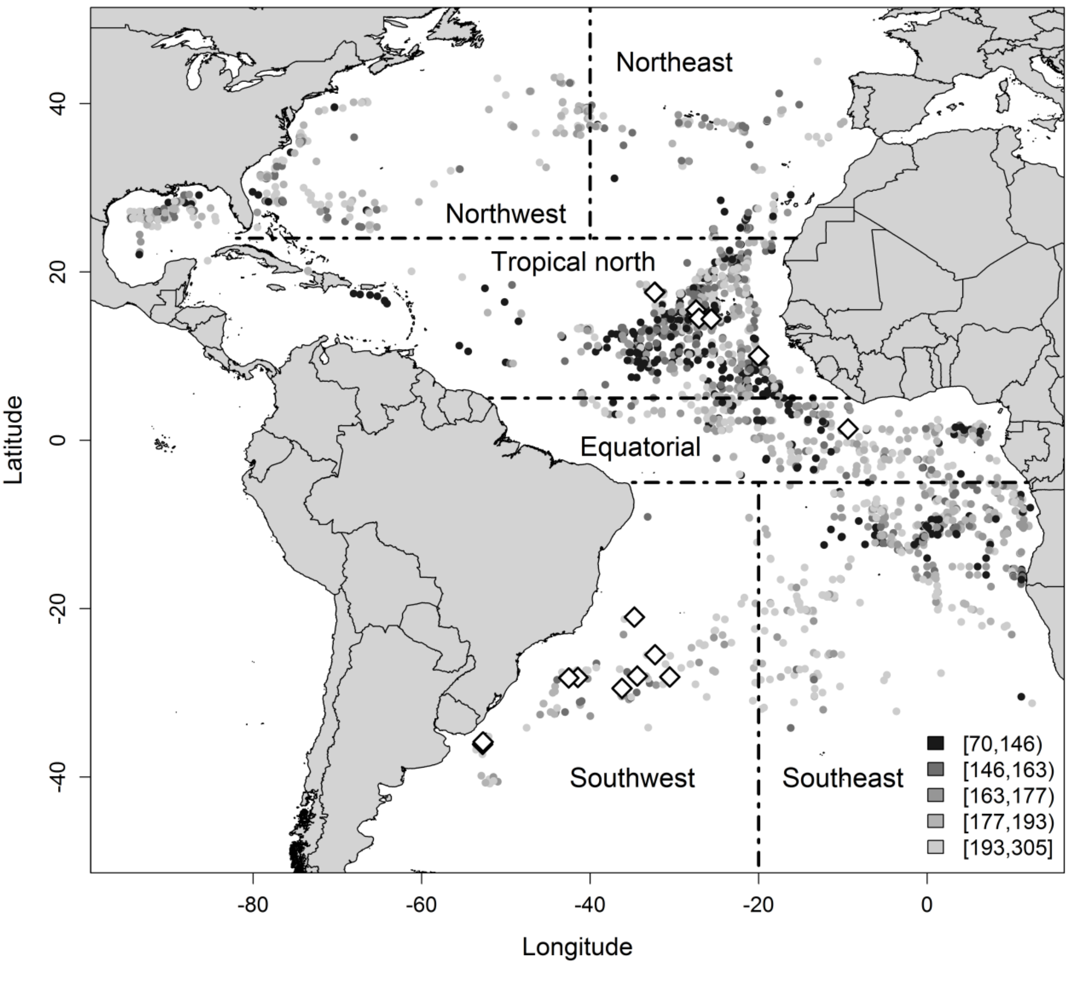

Figure IV.1: Location and sizes (FL, cm) of the bigeye thresher shark (*Alopias superciliosus*) recorded in the six sampling regions of this study. The gray scale of the dots represents specimen sizes, with darker colors representing smaller specimens and lighter colors larger specimens. The categorization of size classes for the map was carried out using the 20% percentiles of the size data. The location of pregnant females recorded by the Spanish, Portuguese and Uruguayan fleets during this study is represented with lozenge symbols.

For the captured specimens, fishery observers recorded data on specimen size, sex, capture location and date. Additionally, in the Portuguese program, maturity stage was also assessed and recorded whenever a dead specimen was captured while retrieving the longline, and in the Spanish, Portuguese and Uruguayan fleets data the observers recorded, when possible, the presence of pregnant females with the respective characteristics of the embryos. All specimens were measured for fork length (FL), except in the case of the Japanese and Taiwanese programs, where the specimens were measured for pre-caudal length (PCL) and total length (TL), respectively. In those cases, the sizes were converted to fork length (FL) using the equations proposed by Liu et al. (1998). Within the Portuguese Program the size of the claspers of males was measured and the maturity stage determined qualitatively, whenever possible. Specimens were considered mature and immature using the following criteria based on the scale proposed by Stehmann (2002): for males, stages 1 (immature) and 2 (maturing) were considered immature while stages 3 (mature) and 4 (active) were considered mature. For females, stages 1 (immature) and 2 (maturing) were considered immature, while stages 3 (mature), 4 (developing), 5 (differentiating), 6 (expecting) and 7 (post-natal/resting) were considered mature (Table IV.1).

IV.2.2. *Data analysis*

Size data were tested for normality with Kolmogorov-Smirnov normality tests (with Lilliefors correction) and for homogeneity of variances, with Levene tests. Given the lack of normality of data and homogeneity of variances, even after transforming the data with square-root and log functions, the specimen sizes were compared between regions, sexes and quarters of the year using non-parametric Kruskal-Wallis tests, and *k*-sample permutation tests using the permutational central limit theorem (Manly 2007). In the cases for which statistical differences were detected, multiple pairwise comparisons tests were carried out to detect between which categories the differences were significant (Siegel and Castellan 1988).

The sex-ratios were calculated and compared between regions with contingency tables and Pearson’s Chi-squared tests. Further, the sex-ratios were also compared between the seasons of the year and size classes (categorized with the 20% percentiles of the data) taking into account the various regions, using Cochran-Mantel-Haenszel (CMH) chi-squared tests. This test allows detecting eventual seasonality of size related effects in the sex-ratios conditional to each of the regions analysed.

Table IV.1: Maturity stages for the bigeye thresher (*Alopias superciliosus*) used in this study, based on the Stehmann (2002) scale.

Sex	**Maturity**	**Stg**	**Stage**	**Description**
Male	Immature	1	Immature	Small claspers, shorter than pelvic fins and flexible. Testes small, sperm ducts thread-like.
		2	Maturing	Claspers equal or longer than the pelvic fin, still flexible. Testes larger, sperm ducts beginning to coil.
	Mature	3	Mature	Claspers fully formed and stiff. Gonads enlarged filled with sperm. Sperm ducts tightly coiled filled with sperm.
		4	Active	Claspers dilated and swollen. Testes segmentated and well irrigated.
Female	Immature	1	Immature	Ovaries small, their internal structure granulated. Oviducts (uteri) narrow, thread-like.
		2	Maturing	Ovaries somewhat enlarged. Oocytes becoming differentiated to various small sizes. Wider uteri.
	Mature	3	Mature	Ovaries large, well rounded and with many oocytes. Oocytes enlarged, all about the same size.
		4	Developing	Uteri well filled and rounded with seemingly unsegmented yolk content.
		5	Differentiating	Uteri well filled and rounded with segmented content of large yolk. Small embryos.
		6	Expecting	Embryos fully formed, yolk sacs reduced. Embryos can be counted, measured and sexed easily.
		7	post-natal/ resting	Ovaries at resting stage. Uteri empty but still widened.

With the maturity stage data recorded by the Portuguese observer program, maturity ogives were developed to estimate the median size at maturity (L_{50}), or length at which 50% of the sharks were mature. For each sex, parameters, standard errors, and 95% confidence intervals (CIs) were estimated.

The maturity ogives were fitted by non-linear least-squares (NLS) regression, using the equation:

$$P_{Li} = \frac{1}{1+e^{-b(L_i - L_{50})}}$$

where P_{Li} is the proportion of mature individuals in size class L_i (using 5cm FL size classes), b is the slope and L_{50} is the size at which 50% of individuals mature. Maturity ogives were fitted for both sexes separately and L_{50} estimates were compared between sexes by analyzing overlaps in the 95% CIs.

The relationship between fork length (FL) and clasper length (CL) was also analysed using a linear regression model. In addition, a segmented regression model (SRM) was used to estimate the transition points and slopes in the regression between fork length and clasper length. These breakpoints have been defined to identify the three FL intervals with different slopes that represent the three maturity stages of male elasmobranchs: “immature”, “maturing” and “mature” (Segura et al. 2013). Thus, the breakpoints are defined as the values of the explanatory variable (FL) at which the changes in slope occur (Muggeo 2003). Standard errors were calculated for all the estimated parameters and the coefficients of determination were calculated to test the goodness-of-fit. Furthermore, to assess model adequacy to the data, the Akaike information criterion value (AIC) was calculated for both models (linear regression and SRM).

A logistic-binomial generalized linear model (GLM) was created to determine the influence of each region, sex and quarter of the year on the odds-ratios of capturing juvenile specimens, considering the estimated median sizes-at-maturity. The significance of the model parameters was tested with Wald statistics and likelihood ratio tests (LRT), comparing nested models. Model goodness-of-fit was assessed with the Nagelkerke coefficient of determination (R^2, Nagelkerke 1991). The discriminative capacity of the models was determined by the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) curves, with the calculation of the model sensitivity (capacity to correctly detect the event, in this case defined as the capture of juveniles), and model specificity (capacity to correctly exclude the non-events, in this case the capture of adults). Cross validation was carried out using a *k*-fold cross validation procedure (with $k = 10$) to estimate the expected level of fit of the models to new data, and to assess eventual over-fitting problems (Fushiki 2011). Because the models in this study are of the binomial type, the cross validation procedure was used to estimate the misclassification error rate. The odds-ratios of the parameters, with their respective 90% CIs, were calculated and used for model interpretation. The equatorial region and quarter 1 were used as the baseline parameters, and the odds-ratios calculated comparatively for the other regions and quarters of the year, taking into account their interaction effects.

Analysis for this paper was carried out using the R language for statistical computing (R Core Team 2013). Besides the R core program functions, some additional libraries were used, specifically “segmented” for the SRM models (Muggeo 2003), “gmodels” for the contingency table analysis (Warnes et al. 2012), “ggplot2” for the graphical analysis (Wickham 2009), and “maps” (Becker et al. 2013), “maptools” (Bivand and Lewin-Koh 2013) and “mapplots” (Gerritsen 2013) for the maps.

IV.3. . Results

IV.3.1. *Size distribution*

A total of 5590 bigeye thresher shark specimens were recorded within the scope of this study (2547 from the Spanish fleet, 1219 from the Taiwanese fleet, 1211 from Portuguese fleet, 426 from the USA fleet, 134 from the Japanese fleet and 53 from the Uruguayan fleet. The specimens ranged in size from 70 to 305 cm FL (70-300 cm FL for females and 75-305 cm FL for males), covering most of the known size-range of the species. The sample was composed mostly of specimens captured in the tropical north (38.9%) and southeast regions (36.4%), followed by 9.1% in the northwest, 9.1% in the equatorial, 4.0% in the northeast and 2.5 in the southwest (Figure IV.1). The spatial distribution of the effort of those fleets during the years for which data was available also covered a wide geographical area in the entire Atlantic Ocean. However, some areas had more effort, specifically along the temperate, tropical and equatorial eastern Atlantic, and also in some areas of the northwest Atlantic (Figure IV.2).

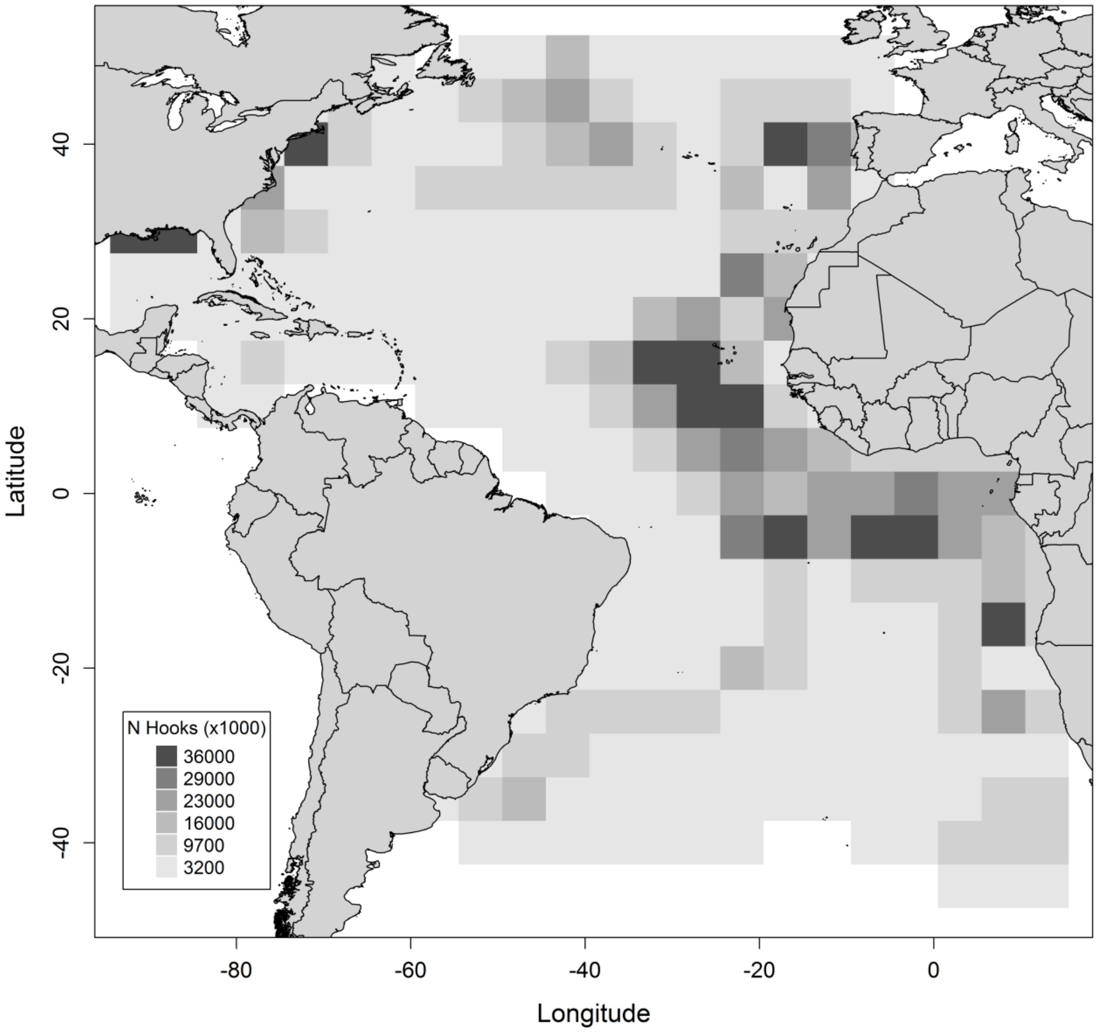

Figure IV.2: Effort distribution (number of hooks) for the US (1992-2009), Spanish (1993-2009), Japanese (1997-2009), Portuguese (2003-2009), Uruguayan (2003-2009) and Taiwanese (2004-2009) pelagic longline fleets in the Atlantic Ocean. The values in the legend refer to the maximum values within each effort class.

Considerable variability was observed in the size distribution of males and females among the Atlantic regions. The larger-sized specimens tended to be captured mainly in the higher latitudes, predominantly in the northwest and southwest Atlantic, while smaller specimens tended to be captured mainly in the tropical north and northeast areas (Figure IV.3). It was also noteworthy that a very low prevalence of the smaller sized specimens (<150 cm FL) was recorded in all regions (Figure IV.3). These regional trends tended to be common for both males and females, even though some differences between sexes were detected. In general, in the higher northern and southern latitudes males tended to be larger than females in the eastern regions (northeast and southeast), while females tended to be larger in the western regions (southwest and northwest) (Figure IV.4). In the equatorial area and tropical north, males also tended to be larger than females (Figure IV.4).

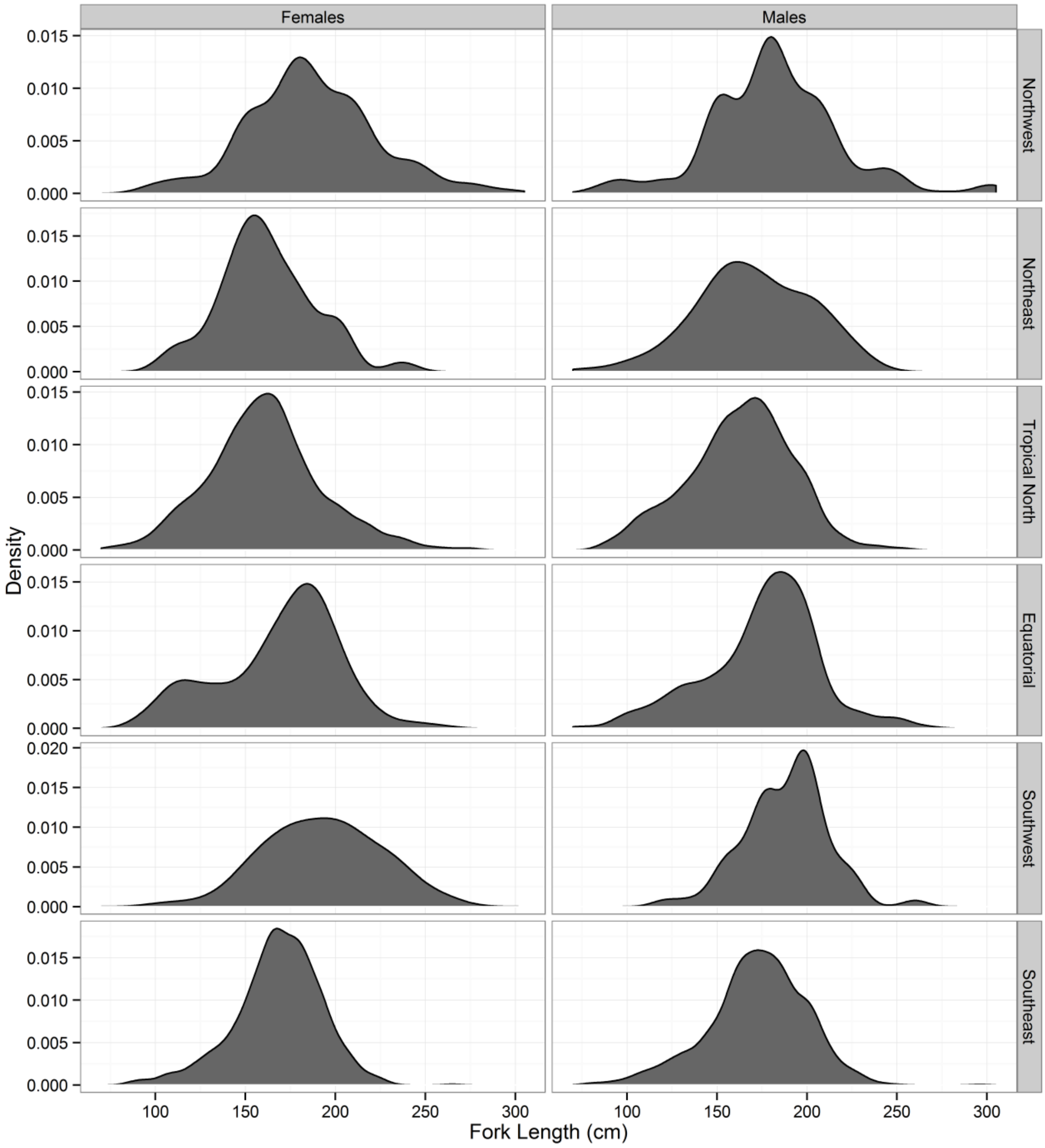

Figure IV.3: Length-frequency distributions of male and female bigeye thresher sharks (*Alopias superciliosus*) caught in six sampling regions of the Atlantic Ocean.

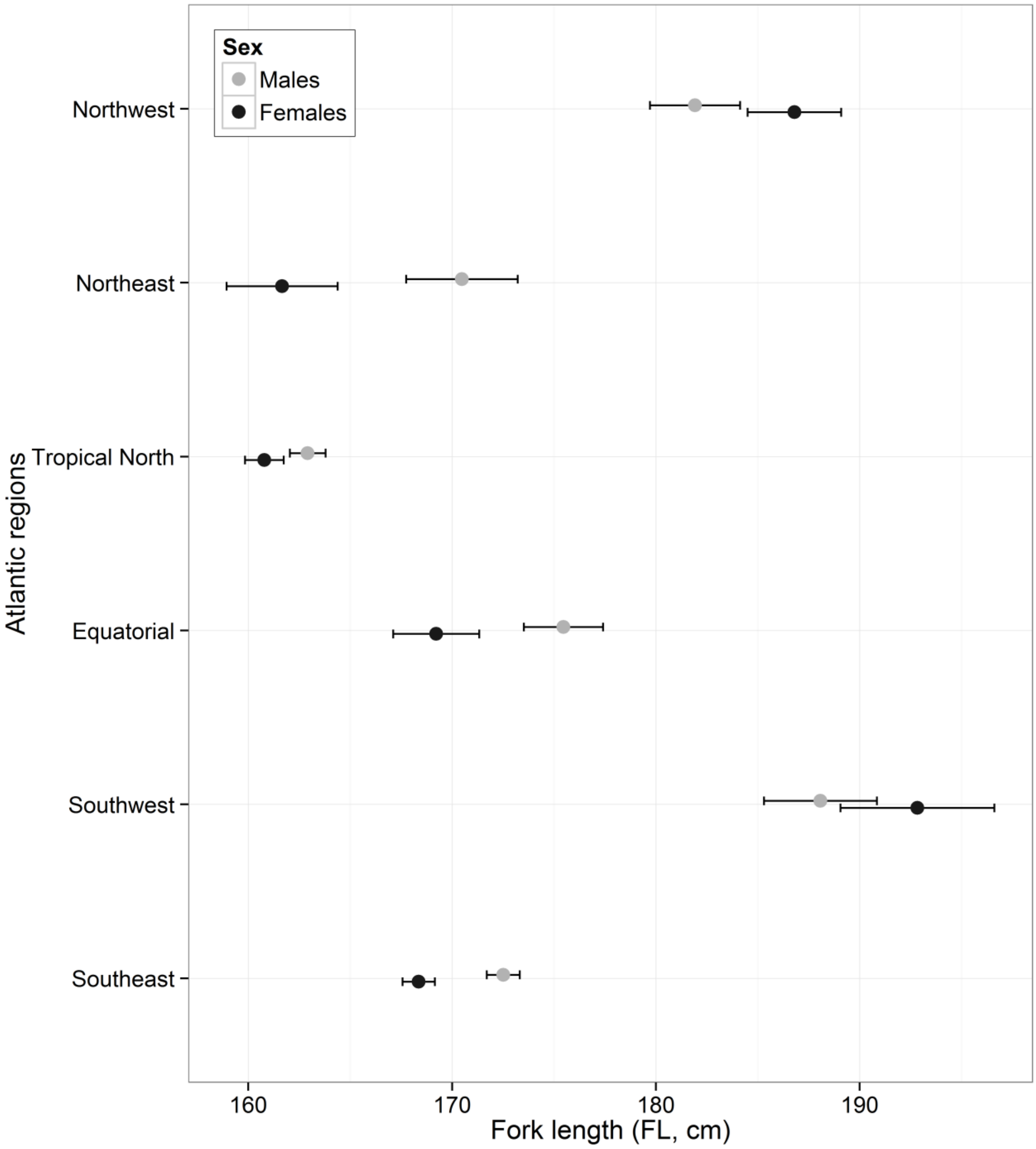

Figure IV.4: Mean sizes of male and female bigeye thresher sharks (*Alopias superciliosus*) caught in six sampling regions of the Atlantic Ocean. The error bars are ± 1 standard error.

Seasonality also seems to influence the size of captured bigeye thresher sharks. In the northern regions an opposite trend was observed when comparing the northwest and northeast, with sizes tending to increase throughout the year in the northwest and decrease in the northeast, both with similar size ranges except for the 4th quarter in the northeast where the sizes were much smaller Figure IV.5). In the southeast and southwest regions smaller specimens were caught in the 2nd and 3rd quarters and larger ones in the 1st and 4th quarters Figure IV.5). In the tropical north the sizes were much smaller and tended to be relatively similar along the year (with even smaller sizes in the 3rd quarter), while in the equatorial region there was a tendency for increasing sizes along the year Figure IV.5).

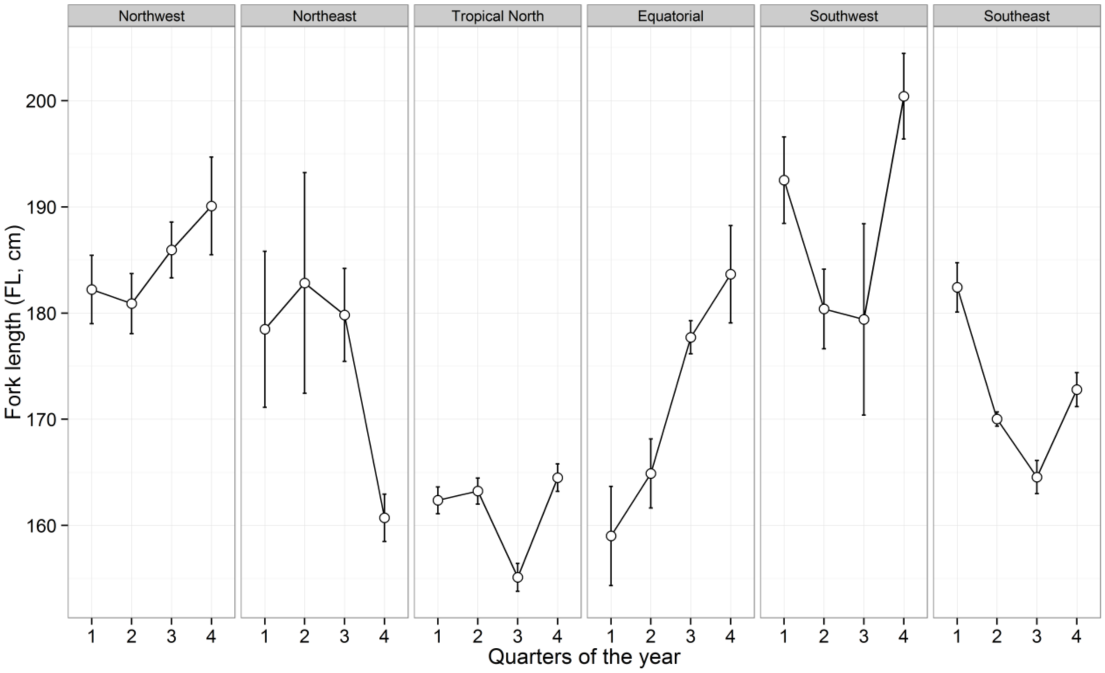

Figure IV.5: Mean size of bigeye thresher sharks (*Alopias superciliosus*) caught in six sampling regions of the Atlantic Ocean during the four quarters of the year. The error bars are ± 1 standard error.

Size data were not normally distributed (Lilliefors test: D = 0.042, p-value < 0.001) and the variances were heterogeneous among regions (Levene test: F = 15.01, df = 5, p-value < 0.001) and quarters (Levene test: F = 24.71, df = 3, p-value < 0.001), and homogeneous among sexes (Levene test: F = 0.61, df = 1, p-value = 0.4358). Univariate non-parametric statistical tests revealed that sizes were significantly different among regions (K-W: chi-squared = 333.98, df = 5, p-value < 0.001; permutation test: chi-squared = 334.14, df = 5, p-value < 0.001) and between sexes (K-W: chi-squared = 23.86, df = 1, p-value < 0.001; permutation test: chi-squared = 13.46, df = 1, p-value < 0.001), but not among quarters of the year (K-W: chi-squared = 5.35, df = 3, p-value = 0.148; permutation test: chi-squared = 4.87, df = 3, p-value = 0.181).

IV.3.2. *Sex ratios*

Of the total bigeye thresher sharks recorded, 2664 (47.7%) were females and the remaining 2926 (52.3%) were males, with some local variability recorded in the sex ratios (Figure IV.6). Particularly, there seemed to be some evidence of the presence of more males in coastal waters of central Africa and in oceanic south Atlantic waters, while around some islands, such as in the Cape Verde archipelago, the sex ratio was highly biased towards the presence of more females (Figure IV.6).

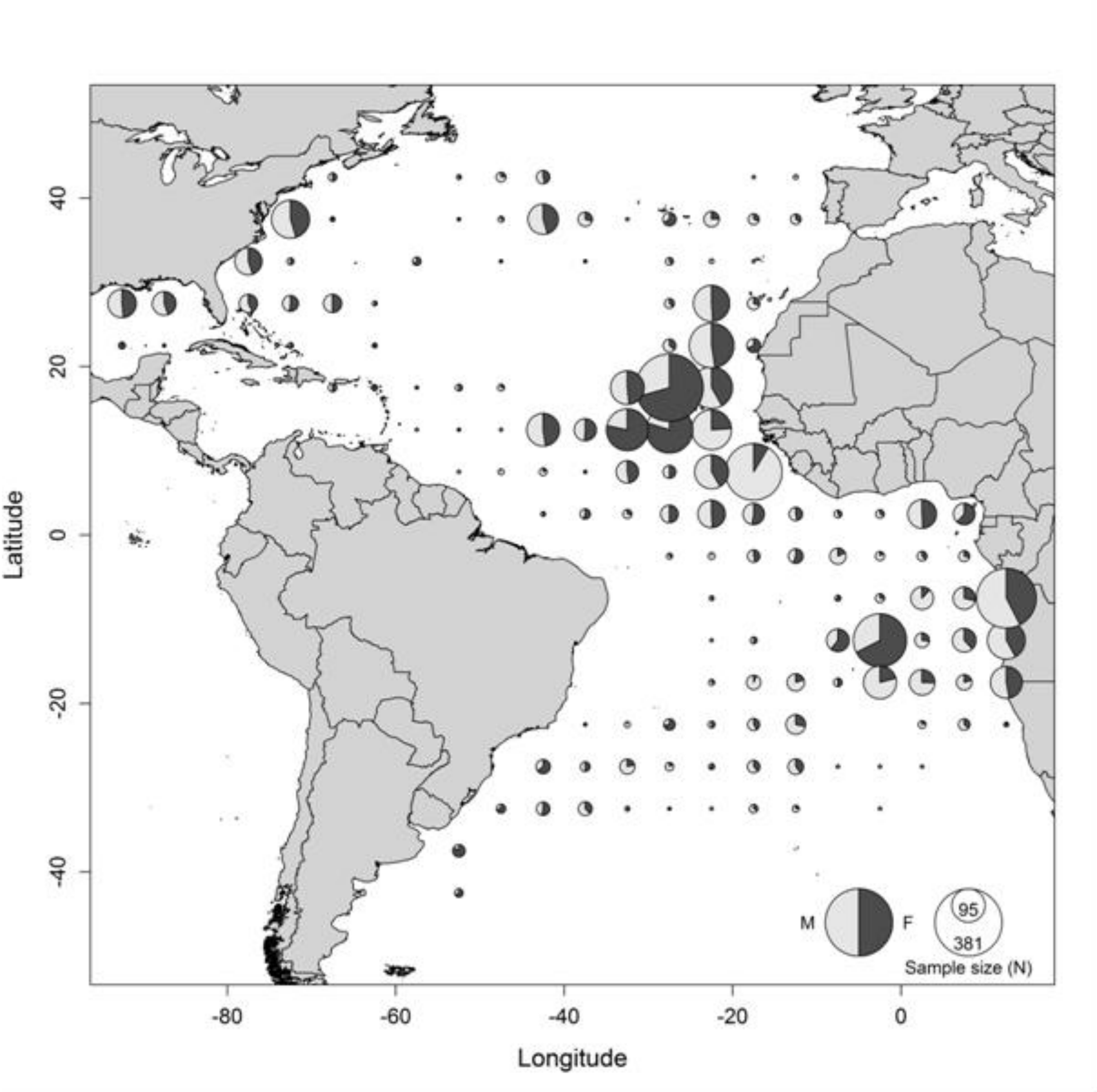

Figure IV.6: Map of the bigeye thresher shark (*Alopias superciliosus*) sex-ratios recorded by 5ºx5º degrees squares during this study. The circle sizes are proportional to the sample size (N) in each square.

When comparing the major regions defined in this study there were significant differences in the sex ratios (prop. test: chi-squared: 16.34, df = 5, p-value = 0.006), with most regions having a higher proportion of males, particularly in the northwest, northeast and southeast, while in the tropical north there was a slightly higher proportion of females (Figure IV.7). For the tropical north and southwest the sex ratios were very similar between males and females (Figure IV.7). There were also significant differences in sex ratios among seasons when those were compared conditionally within the different regions (CMH test: chi-squared = 13.03, df = 3, p-value = 0.005). While females tended to be less frequent than males for all regions and seasons, a higher proportion of females was observed during the 2nd quarter of the year in the northeast and during the 3rd quarter in the southwest. In contrast, a much lower proportion of females was observed in the 2nd quarter in the tropical north compared to a generally higher proportion of females in this region throughout the rest of the year (Figure IV.8). In the equatorial region the sex ratios remained relatively constant throughout the year with values of approximately 50% for each sex (Figure IV.8**)**.

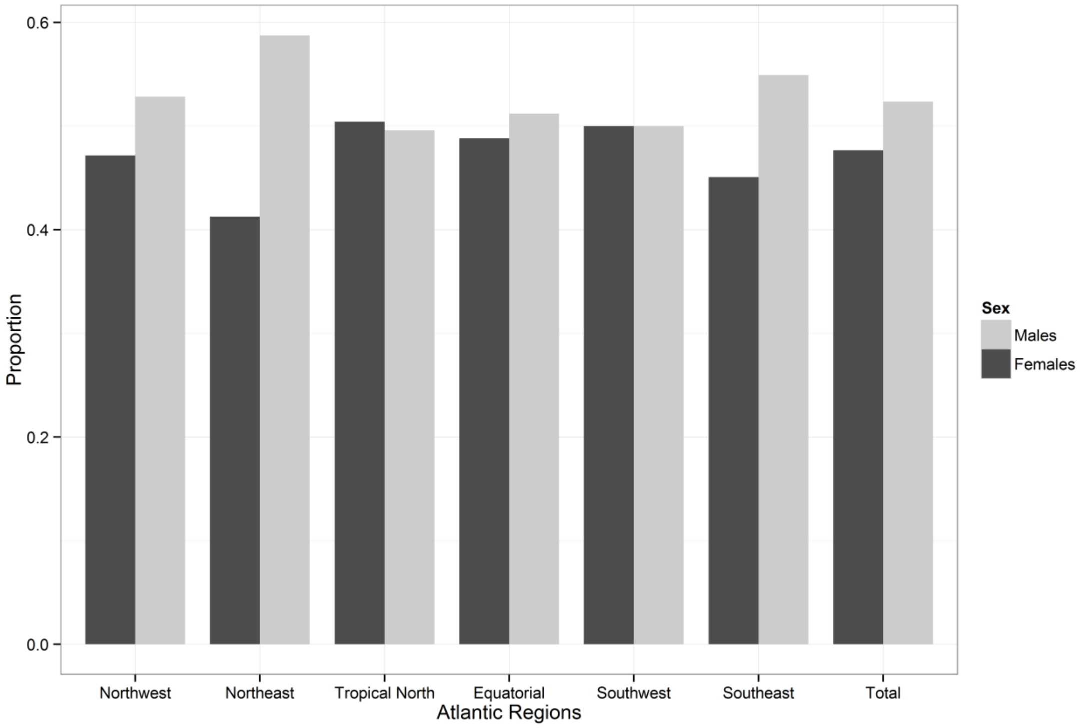

Figure IV.7: Sex ratios of the bigeye thresher shark (*Alopias superciliosus*, all sizes combined) in the six Atlantic regions considered in this study.

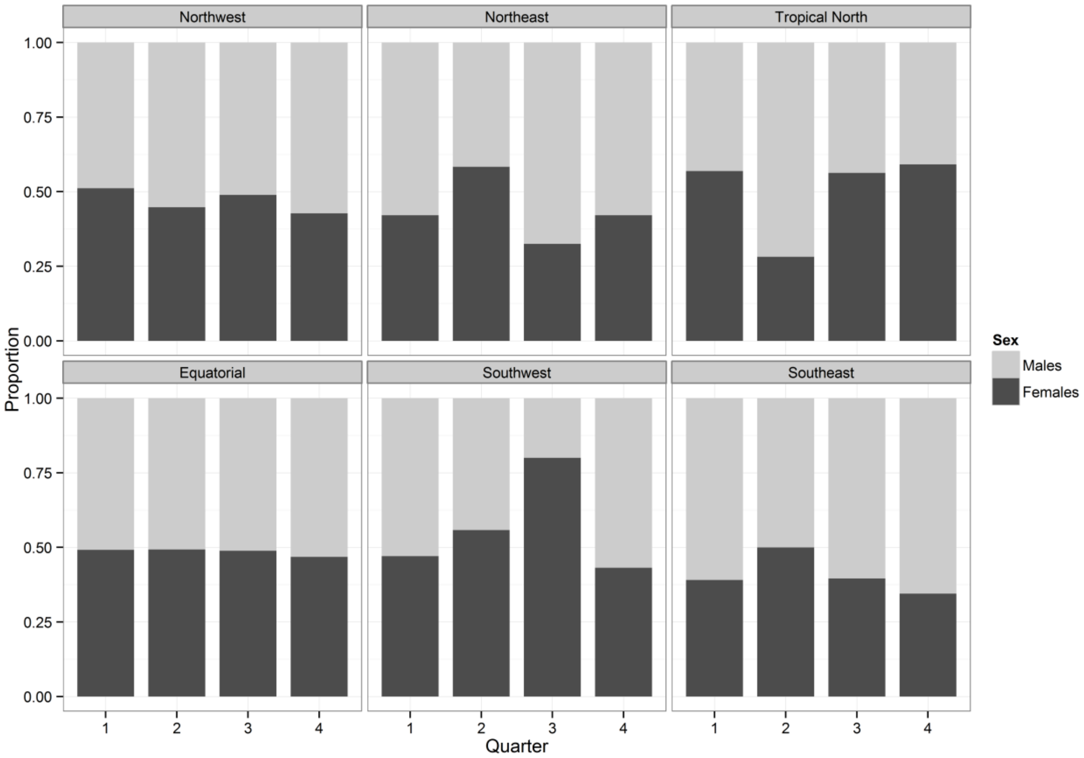

Figure IV.8: Sex ratios of bigeye thresher sharks (*Alopias superciliosus*, all sizes combined) per quarter of the year, in the six regions of the Atlantic considered in this study.

Significant differences were also detected in the sex ratios among sizes tested conditionally within the different regions (CMH test: chi-squared = 22.03, df = 4, p-value < 0.001). A higher proportion of males was observed in the larger size classes in the northeast, southeast and equatorial, while in the northwest there was a tendency for a higher proportion of females in the larger sizes (Figure IV.9). In the tropical north and southwest there were higher proportions of females both in the smaller and larger size classes, and more males in the middle sizes (Figure IV.9).

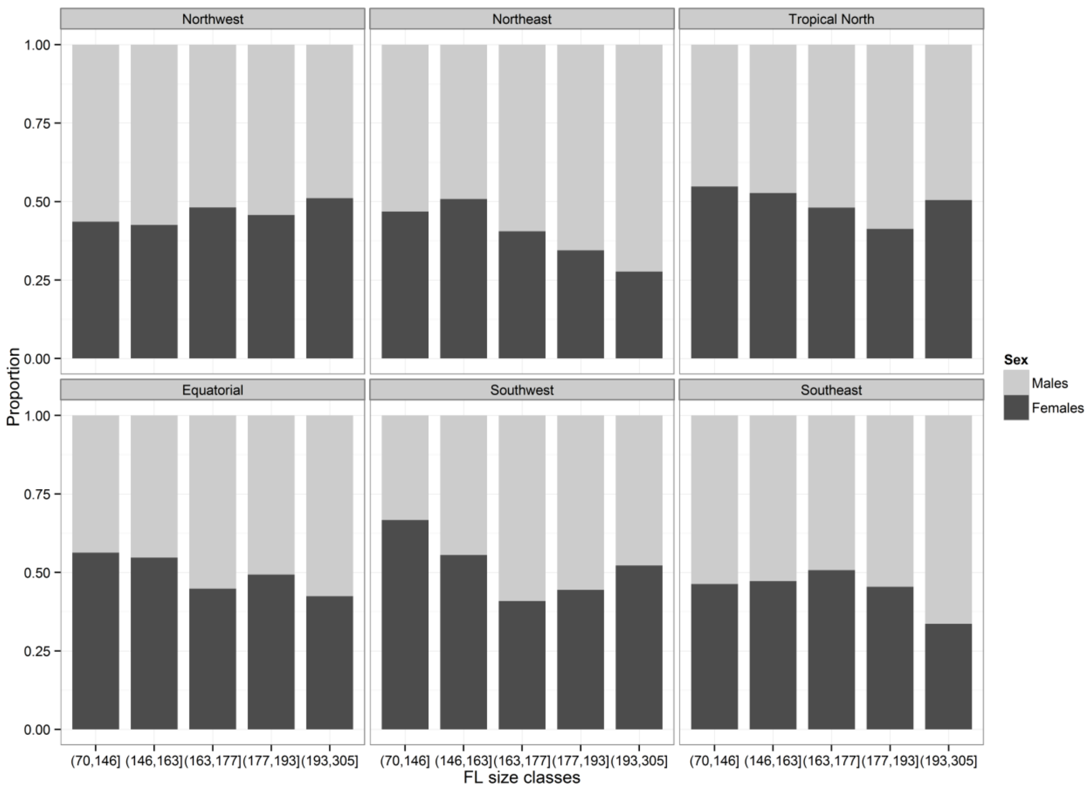

Figure IV.9: Sex ratios of bigeye thresher sharks (*Alopias superciliosus*) per size class, in the six regions of the Atlantic considered in this study. The categorization of size classes carried out using the 20% percentiles of the size data.

IV.3.3. *Median size at maturity*

Maturity information was available for 642 specimens, from which 257 were females (232 immature and 25 mature) and 385 were males (157 immature and 228 mature) (Table IV.2). Sample size of mature females was thus low. For this reason, maturity ogives and the clasper length vs. FL relationship were calculated using combined data from all regions.

Estimated maturity ogives are presented in Figure IV.10 and the respective equations are:

$$PLi = \frac{1}{1+e^{-0.06(Li-208.64)}} \quad \text{for females}$$

and

$$PLi = \frac{1}{1+e^{-0.07(Li-159.24)}} \quad \text{for males.}$$

Table IV.2: Bigeye thresher (*Alopias superciliosus*) observed size ranges and estimated length at 50% maturity (L_{50}) with 95% confidence intervals for males and females obtained in this study. LCL is lower confidence limit, UCL is upper confidence limit, L_{max} is maximum fork length observed.

Sex	**Size range (cm FL)**				**L_{50} (cm)**	**95% CI**		**L_{50} / L**
	Immature	**n**	**Mature**	**n**		**LCL**	**UCL**	
Females	100-220	232	140-264	25	208.6	204.8	212.9	0.79
Males	90 - 200	157	130 - 260	228	159.2	156.5	162.0	0.61

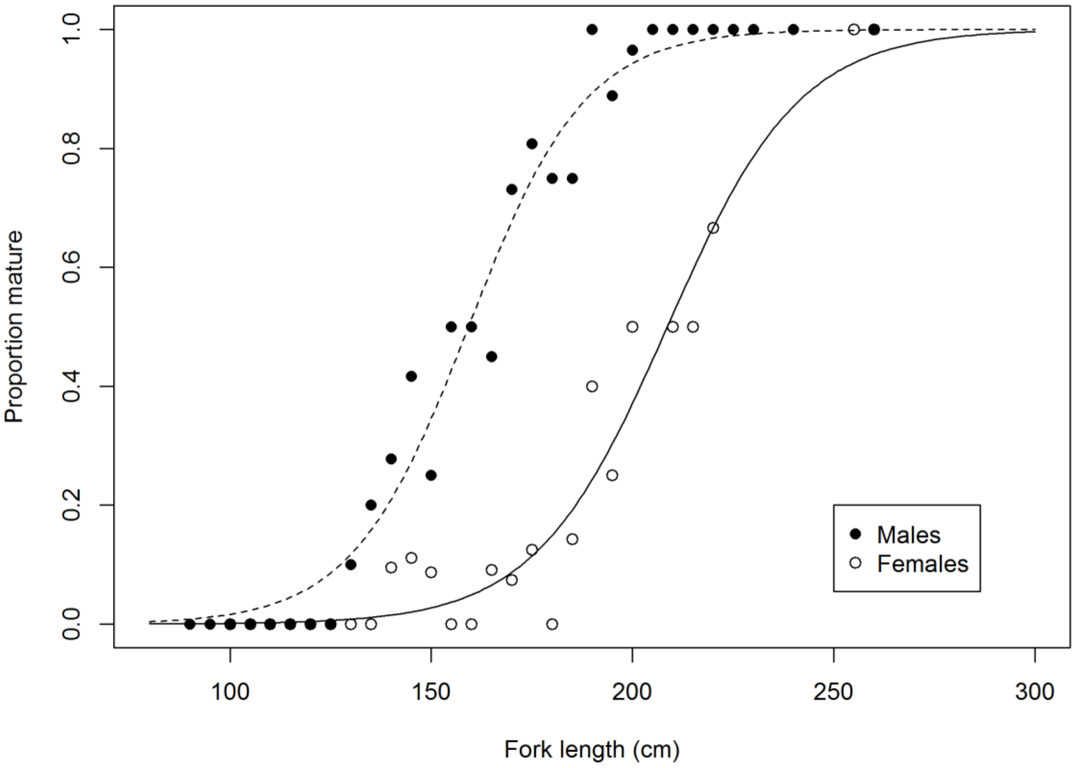

Figure IV.10: Observed proportion mature by size class (dots, black for males and white for females) and fitted maturity ogives for male and female bigeye thresher sharks (*Alopias superciliosus*). Sizes were grouped into 5 cm FL classes.

Female bigeye thresher sharks mature at larger sizes than males (Table IV.2). Differences between sexes were significant because the 95% CIs of L_{50} do not overlap. Both sexes are late maturing, with females maturing at 208.63 cm FL (79% of the maximum observed size) and males at 159.24 cm FL (61% of the maximum observed size). The largest immature female was 220 cm FL, while the smallest mature female was 140 cm FL. For males, the largest immature specimen was 203 cm FL, while the smallest mature specimen was 130 cm FL.

The claspers of 372 male specimens were measured and their lengths were plotted against FL (Figure IV.11). A linear regression fitted the FL vs. clasper length data well ($CL= 0.26FL - 18.97$; $r^2= 0.96$, AIC= 143.38), but the SRM had an even higher coefficient of determination and lower value of AIC ($r^2= 0.99$, AIC= 118.25), indicating a better goodness-of-fit to the data than the linear regression. Two breakpoints were estimated for bigeye thresher males with the SRM, resulting in three linear phases such that:

(1) $CL= 0.03FL + 5.06$ if $FL < 122.5$ cm

(2) $CL= 0.38FL -37.97$ if $122.5 \leq FL \leq 173.3$ cm

(3) $CL= 0.2FL - 6.78$ if $FL > 173.3$ cm

These three linear phases represent the successive maturity stages effectively modeled by the SRM. Thus, phase 1 contains the immature sharks characterized by a subtle slope close to zero; phase 2 represents the transitional “maturing” stage with the steepest slope; and phase 3 presents a flatter slope containing only the mature specimens.

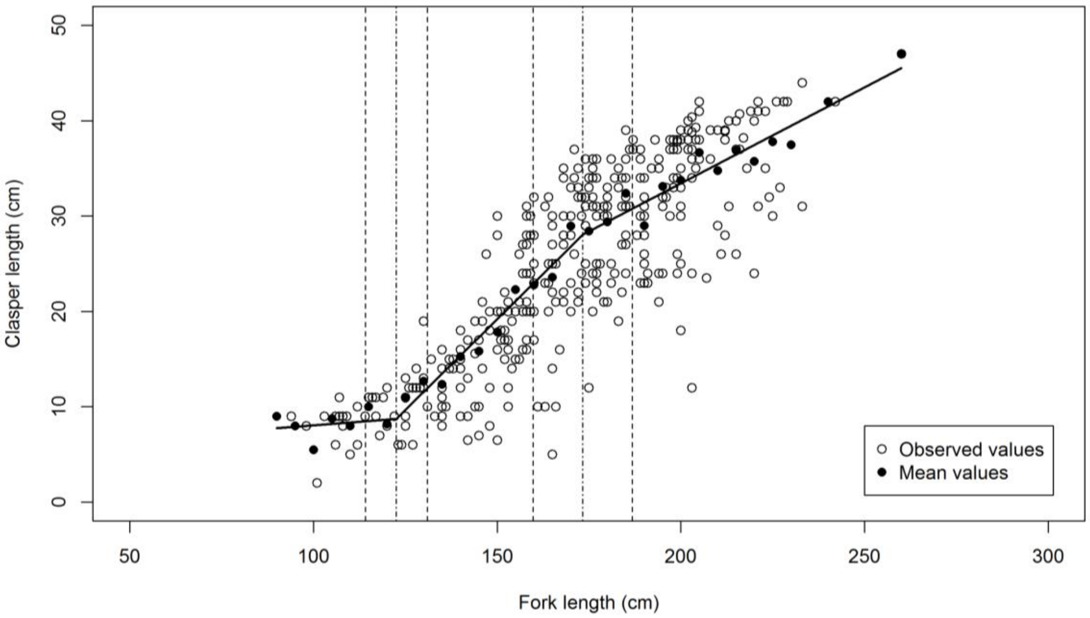

Figure IV.11: Clasper length vs. fork length (FL) of male bigeye thresher sharks (*Alopias superciliosus*). The black line represents the segmented fitted model between fork length and clasper length. For calculating the segmented model, the median clasper size of 5-cm size classes was used instead of the original clasper sizes. The dot-dash lines represent the estimated breakpoints and the associated dash lines, their 95% confidence intervals.

IV.3.4. *Litter size, embrionary development and presence of pregnant females*

Overall, 14 pregnant females were observed, plus two that showed signs of recent mating but still had no visible embryos in the uteri. Each of the pregnant females had two embryos, specifically one in each of the uterus.

The occurrence of pregnant females was recorded mainly in two regions of the study area, specifically in the tropical northeast between 1-17ºN / 9-32ºW, and southwest between 21-36º S / 30- 52ºW (Figure IV.1). In the tropical northeast Atlantic, the smallest pregnant female recorded had 210 cm FL and the largest 240 cm FL, and the recorded embryos ranged in size between 26 and 90 cm FL. In the southwest Atlantic, the smallest pregnant female recorded had 209 cm FL and the largest 256 cm FL, with the two females that showed recent signs of mating also recorded in this area and having 207 cm FL. In the southwest Atlantic, the recorded embryos ranged in size between 4 and 73 cm FL. It should be noted that the embryos measuring 4 cm were recorded in one female in the early pregnancy stages with the embryos still encapsulated, in a region closer to the Uruguayan coast. In terms of embrionary development along the year, the largest embryos were recorded in October-November in the tropical northeast Atlantic and in March in the southwest Atlantic. Moreover, during the month of March in the southwest Atlantic, embryos with both the largest and smallest sizes were observed.

IV.3.5. *Expected distribution of juveniles and adults*

Considerable variability was observed in the distribution of juvenile and adult specimens, when considering sex, region, and season factors, but in general most regions and seasons tended to have a high proportion of juvenile females and adult males (Figure IV.12).

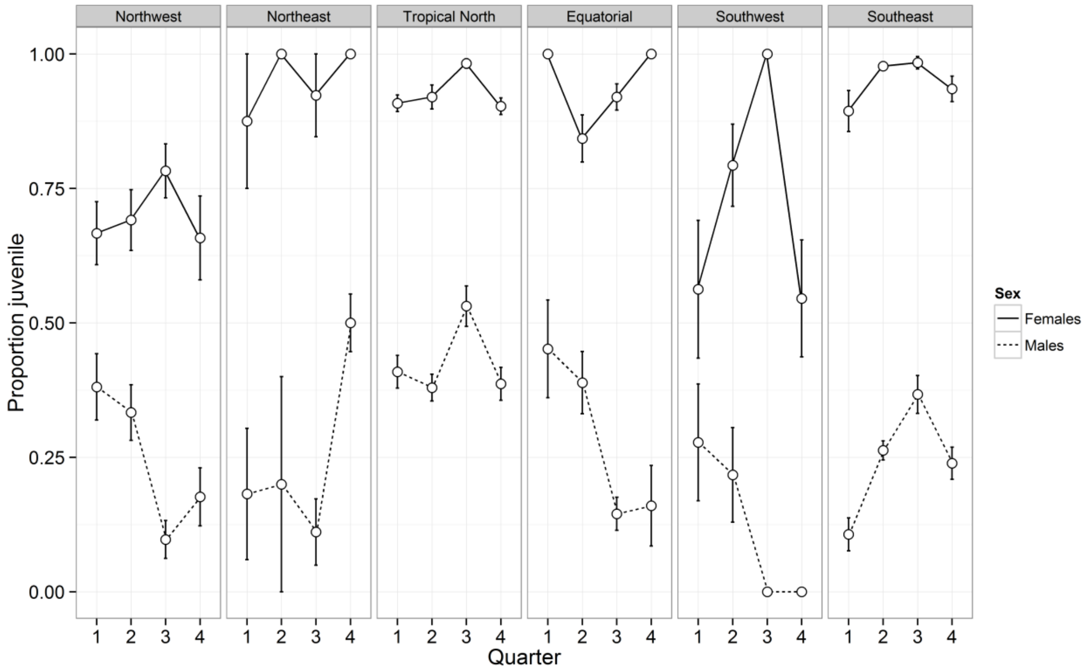

Figure IV.12: Proportion of juvenile bigeye thresher sharks (*Alopias superciliosus*) caught in the six sampling regions of the Atlantic Ocean in each quarter of the year. The error bars are ± 1 standard error. The size range considered was 70-300 cm FL for the females and 75-305 cm FL for the males.

The final estimated logistic-binomial GLM considered the factors sex (deviance explained = 2337.6, df=1, p-value < 0.001), region (deviance explained = 110.1, df=5, p-value < 0.001) and quarter (deviance explained = 5.6, df=3, p-value = 0.132), and also the interaction between quarter and region (likelihood ratio test for nested models: deviance explained = 95.1, df=15; p-value < 0.001). Even though the variable quarter was not significant in terms of single effect, the presence of a significant interaction with region justified having this variable, as well as the interaction, in the model. In terms of goodness-of-fit, the final model had a Nagelkerke R^2 of 0.538 and an AUC of 0.855, with a sensitivity of 72.0% and a specificity of 90.1%. The *k*-fold cross-validation procedure resulted in a predicted error for new data of 20.9%.

Compared to the baseline combination (equatorial region and quarter 1), the odds of capturing juveniles increased in some area-season combinations, whereas they decreased in others. Specifically, the odds-ratios of capturing more juvenile specimens increased significantly in the northeast quarter 4, tropical north quarters 2, 3 and 4, southwest quarters 2 and 3, and southeast quarters 2, 3 and 4 (Figure IV.13). By the contrary, the odds of capturing more juveniles decreased significantly in several regions earlier in the year, specifically in the quarter 1 of the northeast, northwest, southwest and southeast, as well as in the equatorial region in quarters 2, 3 and 4 (Figure IV.13). Additionally, the odds of capturing juvenile males were substantially lower (96.3%, with 90% CI varying between 95.7% and 96.8%) than the odds of capturing juvenile females.

IV.4. Discussion

Differences in the length-frequency distributions and proportions of juvenile and adult specimens were found among the regions of the Atlantic Ocean examined. The most significantly different region seemed to be the tropical north Atlantic, where specimens tended to be smaller and the proportion of juveniles (both males and females) higher throughout the entire year.

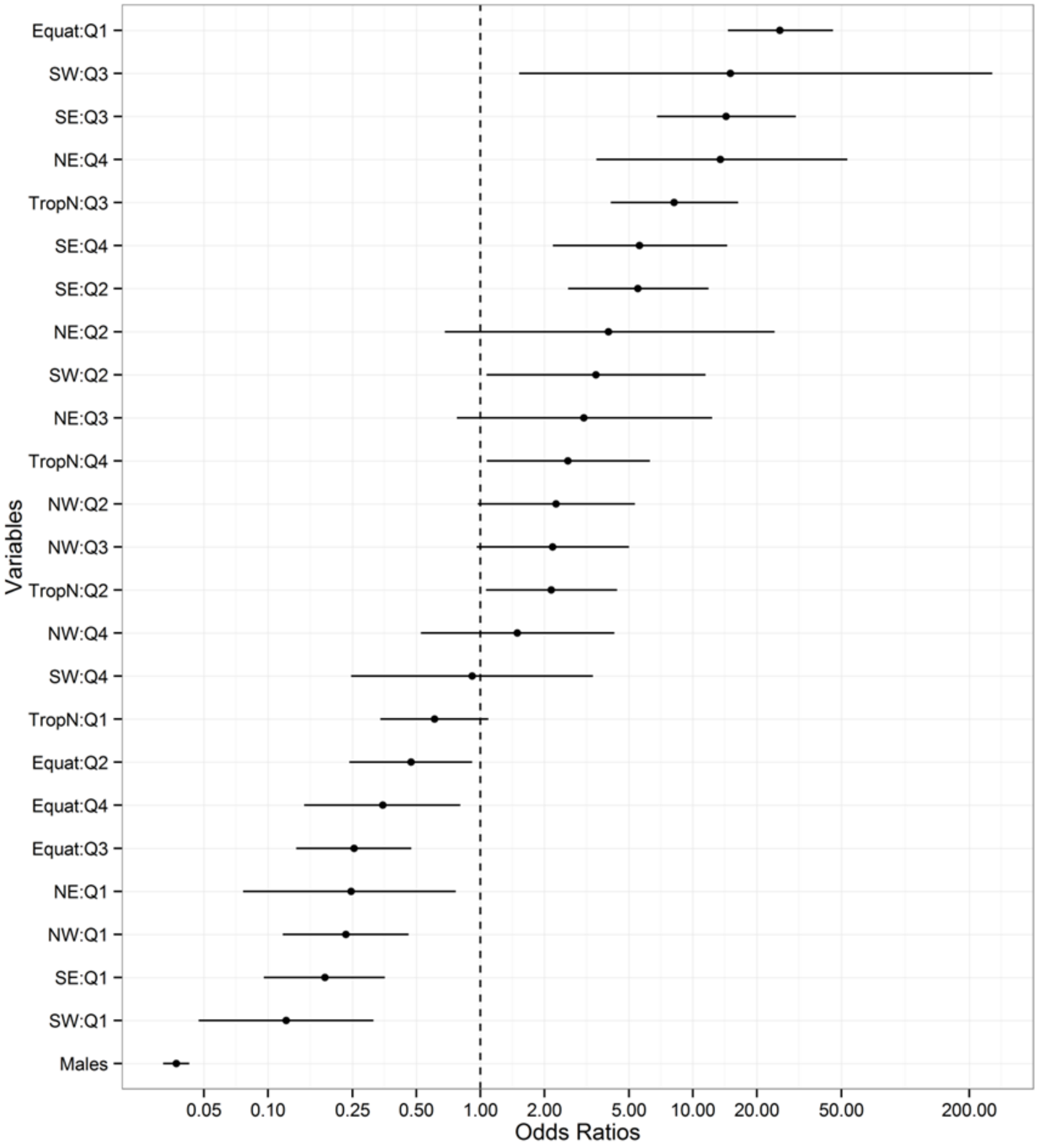

Figure IV.13: Odds ratios (with 90% confidence intervals) of capturing juvenile (<159.2 cm FL for males and <208.6 cm FL for females) bigeye thresher sharks (*Alopias superciliosus*) in each of multiple region:quarter combinations, as well as for the single effect for sex. The x-axis is in a base 10 logarithm scale.

The reasons for these differences are not entirely understood yet, but it is possible that there are migratory and habitat segregation patterns by growth stages between the regions and seasons of the year, with smaller and younger sharks concentrating predominantly in the tropical northern region, while the larger adults seem to prefer the temperate areas of the northern and southern Atlantic. However, it is important to note that the data used in our study comes from several different fleets, with different fishing métiers that target different species, and as such the size ranges and abundance reported by each fleet for each region are also being affected by fleet selectivity. With regards to the spatial distribution of the data, and while part of the observations reported reflect the species spatial dynamics, there is also some influence from the sampling effort within each fleet, and therefore the reported data may not be entirely representative of the prevalence of the species at each locations.

The maximum sizes observed in our sample (504 cm TL for males and 496 cm TL for females, after conversion from FL) were higher than reported in the literature (484 cm TL reported by Thorpe 1997; 357 cm TL for males and 422 cm TL for females reported by Liu et al. 1998; 410 cm TL for males and 461 for females reported by Moreno and Morón 1992). Additionally, the smallest specimens in our sample were 126 cm TL, which is slightly lower than the size at birth of 135-140 cm TL suggested by Chen et al. (1997), and within the 100-140 cm TL suggested by Compagno et al. (2005). This indicates that the sample in our study is covering most of the size classes of the species. However, a very low prevalence of the smaller size classes (particularly specimens with < 150 cm FL) was reported in our study in most of the analysed regions. This might be related with the fact that the fleets analysed are operating mainly in oceanic waters, while the smaller sized specimens may be occurring in other regions not covered in our study, such as more coastal regions where they would be accessible and taken by coastal fleets operating with other fishing gears such as nets and coastal longlines. This higher prevalence of juveniles in more coastal waters has been previously recorded for some other oceanic species, and a similar life history pattern may be occurring with the bigeye thresher shark. Another possible hypothesis would be to consider that the lack of smaller sized specimens might be related with fishing gear selectivity, but given that the bigeye thresher sharks are born at relatively larger sizes, if those smaller specimens were present in oceanic waters then they would likely also be captured by those pelagic longlines. As such, the hypothesis of a life history cycle with the occurrence of smaller specimens in more coastal areas and larger specimens in more oceanic waters is likely to be occurring with the bigeye thresher shark.

As documented for other shark species (Cortés 2000), the estimated median size at maturity was significantly higher for females (208.6 cm FL, 349.1 cm TL) than males (159.7 cm FL, 269.8 cm TL). Although the number of mature females in the present study was small, these values for the bigeye thresher in the Atlantic are very close to the sizes at first maturity reported by Moreno and Morón (1992) for the northeast Atlantic (from Cape São Vicente to the Ivory Coast) and Western Mediterranean Sea (340 cm TL for females and 270 cm TL for males, or 200.2 cm FL and 159.9 cm FL respectively). In Taiwanese waters, Chen et al. (1997) reported median sizes at maturity of 336.3 cm TL (estimated 198.2 cm FL) for females and 279 cm TL (estimated 165.2 cm FL) for males, values which are just slightly lower and higher than ours for females and males, respectively. For the northwestern Atlantic, Stillwell and Casey (1976) suggested 350 cm TL (estimated 206 cm FL) as size at first maturity for females and 295 cm TL (estimated 174.3 cm FL) for males, values almost identical to ours for females and a little higher for males. Significant differences between median sizes at maturity have also been reported for the common thresher (*A. vulpinus*) in the north Atlantic, with 216 cm FL for females and 188 cm FL for males (Natanson and Gervelis 2013) (Table IV.3).

Table IV.3: Summary of thresher shark (genus *Alopias*) size at maturity previously reported in the literature, with a comparison to the estimates presented in this study. * Studies that reported the estimates in fork length (FL) were converted to total length (TL) to facilitate comparison.[a]: Studies that reported median size at maturity. [b]: Studies that reported size at first maturity from observational data.

	Size at maturity (TL, cm)		**Region**	**Species**
	Males	**Females**		
Current study*,[a]	269.8	349.1	Atlantic	*A. superciliosus*
Moreno and Morón (1992)[b]	270	340	Atlantic	*A. superciliosus*
Chen et al. (1997)[a]	270–288	332–341	Pacific	*A. superciliosus*
Stillwell and Casey (1976)[b]	295	350	NW Atlantic	*A. superciliosus*
Cailliet and Bedford (1983)	333	260-315	Pacific	*A. vulpinus*
Smith et al. (2008a) [a]	293–311	303	Pacific	*A. vulpinus*
Natanson and Gervelis (2013)*,[a]	333	386	NW Atlantic	*A. vulpinus*
Liu et al. (1999) [a]	267-276	282–292	Pacific	*A. pelagicus*

The SRM of male size vs. clasper length predicted that the onset of maturity in male bigeye thresher sharks starts at ca. 122.5 cm FL (first breakpoint) and that all males in the population are mature at ca. 173.3 cm FL (second breakpoint). The fact that the median size at maturity estimated through the maturity ogive (L_{50}= 159.2 cm FL) is included between the two breakpoints of the regression, seems to support the effectiveness of this method. Furthermore, other authors have used this approach as it provides an objective and direct estimate of the maturity stages of male elasmobranchs (using only clasper measurements) instead of relying on a subjective classification which depends on the observer’s ability and may vary between different observers (Segura et al. 2013). In addition, it is a non-invasive method and can be applied to existing common fisheries data (Segura et al. 2013).

The estimated median size at maturity occurs at ca. 79% of the maximum observed size for bigeye thresher females and 61% for males. After examining 164 shark species, Cortés (2000) concluded that on average shark size-at-maturity takes place at about 75% of the maximum observed size. Thus, the values presented here follow this general trend, although our male estimation is a slightly lower than the average. Furthermore, it has been documented that the ratio of size at maturity and maximum observed length (L_{50}/L_{max}) ranges from 0.5 to 0.95 for sharks, with most being between 0.65 and 0.8 (e.g. Joung and Chen 1995). The ratios obtained in the present study are comparable to the values of 0.77 and 0.67 for females and males, respectively, obtained by Moreno and Morón (1992). Stillwell and Casey (1976) reported a similar ratio to ours (0.77 vs. 079) for females in the northwestern Atlantic but a higher value for males (0.79 vs. 0.61). In the Pacific Ocean, Chen at al. (1997) suggested an identical ratio to ours for females (0.79) and a higher value for males (0.78). Following the same trend of this study, ratios of 0.8 and 0.7 were estimated in the north Atlantic for female and male shortfin mako, also a Lamniformes species (Natanson et al. 2006). Joung and Chen (1995) proposed three stages of maturity based on the L_{50}/L_{max} ratio: 1 = early maturity ($L_{50}/L_{max}<0.65$), 2 = standard maturity ($0.65< L_{50}/L_{max}<0.8$), and 3 = late maturity ($L_{50}/L_{max} >0.8$). The bigeye thresher can thus be considered to follow a standard maturity pattern, with females tending toward late maturity, while males are closer to early maturity.

The fitted logistic-binomial GLM had a high goodness-of-fit with relatively high r^2 and AUC values, and the cross-validation procedure resulted in a low misclassification error rate. Values of AUC between 0.8-0.9, which is the case of the present study, are considered excellent (Hosmer and Lemeshow 2000), and as such the goodness-of-fit of the presented model also seems very good, with the model having the capacity to correctly predict the capture of juveniles in 72.0% of the cases, while at the same time correctly predicts the capture of adults in 90.1% of the cases. The cross-validation misclassification error rate was estimated at 20.9%, which also seems very reasonable, meaning that most of the times the model is correctly discriminating between the capture of juvenile versus adult specimens under the analysed variables. One advantage of this model that covered a wide Atlantic region is that it provides a very general overview in terms of large-scale oceanic areas, with the downside of losing some detail in specific regions and seasons. As such, this model and odds-ratios outputs should be regarded mainly as general values in the context of these large-scale oceanic areas, bearing in mind that exceptions are very likely to occur in specific and smaller-scale areas. The tropical north region seemed to differ from the remaining areas because in most seasons the odds of capturing more juveniles than adults increased significantly. Similarly, in some of the other regions there were also increased odds of capturing more juveniles, but those were dependent on specific seasons, as for example in the southwest and southwest region in the 3rd quarter.

Moreno and Morón (1992) suggested the existence of a nursery area for this species off the Southwestern Iberian Peninsula in the northeast Atlantic, based on the records of several pregnant females captured in that region. Based on our study, we hypothesize that such an area may exist and possibly extend further south, into the tropical northeast Atlantic and equatorial waters closer to the African continent. This seems to be validated by the fact that smaller and mainly juvenile specimens tended to be captured in this region, but also because a few pregnant females, both mid- and late-term (stages 5- differentiating and 6-expecting), were also recorded in the region. Additionally, the tropical northwestern Atlantic, particularly in areas closer to the Caribbean Sea and in Florida, may also serve as a nursery as some very small specimens (within the range of sizes at birth described by Chen et at. 1997 and Compagno et al. 2005) were captured in that region, added to the fact that a previous study (Gilmore 1983) reported embryos dissected from pregnant females captured in that region. Finally, another cluster of pregnant females was recorded in the southwest Atlantic, some closer to the Rio Grande Rise and a few inside the Uruguayan EEZ and those may also be serving as a nursery area for this species in the south Atlantic. In that region, a previous study by Amorim et al. (1998) had also reported the presence of pregnant females and analysed their embryos. As such, we can hypothesize that at least those areas may constitute nursery areas for the bigeye thresher, but we cannot exclude the possibility of other nurseries in the Atlantic. In some cases we have size observations but without reproductive data, as the observations used in this study depend on the specific objectives of the projects and programs collecting the data. Furthermore, while the geographical coverage of our study is wide, there are areas that were not covered and we cannot exclude the possibility of the presence of pregnant females and small juveniles in those areas.

In terms of embryo development and reproductive seasonality, the presence of the largest embryos (closer to the size at birth) in October/November in the northeast Atlantic and in March in the southwest Atlantic, seem to suggest that birth may be taking place during late summer and autumn in both hemispheres, and corroborates what has been previously suggested for both regions, particularly by Moreno and Morón (1992) for the northeast and Amorim et al. (1998) for the southwest Atlantic. In contrast, in the Pacific Ocean Matsunaga and Yokawa (2013) reported that neonates (<80 cm pre-caudal length) were captured mainly during winter and spring in the area between 10-15N, which suggests a different seasonality for the reproductive cycle and birth season in that ocean. However, it should be noted that the sample size for this analysis in the Atlantic was very small, given that the capture of pregnant females of this species by pelagic longliners is relatively rare (as noted previously by Moreno and Morón 1992), and not all the sampling programs participating in this study record those observations. Additionally, in some periods, namely during March in the southwest Atlantic, embryos of different sizes were recorded including both the smallest and the largest in the region. As such, these parameters still remain highly uncertain, and the previously mentioned embryo development and reproductive seasonality should be considered as hypotheses that need further investigation.

All thresher sharks are listed as “Vulnerable globally” by the IUCN and are known to have vulnerable life history, resulting in a low capacity to recover even from moderate levels of exploitation (Amorim et al. 2009). The sizes at maturity obtained in the present study indicate that the bigeye thresher reaches maturity at a larger size than the other species of the Alopiidae family, as stated by Smith et al. (2008a). Assuming that age at maturity is also reached at a late age, and together with its very limited fecundity, this suggests that the reproductive potential of the bigeye thresher is very low. The distributional patterns of sizes and maturity stages in the six regions during different seasons of the year can be used to better inform future management decisions and conservation initiatives for this species in the Atlantic Ocean.

IV.5. Acknowledgments

This work was carried out as part of a cooperative study conducted within the ICCAT-Sharks working group. Sampling and data collection from the Portuguese fishery was obtained and funded within the scope of the EU Data Collection Framework, and as part of the projects SELECT-PAL (PROMAR Proj. 31-03-05-FEP-1), and THRESHER (FCT Proj. PTDC/MAR/109915/2009). Sampling from the Uruguay was conducted by fishery observers from PNOFA. The authors are grateful to all the fishery observers and longline skippers from the several Nations involved in this study. J. Fernandez-Carvalho and R. Coelho were supported by grants from the Portuguese Foundation for Science and Technology (FCT, Fundação para a Ciência e a Tecnologia), specifically grant SFRH/BD/60624/2009 attributed to J. Fernandez-Carvalho and grant Ref: SFRH/BPD/93936/2013 attributed to R. Coelho.

CHAPTER V. AGE ESTIMATION AND GROWTH MODELING OF *A. SUPERCILIOSUS* IN THE ATLANTIC OCEAN, WITH A COMPARISON OF THE GROWTH PATTERNS BETWEEN THE TWO HEMISPHERES. [4]

V.1. Introduction

The bigeye thresher shark, *Alopias superciliosus* Lowe, 1841, is a pelagic shark distinguished by its long whiplike upper caudal lobe and large eyes and grooves (Bigelow and Schroeder 1948). It is distributed circumglobally in the Atlantic (and Mediterranean), Pacific and Indian Oceans, ranging from tropical to temperate seas, occurring mostly in oceanic epipelagic waters and at times in more coastal waters (Cao et al. 2011, Compagno 2001, Nakano et al. 2003, Smith et al. 2008a, Stillwell and Casey 1976, Weng and Block 2004). Like other members of the order Lamniformes, the bigeye thresher is an intrauterine oophagous aplacental viviparous species, usually bearing only two embryos per litter, resulting in an extremely low fecundity (Chen et al. 1997, Compagno 2001, Gilmore 1993, Moreno and Morón 1992). In fact, the bigeye thresher has been described as having one of the lowest intrinsic rates of population increase amongst elasmobranchs, highlighting its high vulnerability to exploitation (Chen and Yuan 2006, Cortés 2008, Smith et al., 2008b). According to the International Union for the Conservation of Nature (IUCN) Red List Criteria, this species is classified as “Vulnerable” in Global terms, and “Endangered” in the northwest Atlantic and western central Atlantic (Amorim et al. 2009).

In the Atlantic Ocean, the pelagic longline fisheries targeting swordfish commonly capture several pelagic sharks species as bycatch (Buencuerpo et al. 1998, Coelho et al. 2012a, Megalofonou et al. 2005, Moreno and Morón 1992) including bigeye thresher, whose catches have been estimated to be around 0.2% of the total shark bycatches for the Atlantic (Mejuto et al. 2009). The International Commission for the Conservation of Atlantic Tunas (ICCAT), responsible for the management of this

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[4] ***Based on the manuscripts***:
Fernandez-Carvalho J, Coelho R, Erzini K, Santos MN. 2011. Age and growth of the bigeye thresher shark, *Alopias superciliosus*, from the pelagic longline fisheries in the tropical Northeastern Atlantic Ocean, determined by vertebral band counts. Aquat. Living Resour. 24 (4): 359–368.

Fernandez-Carvalho J, Coelho R, Erzini K, Santos MN. *Submitted*. Age estimation and growth modeling of the bigeye thresher shark (*Alopias superciliosus*) in the Atlantic Ocean. Fish. Bull.

species in the Atlantic Ocean, recently prohibited the retention and commercialization of bigeye thresher sharks caught in tuna fisheries, recommending the release of live specimens when accidentally captured and requiring that both incidental catches and live releases be recorded in accordance with ICCAT data reporting requirements (ICCAT Rec. 2009/07). However, simply releasing the caught specimens may not be enough to protect this species due to the estimated 51% at-haulback hooking mortality rate in the pelagic swordfish longline fishery, as the majority of the specimens caught are discarded already dead (Coelho et al. 2012a).

Even though oceanic pelagic sharks are impacted by fishing, due to their highly migratory nature they remain among the least studied elasmobranchs, posing particular difficulties for fisheries management and conservation (Pikitch et al. 2008). Knowledge on life history of a species is essential for successful fisheries management, particularly age and growth studies, as they are the baseline for estimating important biological variables such as growth rates, natural mortality and longevity of a species (Campana 2001, Goldman 2004, Goldman et al. 2012). Understanding these biological parameters is important to assess their current population status and to predict how their population size and structure will change over time (Goldman et al. 2012). In fact, it is fundamental to perform precise and accurate age determinations since erroneous understanding of the population dynamics of a species may lead to serious bias in stock assessment, frequently resulting in overexploitation (Goldman et al. 2012). Since elasmobranch species are characterized by slow growth rates (e.g. Coelho and Erzini 2002) and reduced reproductive potential (e.g. Coelho and Erzini 2006), these fishes are extremely vulnerable to fishing pressure, with overexploitation occurring even at relatively low levels of fishing mortality (Smith et al. 1998). Thus, the study of their life history, including age and growth is more critical than for more resilient species (Goldman et al. 2012).

Age determination in fishes is typically conducted by counting periodic growth increments present in calcified anatomical parts that reflect the time of the year in which the calcified material has been deposited (Cailliet et al. 2006). In general, an annual growth ring or *annuli* is composed of one opaque band (representing faster summer growth) and one translucent band (representing winter growth), though the periodicity may be different for some elasmobranchs (Cailliet and Goldman 2004, Caillet et al. 2006). While in teleost fishes most age and growth studies use otoliths or scales, elasmobranch fishes lack these structures. Therefore, vertebrae are the most widely used structures for age determination, although dorsal spines (usually in the Squalidae family) and caudal thorns (in skates) have also been used (Campana 2001, Caillet and Goldman 2004, Coelho and Erzin 2007, 2008, Goldman 2004, Moura et al. 2007). As the pattern of calcification can vary greatly within and among taxonomic groups of elasmobranchs, a species-specific approach is necessary for their age and growth studies since it cannot be assumed that the banding pattern of one species is representative of another (Goldman 2004).

Several techniques have been used for growth band enhancement in elasmobranch vertebrae and slight differences between methodologies may make one better for obtaining accurate results in a particular species (Goldman 2004). Some examples are: X-radiography (e.g., Natanson and Cailliet 1990, Cailliet et al. 1983), X-ray spectrometry (Jones and Green 1977), cedarwood oil immersion (Neer and Cailliet 2001), alizarin red (LaMarca 1966), silver nitrate (e.g., Neer and Cailliet 2001), crystal violet (e.g. Johnson 1979), graphite microtopography (Neer and Cailliet 2001) and the use of copper-, lead- and iron-based salts (e.g., Gelsleichter et al. 1998). In Lamniformes, several studies have used X-radiography on whole vertebrae (e.g., Cailliet and Bedford 1983, Liu et al. 1998), while others were based on counting growth bands using digital images of vertebral sections (e.g. Natanson et al. 2002, Ardizzone et al. 2006).

In the case of the bigeye thresher shark, little life history information is currently available, especially for the Atlantic Ocean, probably due to its low prevalence in longline catches (Berrondo et al. 2007, Castro et al. 2000, Mejuto 1985, Mejuto and Garcés 1984, Mejuto et al. 2009). Gruber and Compagno (1981) explored the age and growth of this species based on a limited dataset of mostly museum specimens captured in the Pacific and Atlantic Oceans. In the Pacific Ocean, an extensive age and growth study was carried out by Liu et al. (1998) in Taiwanese waters. In addition, some reproductive parameters have been reported for the Pacific (Chen et al. 1997, Gilmore 1993, Gruber and Compagno 1981) and Atlantic Oceans (Moreno and Morón 1992). Thus, the bigeye thresher is one of the pelagic shark species for which there is a major need of improved biological data. Furthermore, the species was classified as being at high risk in an Ecological Risk Assessment (ERA) of pelagic sharks caught in Atlantic pelagic longlines, highlighting the urgent need for better basic biological information on this species (Cortés et al. 2010).

Therefore, the objective of this study was to improve the knowledge on biological information for the bigeye thresher, by providing new information on the age and growth parameters for the species throughout the Atlantic Ocean. A secondary objective was to compare several procedures used for growth band enhancement in elasmobranchs, in order to determine the best technique for ageing bigeye thresher vertebrae.

V.2. Material and Methods

V.2.1. *Sampling*

All samples were collected by fishery observers from the Portuguese Institute for the Ocean and Atmosphere (IPMA, I.P.) onboard Portuguese commercial longline vessels targeting swordfish in the Atlantic Ocean. Vertebral samples were collected only from bigeye thresher specimens that were retrieved already dead when hauling the longline. A total of 546 vertebra samples were collected from September 2007 to December 2009 throughout the Atlantic Ocean, between latitudes 38 ºN and 35 ºS (Figure V.1).

All specimens were measured on board for fork length (FL), in a straight line, and the sex was determined. A section of 4 to 8 vertebrae was extracted from the region below the anterior part of the first dorsal fin. All samples were kept frozen while on the vessels and during transportation to the laboratory.

In the laboratory, the organic tissue of the vertebrae was first removed manually with scalpels, and then by soaking the vertebrae in 4-6 % sodium hypochlorite (commercial bleach) for 10 to 20 minutes, depending on size. Once cleaned, the vertebrae were stored in 70 % ethanol, then air-dried for 24 h before mounting in a microscope slide using thermoplastic cement. Once mounted, the vertebrae were sectioned sagittally with a Buehler low-speed saw, using two blades spaced approximately 500 μm apart. The resulting section included the focus of the vertebra and the two halves (one on each side of the focus), in a form typically called a “bow-tie”.

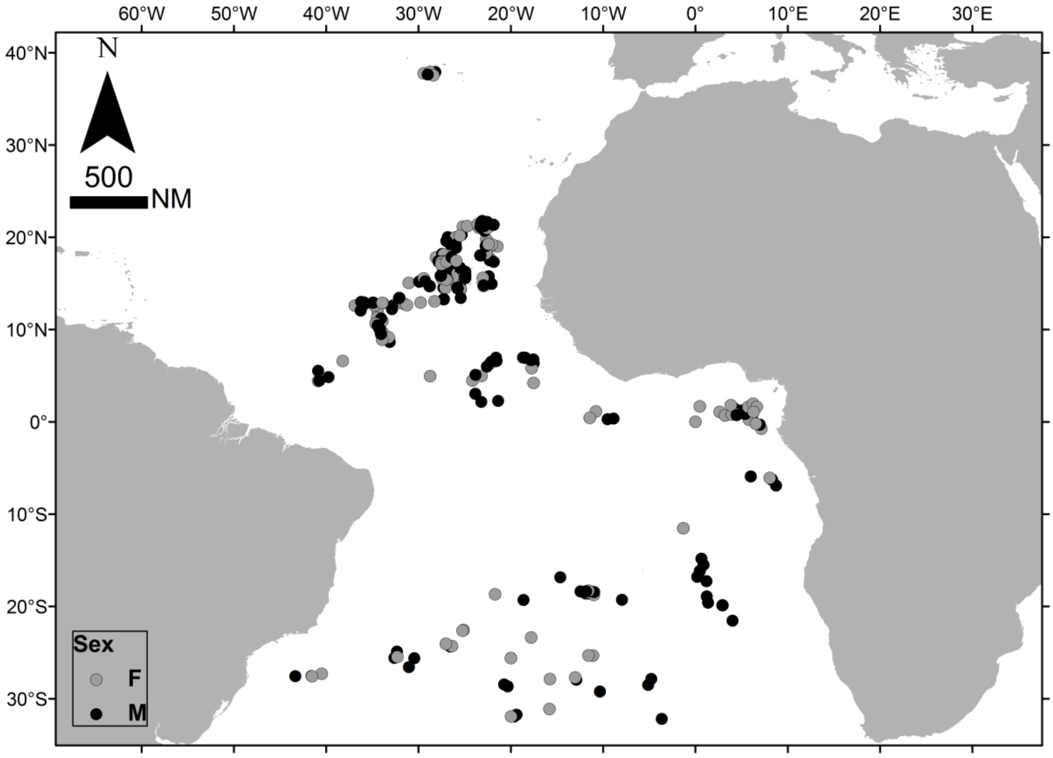

Figure V.1: Location of the catches of bigeye thresher shark (*A. superciliosus*) used for this study. Grey circles represent females (F) and black circles males (M).

Contrary to carcharhinid sharks, which are characterized by having relatively hard vertebrae with solid centra, the vertebrae of lamnoid sharks are typically poorly calcified, with fewer radials and large interstitial spaces in the intermedialia, resulting in a softer and fragile centra (Goldman 2004). Since this poor calcification of the bigeye thresher vertebrae was verified and confirmed in our specimens, special attention had to be taken when sectioning the vertebra so that the final section included the calcified radials of the intermedialia. Thus, when positioning the double saw against the vertebrae, it was confirmed that radials would be included between the two blades.

V.2.2. *Band enhancement techniques*

Several growth band enhancement methods used in elasmobranchs were tested to determine which was most appropriate for the vertebrae of this species. Vertebrae from

30 randomly selected specimens were prepared following four methodologies: no staining, staining with crystal violet (Johnson 1979), staining with alizarin red (LaMarca 1966) and X-raying of whole vertebrae (Cailliet et al. 1983).

The alizarin red staining procedure involved soaking the dried vertebral sections for 10 to 20 minutes, depending on the size of the vertebra. For crystal violet, the procedure was similar but the soaking time was shorter, ranging from 5 to 15 minutes. Once the staining was completed, the vertebral sections were maintained between two microscope slides (wrapped in folded paper to absorb the extra dye) to apply pressure for at least 24 hours in order to prevent curling and bending of the corners of the vertebral sections during drying. The bigeye thresher, like other Lamniformes sharks, seems liable to this problem due to the above-mentioned low calcification of the vertebral intermedialia. Once dried, the sections were mounted onto microscope slides using Cytoseal 60. Growth bands were examined under a dissecting microscope using transmitted white light. A preliminary trial was conducted to test compare X-rays of sectioned and whole vertebrae. As the latter showed better results, whole vertebra were X-rayed using digital film with an exposure of 5 seconds at 40 volts.

To test the different band enhancement techniques, the 30 vertebra (multiplied by 4 techniques) were read three times by one reader. In order to compare the ageing precision of each technique, both the coefficient of variation (CV) (Chang 1982) and the average percent error (APE) (Beamish and Fournier 1981) were calculated and compared. Bias plots were used to graphically assess the ageing accuracy of the techniques (Campana 2001), using the median value from the three readings as, excluding the crystal violet stained sections, which presented at least two identical readings for all vertebrae, several vertebrae presented different estimations for the three readings. Furthermore, a Bowker's test for symmetry (Hoenig et al. 1995) was used to test for systematic bias in the determination of age using the different techniques. In addition, the percentage of agreement (and percentage of agreement within one growth band) among the techniques was also calculated.

Once crystal violet staining had been chosen as the most appropriate band enhancement technique, all the remaining vertebrae were prepared following this protocol.

V.2.3. *Age estimation and comparison of the readings*

The vertebral sections of 117 specimens (reference set) were micro-photographed, and the centrum radius (CR) was measured digitally using Image J software (Abramoff et al. 2004) (Figure V.2). A linear regression was calculated between the centrum radius and the specimen FL. The significance of the regression was tested with an ANOVA, testing H0: slope parameter of the regression (β1) = 0. The coefficient of determination (R2) of the linear regression was determined and used to assess the quality of the fit.

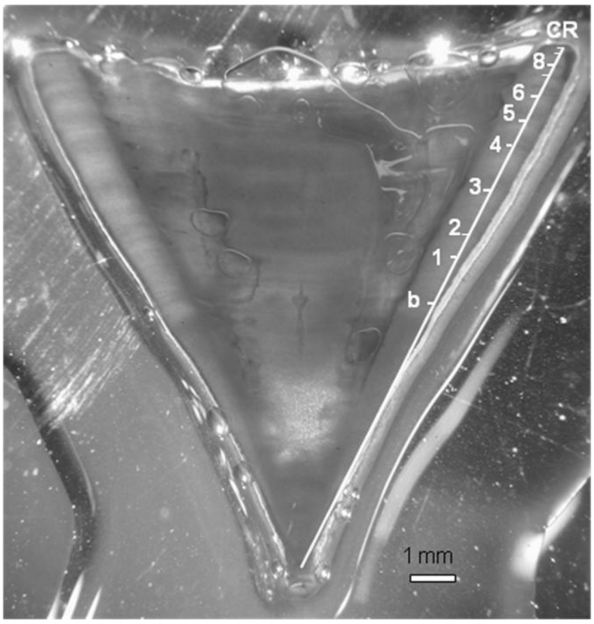

Figure V.2: Vertebral section from a bigeye thresher (*A. superciliosus*) female of 186 cm FL, with 9 visible growth bands. b = birth mark CR = centrum radius (white line).

After a preliminary first reading to adjust to the banding pattern of this species, a reference set of 117 vertebrae (from the 546 total vertebrae) was independently read by two readers three times in order to guarantee quality control and precision of the readings. To prevent bias while counting the bands, the two readers had no knowledge of the length or sex of each shark. After this step, the remaining sample was then read three times by the primary reader, and only those vertebrae whose band counts were the same for at least two of the three readings were accepted for the age and growth analysis. Each reading was finalized before starting the next one to prevent reader familiarity with any particular vertebrae.

In order to verify the temporal periodicity of band formation in the vertebral centra, a marginal increment analysis was initially attempted. However, due to the narrowness and faintness of the bands at the margin of the vertebrae, it was impossible to objectively determine and measure the marginal growth. Thus, a centrum edge analysis was conducted to the reference set (n=117) by identifying whether the last band in each of the vertebrae was opaque or hyaline (translucent). The proportion of vertebrae with either opaque or hyaline bands as the last band was calculated by month, and the proportions compared between months. Since samples were not available for all months, the available months were grouped in two categories: a) June and July, corresponding to a summer period; and b) October to January, corresponding to a winter period. A X^2 test of proportions was carried out to examine whether the proportions of opaque and hyaline edge bands between those two seasonal groups were significantly different. Though no validation *per se* was conducted, the temporal periodicity of band formation was assumed to be annual, (see section V.4. Discussion).

In order to compare the ageing precision between the three readings, both the coefficient of variation (CV) (Chang 1982) and the average percent error (APE) (Beamish and Fournier 1981) were calculated and compared. The percentage of agreement (PA) (and percentage of agreement within one growth band, PA ± 1 year) among the readings was also calculated. Bias plots were used to graphically assess the ageing accuracy between the three readings (Campana 2001). Furthermore, contingency tables and chi-square tests of symmetry (Evans and Hoenig 1998, Hoenig et al. 1995) were used to test if the differences between the three readings were due to systematic bias or random error. The symmetry of all three readings was tested simultaneously by plotting triplets of readings on a hexagon plot (Evans and Hoenig 1998). All symmetry analysis was carried out using the R language for statistical computing (R Core Team 2013), using the package 'fishmethods' (Nelson 2013). The hexagon plots for the triplets of readings were created and interpreted using R code provided by John M. Hoenig (pers. comm.)[5].

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[5] Dr. John M. Hoenig. Professor of Marine Science. Virginia Institute of Marine Science, USA.

V.2.4. *Growth modeling*

Five growth models were used and compared to describe the growth of this species, three variations of the von Bertalanffy growth function (VBGF) and two of the Gompertz growth function (GGF). The VBGFs used were a re-parameterization of the 3 parameters VBGF to estimate L_0 (size at birth) instead of t_0 (theoretical length at age 0) as suggested by Cailliet et al. (2006), a modified 2 parameters VBGF using a known and fixed size at birth (L_0) and a generalized VBGF with 4 parameters:

The 3 parameters von Bertalanffy growth model (VBGF) derived to estimate the size at birth (L_0) is:

$$Lt = L_{inf} - (L_{inf} - L_0)e^{-kt}$$

Where:

Lt = mean length at age t;
L_{inf} = asymptotic maximum length;
k = growth coefficient;
L_0 = length at birth

The modified 2 parameters VBGF with a fixed size at birth (VBGF with fixed L_0) is:

$$Lt = L_{inf}(1 - be^{-kt})$$

Where $b = (L_{inf} - L_0)/L_{inf}$

For the latter model, a L_0 value of 84 cm FL was used. This value was chosen following the size at birth of 135 to 140 cm TL estimated for this species by Chen et al. (1997). This value is comparable with the smallest free swimming sizes reported to date (130 cm TL, Bigelow and Shroeder 1948; 155 cm TL, Stillwell and Casey 1976; 159 cm TL, Gruber and Compagno 1981; 156 cm TL, Moreno and Morón 1992). The mean value of this range (135 to 140 cm TL) was converted to FL (84 cm FL) using the equation:

$$FL = 0.58\ TL + 4.83$$

(n = 390; $R^2 = 0.92$; SE intercept=2.41; SE slope=0.01; Regression ANOVA: F = 4675; p-value < 0.01) (IPMA *unpublished data*).

The generalized VBGF with 4 parameters was defined by Richards (1959) as:

$$L_t = L_{inf}(1 - e(-k(1-m)(t-t_0)))^{1/(1-m)}$$

Where t_0 = theoretical age at zero length

m= fitted fourth function parameter

Two versions of the Gompertz growth function (Ricker 1975) were fitted, with 3 parameters (GGF) and 2 parameters (GGF with fixed L_0). The same value of size at birth as in the VBGF (84 cm FL) was used:

$$Lt = L_0 e^{G[1-e(-kt)]}$$

Where *G* is the instantaneous rate of growth at time *t*,

Lt = mean length at age *t*;

k = rate of decrease in *G*;

L_0 = length at birth

The size distribution of the sample was plotted and analysed in R (R Core Team 2013) using ggplot2 (Wickham 2009). All growth models were fitted in R, using non linear least squares with the Gauss-Newton algorithm (nls function in R), except the generalized VBGF that was fitted using non linear least squares with grid-search (package nls2, Grothendieck 2013). For each model, the parameters and standard errors (SE) were estimated, and the 95% confidence intervals calculated. Furthermore, to assess model adequacy to the data, the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) values were calculated for each model, and the results compared. A Likelihood Ratio Test (LRT), as defined by Kimura (1980) and recommended by Cerrato (1990), was used to test the null hypotheses (H_0) *that there is no difference in growth parameters between males and females*. The growth parameters of the north and south Atlantic samples were also compared. For the purposes of this analysis, the two hemispheres were separated based on the 5ºN parallel, as recommended in the ICCAT Manual for shark species (ICCAT 2006-2013).

V.3. Results

V.3.1. *Sample*

A total of 546 samples of vertebrae of bigeye thresher were collected, from which 501 had a valid reading and thus were used for the age and growth analysis. From these, 258 were females (52%) and 241 males (48%), while the sex of two specimens could not be determined. The size distributions of the specimens used in this study ranged from 102 to 265 cm FL for females and 94 to 260 cm FL for males (Figure V.3).

V.3.2. *Band enhancement techniques*

Before calculating precision indices, it was clear that some techniques enhanced the growth bands better than others. It was difficult to differentiate growth bands and to differentiate the growth bands from the "false checks" or "split bands", as also observed by Goldman (2004), in the unstained vertebrae compared with stained ones (both with alizarin red and crystal violet). In the X-rays, growth bands could be identified near the centrum, but the level of differentiation decreased towards the edges due to a shadow effect covering these areas. It was therefore particularly difficult to obtain valid readings with the X-ray technique, especially in the larger vertebrae.

Staining with crystal violet led to the best precision indices, with 5.7 % CV and 6.6 % APE, followed by the alizarin red stain, with 9.3 % CV and 10.4 % APE. Unstained sections and X-raying resulted in much poorer band discrimination and consequently much worse precision indexes (15.3 % CV, 16.7 % APE and 14.2 % CV, 15.9 % APE, respectively). The same pattern was observed in the percentage of accepted readings, with crystal violet being the methodology with the most vertebrae (100 %) acceptable for use in the models (accepted=agreement achieved in at least two of the three readings), followed by alizarin red staining (83 %), no staining (57 %) and X-raying (53 %).

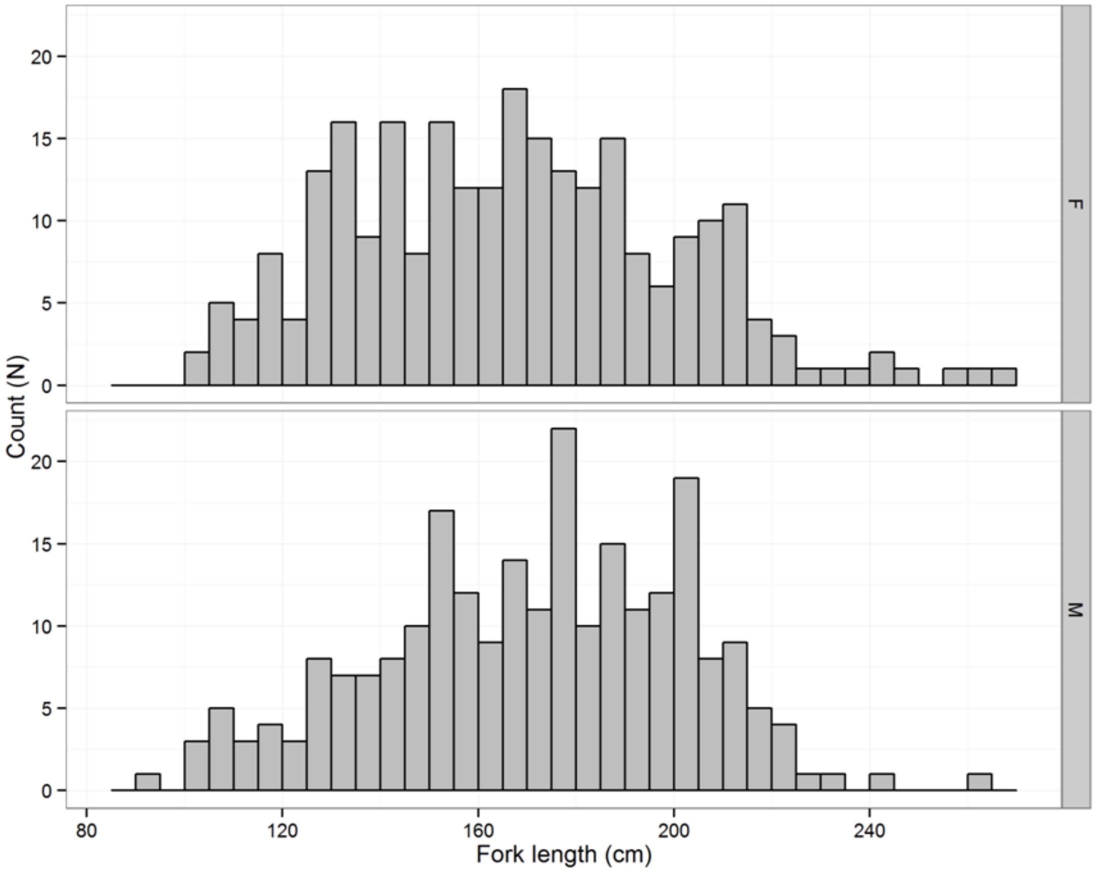


Figure V.3: Length-frequency distribution of the sample of bigeye thresher (*A. superciliosus*) used in this study. Size classes were grouped into 10-cm fork length classes. The two specimens for which the sex was not determined are not represented in the figure.

Age-bias plots were calculated to assess the accuracy of the readings in each technique. Since crystal violet was the methodology with the highest precision index and percentage of accepted readings, the remaining techniques were plotted against it (Figure V.4).

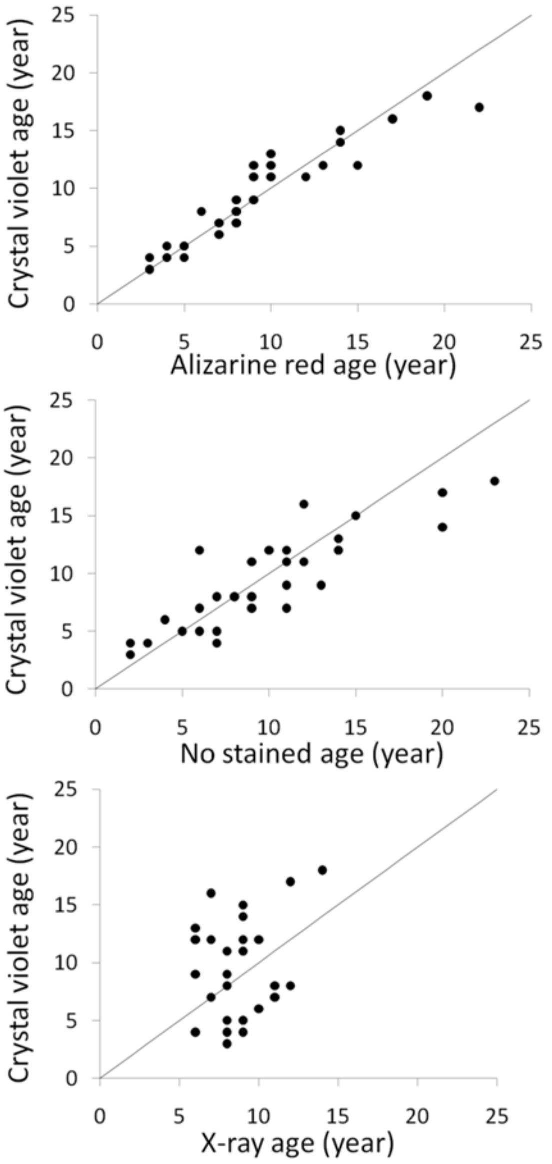


Figure V.4: Age-bias plots of the growth band enhancement techniques tested in this study for bigeye thresher (*A. superciliosus*) vertebrae: Crystal violet, Alizarin red, unstained vertebrae and X-rays of whole vertebrae.

Bowker's test for symmetry showed no systematic bias when comparing readings of the crystal violet treatment with those of alizarin red ($X^2 = 19.0$, df = 18, $p > 0.05$), no staining ($X^2 = 19.0$, df= 21, $p > 0.05$) and X-rays of whole vertebrae ($X^2 = 24.0$, df = 23, $p > 0.05$), suggesting that the differences in the readings of each technique were caused by random error. When analyzing the percentage agreement between the techniques, it was clear that alizarin red staining showed readings most similar to the crystal violet treatment, with 30 % agreement overall and 73 % to within one growth band. Unstained sections had only 13 % readings consistent with the crystal violet readings and 43 % to within one growth band. The X-ray readings showed by far the highest discrepancy with crystal violet values, with only 7 % agreement and 3 % to within one growth band.

V.3.3. *Age estimation and comparison of age readings*

A significant linear relationship was established between FL (cm) and the vertebrae centrum radius (CR, mm), suggesting that there is a direct linear relationship between specimen growth and growth of the vertebrae (Figure V.5):

$FL = 9.88 \, CR + 48.88$

($R2 = 0.73$; Regression ANOVA: $F = 308.9$; $p < 0.01$)

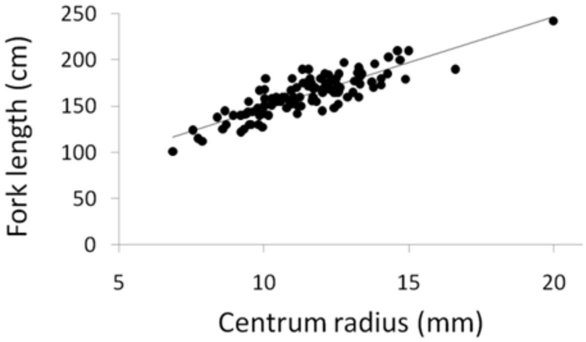


Figure V.5: Relationship between fork length (cm) and vertebrae centrum radius (mm) for bigeye thresher shark (*A. superciliosus*).

Although the sample was not equally distributed along the year, the centrum edge analysis suggested a seasonal pattern of band formation. A higher proportion of vertebrae with opaque last bands were observed during the winter period, from October to January (62 % to 68 %), compared with the summer period, of June and July (15 % to 25 %). The difference in the proportions between those two periods was statistically significant ($X^2 = 13.4$, df = 1, $p < 0.01$).

As expected and seen on other Lamniformes sharks, the vertebrae of bigeye thresher were poorly calcified and in general difficult to read, especially when compared to Carcharhinidae sharks. Nevertheless, the birth band was easily identifiable as it coincides with an angle change in the corpus calcareum of the vertebrae. A high degree of agreement over time was observed between the three readings of the primary reader, with the percentage agreement between the first and second, first and third, and second and third readings being 46%, 43% and 87%, respectively. A total of 96.6% of the vertebrae had at least two identical readings (99.2% within one growth band) and thus were accepted for the growth modeling. The coefficient of variation between the three readings was 10.03% and the average percent error (APE) 7.68%. A high agreement with no systematic bias was observed between the readings when comparing graphically the three readings of the primary reader using the age-bias plots (Figure V.6).

In addition, the symmetry of all three readings was tested simultaneously plotting triplets of readings on a hexagon plot, as suggested by Evans and Hoenig (1998) (Figure V.7). When interpreting the hexagon plot, most of the observations were on the A axis (the horizontal line). This corresponds to the second reading (B) equaling the third reading (C), but the first reading (A) being different from the other two. If all three readings were equivalent (i.e. interchangeable), then there would be an overall symmetry. That is, each triangle would have the same number of observations and the 6 rays going from the center outwards would have the same number of observations (except for discrepancies due solely to sampling error). The pattern obtained in this study revealed that there is no sign of an evolution of the readings towards higher or lower values over time (ageing criteria remained stable rather than having evolved over time). Thus, as time passed, the primary reader´s readings showed less variability but did not change systematically towards higher or lower values, indicating there is little evidence of systematic differences between the readings caused by other reasons than due to random error.

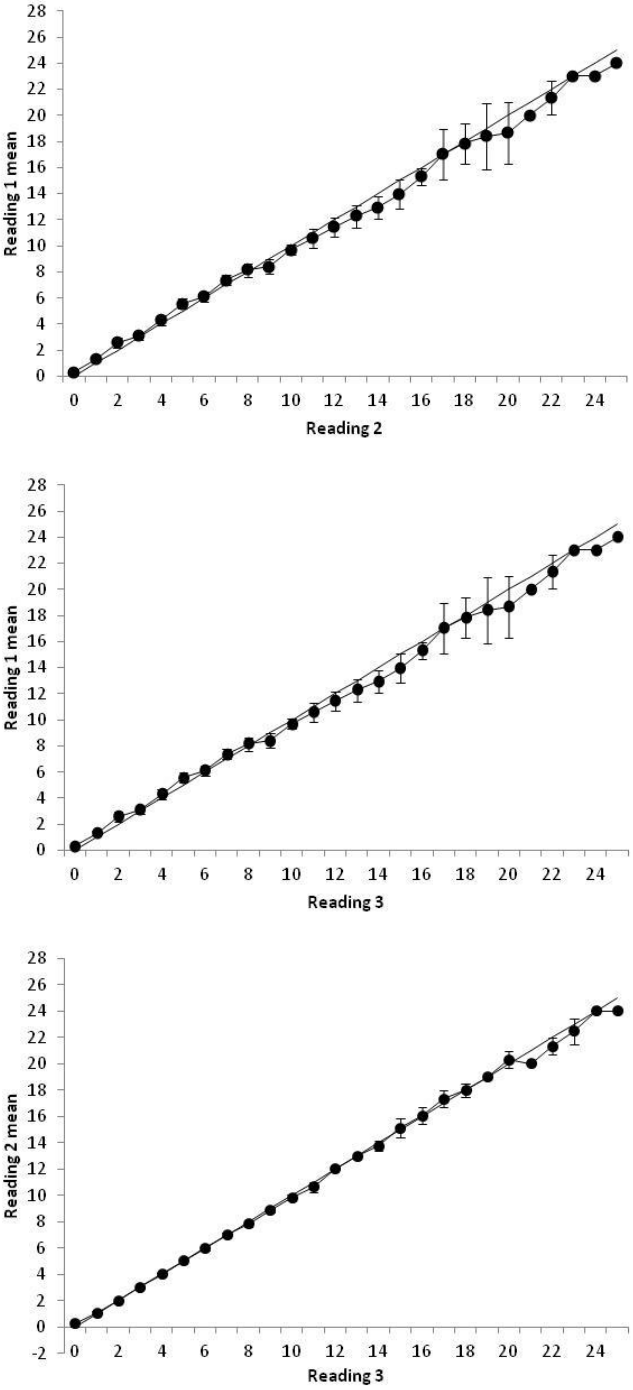


Figure V.6: Age–bias plots of pairwise age comparisons between the three readings carried out by the primary reader based on examination of bigeye thresher shark (*A. superciliosus*) vertebrae.

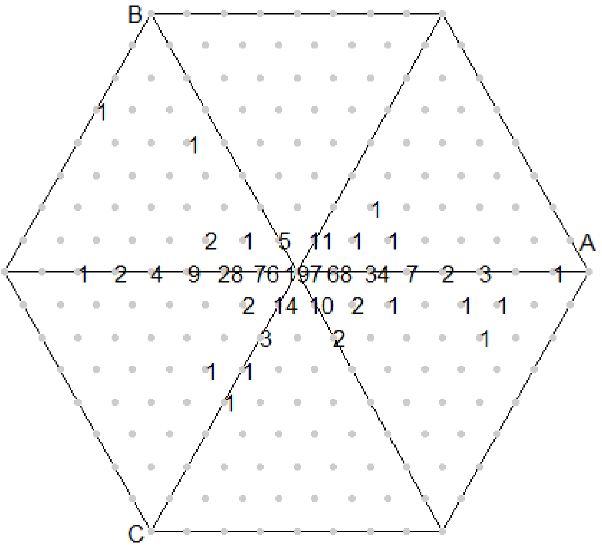


Figure V.7: Hexagon plot representing the triplets of readings on bigeye thresher (*A. superciliosus*) vertebrae.

V.3.4. *Growth modeling*

The ages estimated in this study ranged from 0 (young of the year) to 25 years for both sexes. Of the five growth models used, the generalized VBGF with 4 parameters was the only that did not converge, even when the grid-search technique (with the starting values varying between a range of possible values) was used. Based on both the statistical goodness-of-fit and the resulting biological parameters that seemed realistic, the growth parameters obtained by the regular 3 parameter VBGF were considered the best for describing the growth of this species for both sexes. The estimated Linf values were always higher and the growth coefficients (*k* values) lower when using the VBGF, than those obtained by the VBGF with fixed L_0, for both females (L_{inf}= 284.2 cm FL, *k*= 0.06/yr) and males (L_{inf}= 245.6 cm FL, *k*= 0.09/yr) (Figure V.8; Table V.1). In the case of the Gompertz models a similar pattern was found, with the GGF producing lower growth coefficients in both sexes than the GGF with fixed L_0.

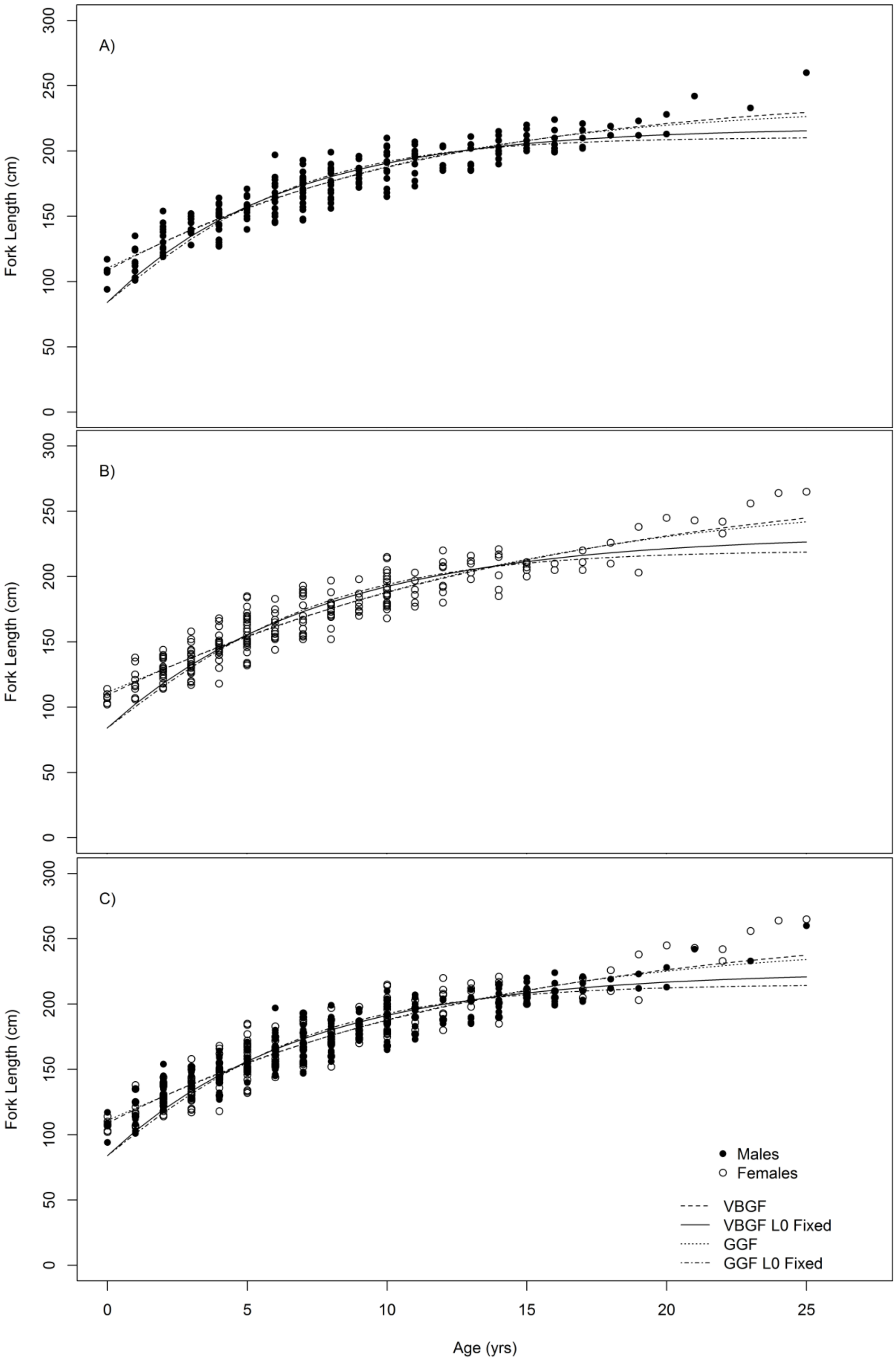


Figure V.8: Estimated ages and growth models for bigeye thresher (*A. superciliosus*) in this study: the von Bertalanffy growth function (VBGF), VBGF with fixed L_0, the Gompertz growth function (GGF) and GGF with fixed L_0 (L0 = 84 cm FL). Growth curves are presented for A) males, B) females and C) sexes combined.

Table V.1: Growth parameters estimated for the bigeye thresher (*A. superciliosus*) from the Atlantic Ocean, obtained with the von Bertalanffy growth function (VBGF), the VBGF with fixed size at birth (L_0), the Gompertz growth function (GGF) and the GGF with fixed L_0 (L_0 = 84 cm FL). For each model the parameters are given with their respective standard errors (SE) and 95 % confidence intervals (CI). The Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) values are given for model comparison within each gender group.

Sex	**Model**	**AIC**	**BIC**	**Parameter**	**Estimate**	**SE**	**95% CI**	
							Lower	**Upper**
Sexes combined	VBGF	3827.1	3843.9	L_{inf}	263.50	7.516	248.75	278.28
				k	0.07	0.006	0.06	0.08
				L_0	108.80	1.623	105.63	112.01
	VBGF Fixed L_0	3984.0	3996.6	L_{inf}	224.70	2.513	219.72	229.59
				k	0.14	0.005	0.13	0.15
	GGF	3837.1	3854.0	G	0.80	0.016	0.77	0.83
				k	0.11	0.007	0.09	0.12
				L_0	110.90	1.494	107.91	113.79
	GGF Fixed L_0	4042.2	4054.8	G	0.94	0.009	0.92	0.96
				k	0.22	0.006	0.20	0.23
Males	VBGF	1831.0	1845	L_{inf}	245.60	7.535	230.73	260.42
				k	0.09	0.009	0.07	0.10
				L_0	108.50	2.306	103.91	113.00
	VBGF Fixed L_0	1908.8	1919.2	L_{inf}	218.10	3.077	211.99	224.11
				k	0.16	0.008	0.14	0.18
	GGF	1835.4	1849.4	G	0.75	0.020	0.71	0.79
				k	0.12	0.010	0.10	0.14
				L_0	110.30	2.143	106.10	114.55
	GGF Fixed L_0	1936.2	1946.6	G	0.92	0.011	0.90	0.94
				k	0.23	0.009	0.21	0.25
Females	VBGF	1993.3	2007.5	L_{inf}	284.20	14.430	255.76	312.60
				k	0.06	0.008	0.04	0.08
				L_0	109.00	2.249	104.61	113.47
	VBGF Fixed L_0	2073.7	2084.3	L_{inf}	231.90	4.037	223.99	239.89
				k	0.13	0.007	0.12	0.15
	GGF	1998.5	2012.8	G	0.86	0.027	0.80	0.91
				k	0.10	0.009	0.08	0.11
				L_0	111.20	47.000	107.20	115.27
	GGF Fixed L_0	2105.9	2116.5	G	0.96	0.014	0.94	0.99
				k	0.20	0.008	0.19	0.22

Significant differences were found between sexes in all the estimated VBGF growth parameters except for the L_0 (L_{inf} LRT, X2 = 6.08, df = 1, p< 0.05; k LRT, X2= 4.13, df = 1, p< 0.05; L0 LRT, X^2 = 1.66, df = 1, p> 0.05; combined parameters LRT, X2= 9.69, df = 3, p< 0.05), based on the Kimura (1980) LRT tests. Females exhibited lower growth coefficients (*k* values) and higher asymptotic size (L_{inf}) than males for all models.

In order to determine if there were differences in the growth of the bigeye thresher between the north and south Atlantic, a VBGF growth model was fitted for each sex and hemisphere. The sample size for this analysis for the north Atlantic consisted of 358 sharks (200 females and 158 males) and for the south Atlantic of a total of 141 specimens (58 females and 83 males). Only the 2 parameter VBGF with fixed L_0 converged for the separate sexes in each hemisphere, while the traditional VBGF converged for the north Atlantic but not for the south. Thus, the VBGF with fixed L_0 was used to obtain and compare the growth parameters for the two hemispheres (Table V.2). The overlaps in the confidence intervals (CI) of the parameters were used for this comparison. There was no overlapping between the north and south CIs, with the exception of a slight overlap in the males' maximum asymptotic size (L_{inf}). The estimated growth coefficients were higher for both sexes for the north Atlantic ($k_{females}$= 0.16, CI= (0.14, 0.18); k_{males}= 0.18, CI= (0.15, 0.21)) than for the southern hemisphere ($k_{females}$= 0.09, CI= (0.07, 0.11); k_{males}= 0.13, CI= (0.11, 0.15)).

Table V.2: Growth parameters estimated for the bigeye thresher (*A. superciliosus*) from the North and South Atlantic Ocean, obtained with the VBGF with fixed size at birth (L_0 = 84 cm FL). For each model, the parameters are given with their respective standard errors (SE) and 95 % confidence intervals (CI).

Sex	**Atlantic**	**Parameter**	**Estimate**	**SE**	**95% CI**	
					Lower	**Upper**
Males	North	L_{inf}	211.77	4.64	202.62	220.93
		k	0.18	0.01	0.15	0.21
	South	L_{inf}	229.00	5.10	218.85	239.15
		k	0.13	0.01	0.11	0.15
Females	North	L_{inf}	219.20	4.34	210.64	227.77
		k	0.16	0.01	0.14	0.18
	South	L_{inf}	265.70	11.34	243.01	288.43
		k	0.09	0.01	0.07	0.11

V.4. Discussion

The vertebrae of the bigeye thresher are very poorly calcified and are therefore difficult to read compared with other sharks such as the Carcharhiniformes. The only extensive study found on the age and growth of the bigeye thresher (Liu et al. 1998) used X-rays of whole vertebrae. Cailliet and Bedford (1983) also used X-rays for ageing of the common thresher *Alopias vulpinus*. In our study, however, the X-ray technique never produced satisfactory results, either in terms of the readings or the costs and logistics. After testing four different techniques, we recommend staining vertebra sections of approximately 500 μm thickness with crystal violet as the best enhancing technique for reading growth bands and estimating ages in this species. Our results suggest that alizarin red staining produces the closest results to crystal violet staining out of the techniques tested, thus we recommend this methodology as a second choice if crystal violet staining is not possible.

Gruber and Compagno (1981) mentioned that the "maximum accurately measured *Alopias superciliosus*" in their study was 461 cm TL (270 cm FL, estimated from our conversion equation) and that the largest male was a 378 cm TL specimen (estimated 222 cm FL) caught off of California. Liu et al. (1998) found maximum sizes of 357 cm TL (estimated 210 cm FL) for males and 422 cm TL (estimated 247 cm FL) for females off Taiwan. Finally, in the northeast Atlantic, Moreno and Morón (1992) caught a male of 410 cm TL (estimated 240 cm FL) and a female of 461 cm TL (estimated 260 cm FL). These previously published values are relatively similar to our own maximum sizes (260 cm FL for males and 265 cm FL for females), suggesting that the sample used in this study covers all size range of the species.

Several approaches were used in this study when evaluating the precision and testing for bias in the age determinations of bigeye thresher shark (PA, PA ± 1 year, APE, CV, Age bias plots, tests of symmetry), as suggested by Goldman et al. (2012). To our knowledge, this was the first study that tested the symmetry of three age counts using a hexagon plot as described by Evans and Hoenig (1998). No systematic bias in band counts was detected when interpreting the hexagon plot, indicating that there is little evidence of systematic differences between the readings being caused by other than due to random error. Although not directly comparable between studies, reference levels of 7.6 % for CV and 5.5 % for APE have been suggested for shark studies, with most studies reporting shark ages based on vertebrae exceeding 10 % CV values (Campana 2001). In this study, values of 10.03% CV, 7.68% APE and 96% PA were determined, which taken together with the age bias and symmetry plot results indicates that our age estimates were consistent and adequate for this species.

Due to the morphology of the vertebrae of the bigeye thresher, characterized by low calcification and narrow and faint bands at the edges, it was not possible to objectively determine marginal growth increments. Few studies on the age and growth of Alopiidae sharks exist, with the majority from the Pacific Ocean (*A. superciliosus*: Liu et al. 1998; *A. vulpinus*: Cailliet and Bedford 1983; Smith et al. 2008a; *A. pelagicus*: Liu et al. 1999) and only one from the north Atlantic (*A. vulpinus*: Gervelis and Natanson 2013). Of these studies, only a few attempted to perform age verification. Liu et al. (1998) verified a one-band (composed of one opaque ring and one hyaline ring) per year periodicity in the bigeye thresher, while Liu et al. (1999) verified the same pattern for the pelagic thresher (*A. pelagicus*), in both cases using marginal increment analysis for populations of the northwest Pacific. In the Atlantic, the preliminary centrum edge analysis (with limited samples from six months of the year) for bigeye thresher, conducted in this study also suggests a seasonal pattern in band formation. Thus, although no age verification was carried out in the present study, assuming a one band per year periodicity for this species seems reasonable in light of the few available studies. Furthermore, age and growth studies of other species of Lamniformes sharks have validated an annual band deposition. Natanson et al. (2002) proposed that vertebral band pairs are deposited annually by using vertebrae from recaptured oxytetracycline-injected porbeagle sharks (*Lamna nasus*). The same periodicity (one band per year) was validated for the shortfin mako (*Isurus oxyrinchus*) both by bomb carbon chronology and oxytetracycline tagging (Ardizzone et al. 2006, Natanson et al. 2006). Finally, Wintner and Cliff (1999) stated that even though they could not determine band periodicity using marginal increment analysis in the white shark (*Carcharodon carcharias*) off the coast of South Africa, one specimen that had been tagged with oxytetracycline and recaptured also suggested annual deposition. Thus, and despite the lack of validation for the bigeye thresher in this study, the growth data presented represents the most comprehensive age estimates for this species for the north and south Atlantic, and as such are an important contribution to our understanding of the biology of this species. Nevertheless, it should be noted that these estimates should be used with caution for stock assessment and management decisions until definitive age verification is accomplished.

All growth parameters estimated by the four converging growth models used in this study had biologically reasonable values. The differences between the AIC values of the VBGF (lowest AIC) growth model and the GGF for both sexes were small (< 5), while the differences between the VBGF and both the VBGF and GGF with a fixed L_0 can be considered high (>10), and as such these models should be discarded, as suggested by Katsanevakis (2006). Nevertheless, it should be noted that when considering VBGF and GGF with a fixed L_0, different authors give different values for size at birth (e.g., Bass et al. 1975, Gilmore 1993, Moreno and Morón 1992) and that changing this value will influence the estimation of the other parameters (Pardo et al. 2013). On the other hand, although the GGF also produced realistic growth parameters, this growth function has been described as better suited for batoids (or elasmobranchs that hatch from eggs), whose volume increases with age more than length (e.g. myliobatiform) (Goldman et al. 2012). As the growth parameters obtained by the regular VBGF had the best statistical fit and were biologically realistic, we recommend its use for describing the growth of bigeye thresher shark.

To our knowledge, the present study is the first comprehensive age and growth study for the bigeye thresher shark covering both north and south Atlantic. The growth parameters obtained in this study are comparable to those generated for the northwest Pacific population by Liu et al. (1998) with some differences. Females from our study seem to grow to a larger size (L_{inf} = 284.2 cm FL), but at a slower rate (k= 0.06) than what has been described for the northwest Pacific (L_{inf} = 241.7 cm FL, k=0.09) (Table V.3). On the other hand, males seem to grow to a slightly larger size (Linf = 245.6 cm FL) but at a similar rate to that described for the northwest Pacific (L_{inf} = 235.5 cm FL, k=0.09) (Table V.3). These differences might be explained by the fact that our sample contained larger sizes, and consequently older ages, for both females and males when compared to the northwest Pacific study (Liu et al. 1998). The values of L_{inf} obtained in our study were close to the maximum sizes of bigeye threshers reported in the literature (Gruber and Compagno 1981, Liu et al. 1998, Moreno and Morón 1992). .

Table V.3: Comparison of von Bertalanffy growth function (VBGF) parameters in age and growth studies carried out worldwide in the Alopiidae family. Linf = asymptotic size, FL; k = growth coefficient, y-1. *: Data for sexes combined. **: Sizes in Precaudal length. NA: Values not available.

Study	**Sex**	**Size range (FL, cm)**	**Sample size (N)**	**VBGF parameters**		**Max. obs age (yrs)**	**Region**	**Species**
				L_{inf}	k			
Present study	Males	94-260	241	245.6	0.09	25	Atlantic wide	*A. superciliosus*
	Females	102-265	258	284.2	0.06	25		
Fernandez-Carvalho et al. (2011)	Males	101-210	42	206.0	0.18	17	NE Tropical Atlantic	*A. superciliosus*
	Females	115-242	73	293.0	0.06	22		
Liu et al. (1998)	Males	NA-213.5	214	235.5	0.09	20	NW Pacific (Taiwan)	*A. superciliosus*
	Females	NA-256.5	107	241.7	0.09	21		
Cailliet and Bedford (1983)	Males	35.1-312.7*	143*	271.1	0.22	15*	NE Pacific (California/Oregon)	*A. vulpinus*
	Females			345.2	0.16			
Smith et al. (2008a)	Males	NA	83	229.7	0.19	19	NE Pacific (California/Oregon)	*A. vulpinus*
	Females	NA	129	253.9	0.12	22		
Gervelis and Natanson (2013)	Males	56.3-264.4*	135	227.9	0.16	22	NW Atlantic (NE USA)	*A. vulpinus*
	Females		173	274.5	0.09	24		
Liu et al. (1999)	Males	NA	323	182.2**	0.12	14	NW Pacific (Taiwan)	*A. pelagicus*
	Females	NA	508	197.2**	0.09	16		

The *k* values obtained in our study for the bigeye thresher are the lowest growth coefficients ever presented for the species and within the Alopiidae family (Table V.3), highlighting the species' slow growth pattern, and consequent vulnerability to fishing pressure and mortality

As described for other shark species, the growth of bigeye thresher males and females was statistically different, with females presenting a lower growth coefficient and higher asymptotic size than the males (e.g. Coelho et al. 2011, Gervelis and Natanson 2013, Piercy et al. 2007). Therefore, it is advisable to use the growth parameters obtained specifically for each gender instead of the parameters obtained for the sexes combined. The growth curves of both sexes were similar until age 10, after which males exhibited a considerable reduction in the growth rate, while females showed a straighter growth curve, with a far less acute reduction in the growth rate than males and at a later age.

Future studies on this species should try to include more samples from the south Atlantic region, and especially of the smaller and larger length classes, as some difficulties occurred when comparing the two hemispheres. This was due to the relatively smaller sample size for the southern region, but also to the fact that most samples from the north Atlantic were collected around the Cape Verde Archipelago, where the majority of the specimens tended to be small. Nevertheless, the differences observed in the growth of the bigeye thresher shark between the north and south Atlantic seems to exist, especially for females, suggesting slower growth rates for the southern population.

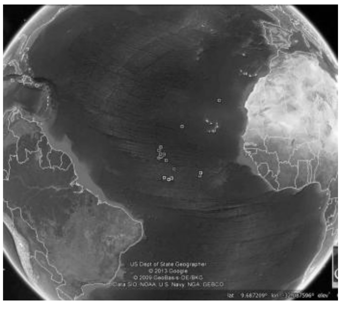
Accurate age information is vital for obtaining quality estimates of growth which are essential for successful and sustainable fisheries management. The growth parameters presented in this study are the first estimates for the bigeye thresher shark covering an extensive area in the Atlantic Ocean and can now be incorporated into stock assessment models to allow more science based fishery management and conservation initiatives. The extremely slow growth rates obtained with our study suggest a high susceptibility to fisheries mortality, and the importance of protecting this species. Although the bigeye thresher is currently managed and some conservation measures are already in place (ICCAT Rec. 2009/07 prohibiting onboard retention), its slow growth rates together with its high at-haulback mortality suggest the need for further studies to implement additional conservation measures, in order to prevent increased fishing mortality and population declines.

V.5. Acknowledgments

This study, including sampling and data collection, was conducted within the scope of Projects THRESHER (FCT Proj. PTDC/MAR/109915/2009), SELECT-PAL (programa PROMar proj. 31-03-05-FEP-1) and the EU Data Collection Framework. The authors thank the skippers and crews of several Portuguese longliners, as well as the technicians (S. Amorim, M. Cerqueira, S. Góis, I. Ribeiro, J.R. Táta and C. Barbosa) for collecting the samples. The authors are grateful to G. Burgess and Dr. A. Piercy (Florida Program for Shark Research/Florida Museum of Natural History) for their recommendations and help on processing the vertebrae, and to Prof. John M. Hoenig (Virginia Institute of Marine Science) for providing the R-code and help with the hexagon plots creation and interpretation. The Portuguese Foundation for Science and Technology (FCT, Fundação para a Ciência e a Tecnologia) funded the PhD grant attributed to J. Fernandez-Carvalho (Ref: SFRH/BD/60624/2009) and the Post-Doctoral grant attributed to R. Coelho (Ref: SFRH/BPD/93936/2013).

SECTION 3:

MOVEMENTS AND HABITAT UTILIZATION



CHAPTER VI. HABITAT USE AND DIEL VERTICAL MIGRATIONS OF *A. SUPERCILIOSUS* DETERMINED BY SATELLITE TELEMETRY. [6]

VI.1. Introduction

Pelagic sharks are captured by a wide range of commercial fisheries but are particularly common as bycatch of pelagic longlines targeting tunas and tuna-like species, as in the case of the longline fisheries targeting swordfish (e.g. Petersen et al. 2009, Coelho et al. 2012a). Understanding the habitat use and foraging ecology of oceanic sharks is crucial, not only for assessing the fishing impacts to these shark species, but also on the marine communities in general given that pelagic sharks are apex predators on the top of the marine food webs. For most of the shark bycatch species the current knowledge on their biology, ecology and habitat use is still very limited, and this includes some of the currently protected species as the bigeye thresher, *Alopias superciliosus*, that is currently prohibited to retain and has to be discarded both in the Atlantic (ICCAT 2009) and Indian (IOTC 2012) Oceans.

The bigeye thresher is a pelagic shark distributed worldwide in oceanic and neritic waters over continental and insular shelves (Gruber and Compagno 1981, Compagno 2001, Smith et al. 2008a). Characterized by having an extremely low fecundity (two to four embryos per reproductive cycle) and slow growth, this species is considered one of the most vulnerable pelagic sharks to fisheries (Smith et al. 1998, Chen and Yuan 2006, Cortés 2008, Cortés et al. 2010). Although, the bigeye thresher is commonly caught in pelagic longline fisheries in all Oceans, the information on the species habitat use and migrations is very limited, which precludes the provision of sound-based scientific advice regarding fisheries mitigation measures aiming the conservation of this species.

Over the past years, the use of satellite telemetry to study the movements and behavior of large highly migratory species like bluefin tuna, *Thunnus thynnus* (Block et al. 2005, Wilson et al. 2005); swordfish, *Xiphias gladius* (Abascal et al. 2015) and pelagic sharks (Kerstetter et al. 2004, Moyes et al. 2006, Campana et al. 2009, Stevens

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[6] ***Based on the manuscripts***: Coelho R, Fernandez-Carvalho J, Santos MN. *Submitted*. Habitat use and diel vertical migrations of the bigeye thresher shark, *Alopias superciliosus*: overlapping with pelagic longline fishing gear. Mar. Environ. Res.

et al. 2010; Abascal et al. 2011) has been increasing. Currently, besides providing estimates of geo-location, pop-up satellite archival tags (PSAT) can also collect and archive physical oceanographic data like water temperature, pressure (depth) and light levels. These types of tags are programmed for a predetermined period of time, after which the tags detach automatically, float to the surface and transmit the stored data to passing satellites of the ARGOS system. The data can then be used to calculate overlaps (both horizontal and vertical) between the species distribution patterns with the pelagic fishing gears, which can assist fishery scientists and managers to implement more efficient management and conservation measures. Some previous studies have deployed satellite telemetry tags on bigeye threshers, but most were in the Pacific and Gulf of Mexico, and analyzed a very limited number (1 to 3) of tag reports (Weng and Block 2004, Stevens et al. 2010, Musyl et al. 2011, Carlson and Gulak 2012).

Given the scarcity of information on habitat use for the bigeye thresher shark and its vulnerability to commercial oceanic fisheries, the main objective of this study was to provide consistent insight regarding the species habitat utilization, particularly in terms of depth related movements and diel cycle patterns. The second objective was to calculate overlaps between the species habitat utilization and pelagic longline fishing gear utilization, specifically the surface longlines that are deployed targeting swordfish and frequently bycatch sharks.

VI.2. Material and Methods

VI.2.1. *Tagging protocol*

The Pop-up Satellite Archival Tags (PSAT) used in this study were built by Microwave Telemetry Inc, and both Standard, X-tags and High Rate (HR) tag models were used (Figure VI.1). The PSATs deployments were carried out by observers from the *Portuguese Sea and Atmospheric Research Institute* (IPMA) onboard vessels from the Portuguese pelagic longline fleet. Tag deployment and pop-up took place between August 2012 and June 2014.

The PSATs were rigged with monofilament leaders secured with copper crimps and encased in surgical silicone tubing. An umbrella-type nylon dart (Domeier et al. 2005) was used to attach the tag laterally to the shark dorsal musculature below the first dorsal fin, using the methodology described by Howey-Jordan et al. (2013). The captured sharks were restrained alongside the vessel or hauled vertically alongside the vessel, were measured for fork length (considering 10 cm size classes) and the sex was recorded while being tagged. Additional data recorded for each tagged specimen included the tagging location (latitude and longitude), date and time. The tags were programmed for deployment periods between 1 and 6 months.

Figure VI.1: Pop-up Satellite Archival Tags (PSAT) used in this study. Type PTT-100 X-Tag built by Microwave Telemetry Inc.

The X-tags used record and archive data on depth and temperature at every 2 minutes interval, daily minimum and maximum depths and temperatures, as well as the light levels and time at sunrise and sunset. After pop-up, the transmitting tags attempt to transmit one depth and temperature data-point within each 15-30 minute period in the time series (depending on deployment period), as well as the full minimum and maximum daily depths and the daily times at sunrise and sunset. The Standard tags work in a similar way but record and archive data with a lower time resolution that was set to 15 minutes intervals. Two of our deployed tags (one standard and one X-tag) were recovered and returned to the manufacturer for the full data download, so in those cases the full dataset was available. For the remaining tags the percentage of transmitted information varied depending on the messages that were successfully transmitted. The HR tags that were also used on some sharks record data every 5 minute intervals and after pop-up attempt to transmit the entire time series with the 5-minute resolution. All data transmissions were made through the ARGOS satellite system, and the transmitted data were decoded by the tag manufacturer.

VI.2.2. *Depth of longline gear operation*

In order to characterize the pelagic longline fishing depth of operation, a total of 60 fishing sets were monitored with Minilog Temperature and Depth Recorders (TDR) build by Vemco. Six Minilogs were used per fishing set and were programmed to record data at every 1-minute intervals. The Minilogs were attached immediately adjacent to the hooks in order to characterize the actual minimum and maximum depth of the hooks during the fishing operations.

The fishing sets were carried out from a commercial Portuguese longline vessel following the general practices of the European longline fleet that operates over a wide Atlantic area targeting mainly swordfish. This fishery operates during the night, with the fishing gear deployment starting in the late afternoon at around 17:00 hr, and haulback starting the next morning from about 06:00 hr. The fishing gear consisted of a standard US style polyamide monofilament mainline, with five branch lines between floats. Each branch line was around 18 m in length and was composed by two sections: the first a 2.5 mm monofilament (9 m length) connected by a swivel to a 2.2 mm monofilament gangion (9 m in length) with a hook in the terminal tackle. Two different size options for the float line are typically used by this fleet (usually either 12 or 16m). Therefore the study design took into account this variability of the fleet fishing strategy, with TDRs being equally deployed on sections using both sizes of float lines.

VI.2.3. *Data analysis*

The archival data (15-30 min intervals in the standard tags, 5 min intervals in the HR tags, and 2 min in the recovered X-tag) were processed and analyzed for the depth and temperature time series profiles along the deployment periods of all sharks. The percentages of habitat utilization in terms of time-at-depth and time-at-temperature were calculated and analyzed separately for the daytime and nighttime periods, to assess the sharks habitat use during those two periods. The habitat utilization was also analyzed separately for males and females, as well as juveniles and adult specimens, to determine if habitat use varies between sexes and maturity stages. For this analysis the depth profiles were categorized into 30m depth classes and the temperature profiles into 2ºC temperature classes. Additionally, the minimum and maximum daily depths recorded were also analyzed.

In terms of geographical locations, an attempt was made to estimate the most probable daily locations using state-space models with unscented Kalman filtering (Lam et al. 2008). Those models try to determine the expected spatial locations in function of the estimated nominal positions and the sea surface temperature (SST), in order to create the most probable track for each specimen movements. However, given the diel vertical movements observed on all specimens, the tags were not able to correctly record the daily sunrise and sunset times and it was not possible to estimate daily geographical positions. Therefore, only the deployment and pop-up locations were analyzed for the geographical locations.

The overlapping between the species habitat utilization and the deployment of the fishing gear was calculated by analyzing the results from the Minilog TDRs. The mean depth of the hooks when using either 12m or 16m float lines were calculated, and the differences tested with permutation tests (Manly 2007). For this, a Monte Carlo approach was used with the data randomized and re-sampled 9,999 times to build the expected distribution of the differences under a random distribution, which was then used to determine the significance of the hook depth differences observed in the sample. The 90% percentiles of the recorded hook depths were calculated, with those limits defined as the overall depth of operation of the fishery. The depth distribution of the specimens were overlapped with the depth distribution of the fishing gear in order to calculate the percentage of overlapping time, both for the night/day periods as well as for the juvenile/adult specimens.

All statistical analysis for this paper was carried out with the R Project for Statistical Computing version 3.0.1 (R Core Team 2013). The state-space models for geo-location were run using library "ukfsst" (Nielsen et al. 2012), the permutation tests using library "perm" (Fay and Shaw 2010), the pyramid plots using library "plotrix" (Lemon 2006) and all other plots using library "ggplot2" (Wickham 2009).

VI.3. Results

VI.3.1. *Tag performance*

Fifteen tags were deployed during 2012 and 2013, mainly in the tropical and sub-tropical region of the northeast Atlantic Ocean (Figure VI.2), given that these are areas of relatively high abundance for the species and also important for the pelagic longline fleets. Data from twelve tags were successfully transmitted, with two having a premature detachment. Two tags were recovered; one of a specimen recaptured by a commercial fishing vessel and another that was found stranded in a beach in the Bahamas after drifting at the sea surface for more than one year after pop-up (Table VI.1). As a result, a total of 907 tracking days were registered, specifically 581 tracking days for females and 326 days for males. Both adults and juveniles of each sex were tracked successfully, and a summary of the tracking days per sex and maturity stage is presented in Table VI.2.

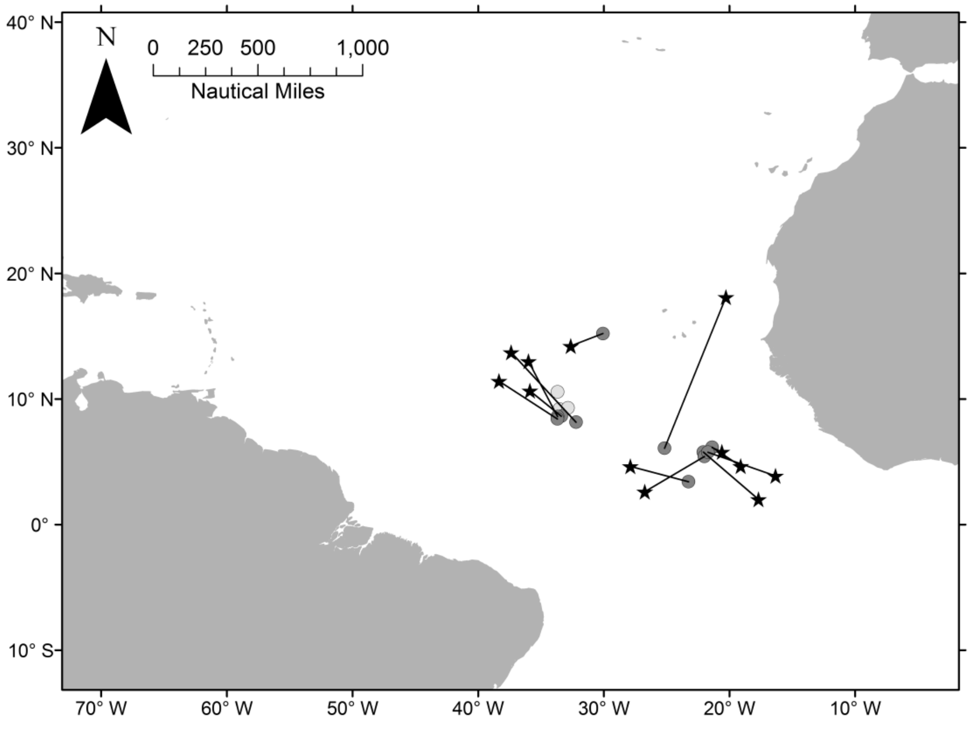

Figure VI.2: Tagging and pop-up locations of the bigeye thresher sharks, *Alopias superciliosus*, tracked with satellite tags in this study. The tagging locations of specimens with successful tag transmissions are represented in dark grey circles, the tagging locations of specimens with tags that failed to transmit are represented with light grey circles, and the pop-up locations are represented with black stars.

Table VI.1: Characteristics of the bigeye thresher sharks, *Alopias superciliosus*, and satellite telemetry tags used in this study, including information on specimen size, sex, tag type, planned duration, effective tracking days and % of transmitted data.

ID	Tag Type	Size (FL, cm)*	Sex	Tagging Date	Planned duration (months)	Tracking days	Transmitted data (%)
113777	Standard	155	Female	26-Aug-12	1	31	100
113778	Standard	135	Male	28-Aug-12	1	31	100
113782	Standard	160	Female	31-Aug-12	4	122	94
113783	Standard	130	Male	31-Aug-12	4	47	100**
119177	X-tag	140	Male	27-Sep-12	6	127	100**
120465	X-tag	180	Female	21-Aug-13	4	122	48
127995	X-tag-HR	215	Female	27-Sep-13	1	31	72
120466	X-tag	190	Male	16-Dec-13	4	121	55
127996	X-tag-HR	150	Female	17-Dec-13	1	33	79
127997	X-tag-HR	180	Female	19-Dec-13	1	30	80
120469	X-tag	195	Female	19-Dec-13	6	182	44
127994	X-tag-HR	170	Female	23-Dec-13	1	30	78

*: Sizes given are the mid points within 10cm FL size ranges; **: Recovered tags.

Table VI.2: Total tracking days of bigeye thresher sharks, *Alopias superciliosus*, per sex (males and females) and maturity stage (juveniles and adults).

Sex	Maturity stage		Total
	Adult	Juvenile	
Female	31	550	581
Male	121	205	326
Total	152	755	907

VI.3.2. *Habitat use*

A marked and constant diel vertical movement was observed for all studied specimens, with the bigeye threshers spending most of the daytime periods in deeper and colder waters and the nighttime periods in shallower warmer waters closer to the sea surface (Figure VI.3). The mean depth during the nighttime periods was 71.9m (SD=54.1) and during the daytime period was 352.8m (SD=72.8), with those differences statistically significant (t-student test: t = -853.1, df = 140148, p-value < 0.01). Even though most of the time at depth was spent close to the 350m depth range, it was also possible to observe that on occasions the sharks performed quick dives followed by quick ascents (Figure VI.4). The maximum depth recorded during this study occurred during one of those quick dives followed by a quick ascent, with the shark reaching a maximum depth of 954.5m and a minimum water temperature of 5.2ºC.

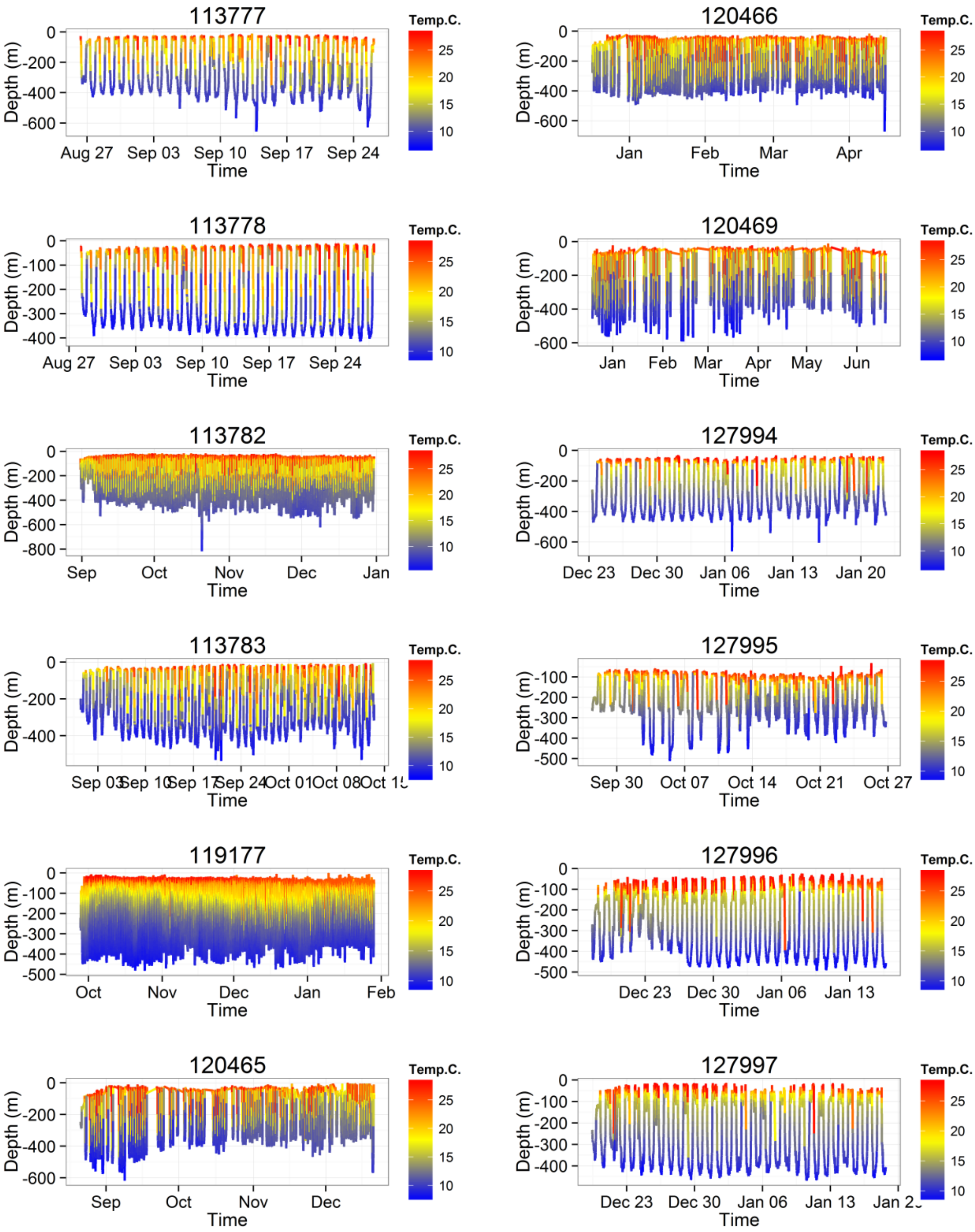

Figure VI.3: Time series of the depth and temperature profiles of the bigeye thresher sharks, *Alopias superciliosus*, tracked during this study. Specimen and tag details are specified in Table 1.

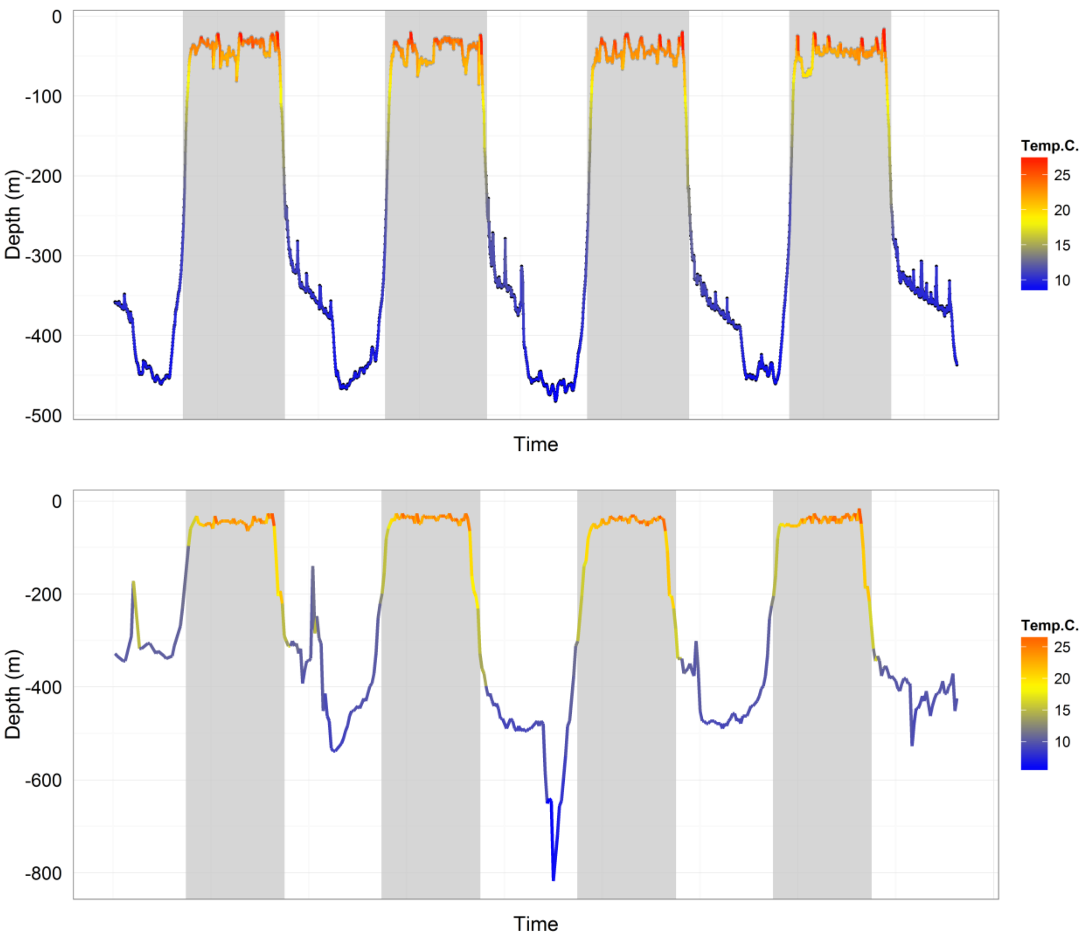

Figure VI.4: Details of diving behavior profiles of bigeye thresher sharks, *Alopias superciliosus*, tagged with satellite telemetry tags. The plot on the top represents the most common diel behavior movements, with the daytime spend in deeper waters and the nighttime in shallower waters. The plot on the bottom shows the occasional deep dives and ascents (in this case in the 3rd day of the time series represented in the plot. In both plots the nighttime periods are shaded in grey.

The patterns of habitat utilization for adults and juveniles followed this common general trend of using shallower waters during the night and deeper waters in the day, but some differences were noted. Specifically, the range of habitat utilization in terms of depth was wider for the juveniles than for the adults, with the juveniles staying in waters shallower than the adults during the night, but in deeper waters than the adults during the day (Figure VI.5). Differences between the sexes were also detected, as well as interactions between sex and maturity stage. During the daytime period the adult males tended to be deeper than the adult females, while the juvenile males tended to be shallower than the juvenile females (Figure VI.6). During the nighttime period both adult and juvenile males tended to be shallower than the females (Figure VI.6).

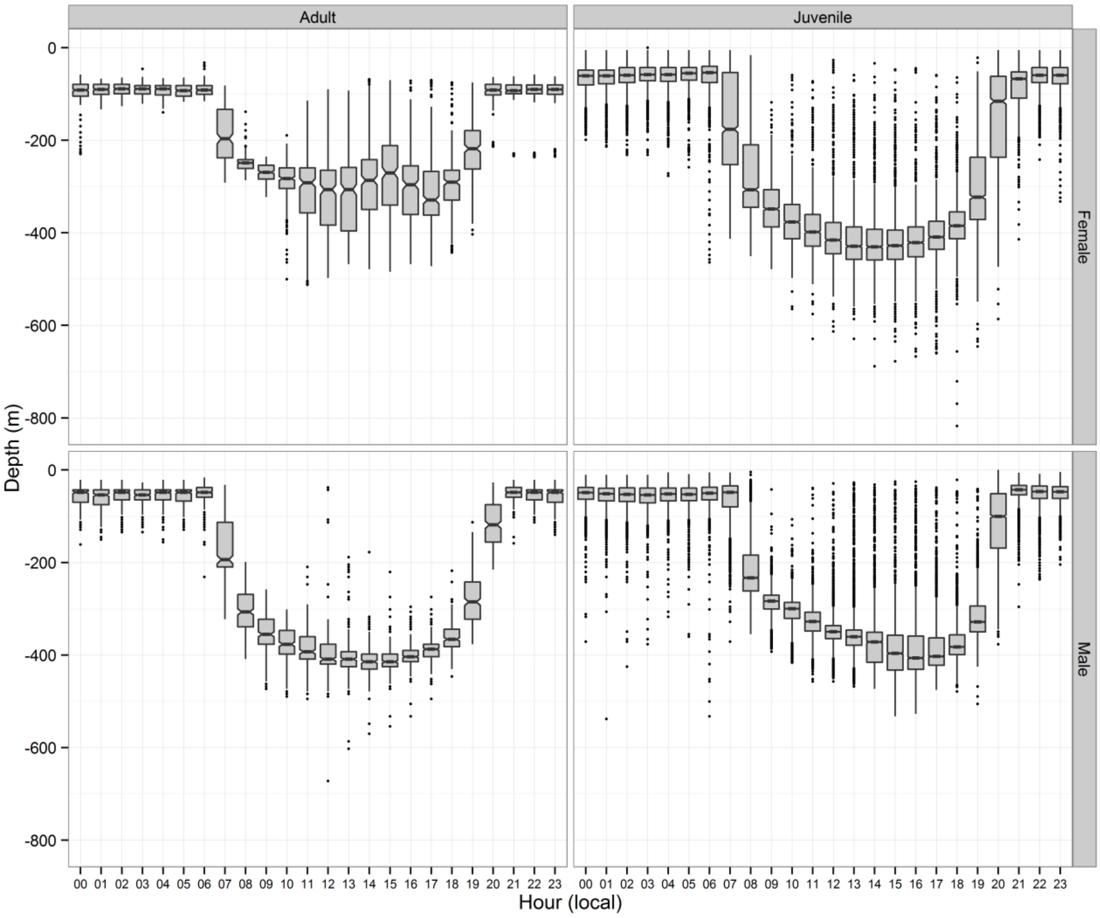

Figure VI.5: Bigeye thresher shark, *Alopias superciliosus*, habitat utilization with the data categorized in one hour time classes, separated by sex and maturity stage.

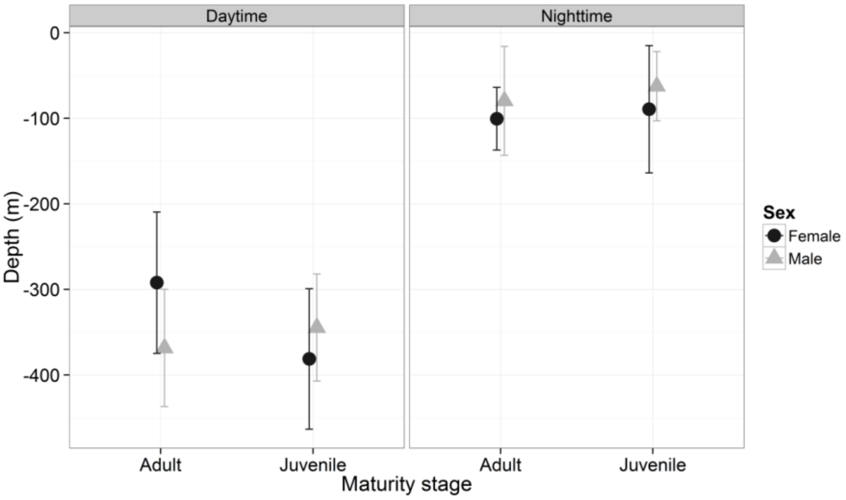

Figure VI.6: Mean depth of bigeye thresher sharks, *Alopias superciliosus*, separated by maturity stage (adult and juvenile) and sex (male and female), during the daytime and nighttime periods. The error bars refer to the standard deviations.

In terms of habitat utilization, for the juveniles the modal class of habitat use during the daytime period was the 330-360m depth class with 18.4% of the daytime period spent there, while the modal class during the nighttime period was the 30-60m depth class where the sharks spent 49.9% of the nighttime period (Figure VI.7). The adults showed some differences compared to the juveniles, as for the adults there was a bimodal distribution for the daytime period, specifically with a peak of 14.1% of the time spent at 240-270m and another peak with 16.9% of the time spent at 390-420m, while the modal class during the nighttime period was the 60-90m depth class where the sharks spent 29.8% of the time (Figure VI.7).

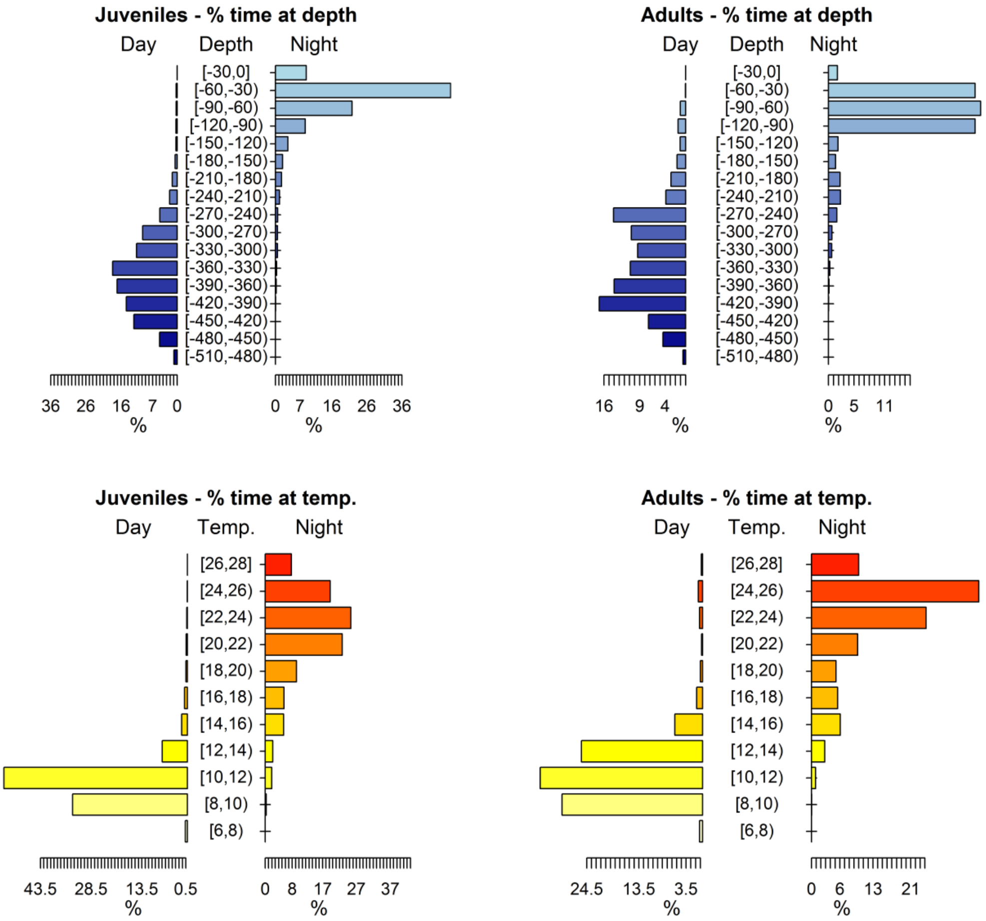

Figure VI.7: Habitat utilization for juvenile and adults bigeye thresher sharks, *Alopias superciliosus*, for the daytime and nighttime periods in terms of depth and water temperature. Depth classes are categorized in 30m intervals and temperature classes in 2°C intervals.

VI.3.3. *Overlap between habitat use and fishing gear operation depth*

By analyzing the time series of the fishing gear deployments it was possible to observe some differences on the depth of operation of the hooks depending on the length of the float lines (Figure VI.8). The average hook depth of this fishery were 40.8m (SD=15.4) and 47.5m (SD=16.7), when using respectively 12m or 16m long float lines (Figure VI.9), with those observed differences statistically significant (Permutation test: observed differences = 6.68; p-value < 0.01).

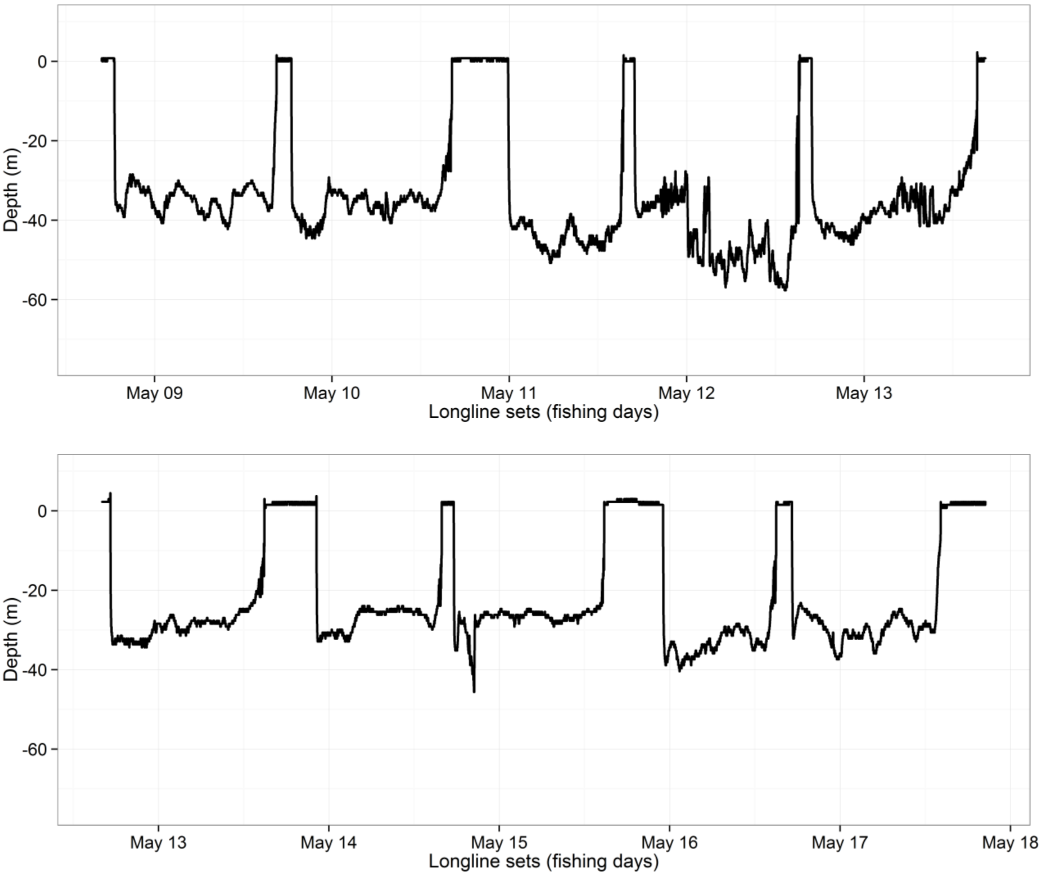

Figure VI.8: Times series (examples) of Minilog deployments on a traditional pelagic longline gear targeting swordfish, using 16m (plot on the top) and 12 m (plot on the bottom) float lines. In these plots, each time series represents a sequence of 5 fishing sets (days).

The 90% percentile depth distribution of the hooks depth were 24.5m-63.1m and 29.8m-70.3m, respectively for the 12m and 16m float lines. When this distribution was overlapped with the species habitat utilization, it was possible to calculate that the overlapping between fishing gear and species habitat use took place almost exclusively during the nighttime period. Moreover, such overlap was more marked in the case of the juveniles. Specifically, during the nighttime period the overlap between the species habitat and fishing gear deployment for the juveniles varied between 56.4-60.2%, while for the adults the overlap varied between 25.4-33.6% (Table VI.3).

Table VI.3: Overlapping, in percentage of time (%), between the depth related habitat utilization of bigeye thresher shark, *Alopias superciliosus*, and the depth of operation of the shallow setting pelagic longline gear targeting swordfish.

Float line length	Daytime		Nighttime	
	Juveniles	Adults	Juveniles	Adults
12m	< 1.0	< 1.0	60.2	25.4
16m	< 1.0	< 1.0	56.4	33.6

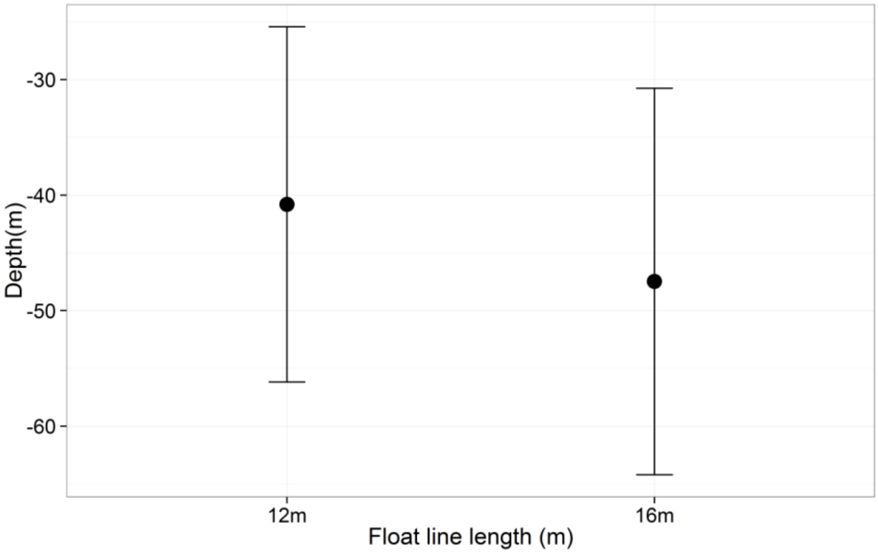

Figure VI.9: Mean depth of operation of a traditional pelagic longline fishery targeting swordfish in the Atlantic Ocean, using either 12m or 16m long float lines. The error bars refer to the standard deviations.

VI.3.4. *Geographical movements*

Due to the fact that all specimens showed strong diel movements, spending the majority of the daytime period at considerable depths, the satellite tags were not able to correctly detect and record the sunrise and sunset times, as well as the daylight period duration, which hindered the estimation of accurate geo-location positions. Even when state-space models were applied and tested, the nominal geo-locations had very large errors and missing data points along several consecutive days, which prevented the models to achieve convergence and reasonable results. Therefore, for this species, only the known deployments positions and pop-up locations were used for the spatial analysis (Figure VI.2). The minimum distances traveled (straight lines between the tagging and pop-up locations) ranged from 94.6 to 1439.9 km (for 30 and 122 tracking days, respectively), with an average daily distance of 13.0 km/day, ranging from 2.3 to 27.0 km/day.

VI.4. Discussion

The present paper provides the most comprehensive study on habitat use and migration of bigeye thresher sharks, based on a large set of specimen tagged with satellite telemetry tags. We were able to tag and track specimens of both sexes, including juveniles and adults of each sex, and therefore the differences in the habitat utilization between sexes and maturity stages were observed and reported for the first time. Only a few studies have tried to determine the habitat utilization of the bigeye thresher, but all tagged and analyzed a very limited number of specimens. Most have also detected the diel vertical movement pattern that we report in our study, but not the differences that we found in terms of differential habitat utilization by sex and maturity stage, mainly because these studies used much more limited sample sizes and were not able to compare sexes or maturity stages.

Moreover, by analyzing data from Minilog TDRs deployed during commercial longline fishing sets we were able, for the first time, to calculate the overlaps between the species habitat utilization and the depth of operation of longline fishing gear. For this particular fishery that uses shallow night set longlines targeting swordfish, it was possible to show that the overlaps are taking place almost exclusively during the night (when the fishery operates) and that the juveniles are potentially more impacted than the adults, as the percentage of time overlapped is greater for the juveniles than for the adults. However, it should be noted that we only calculate and report the percentage of overlapping between habitat utilization and depth of operation of the hooks, not taking into account that the hooks used are baited (typically with squid or mackerel, see Santos et al. 2012, Amorim et al. in press), and that those baits have attractant characteristics (scent) that may cause the specimens to change their behavior and actively swim towards the hooks, if they are sufficiently close to the fishing gear.

A previous study by Weng and Block (2004) analyzed two bigeye thresher sharks tagged with satellite tags (one in the Gulf of Mexico and another in the Pacific Ocean close to Hawaii), and reported that, like in our study, both specimens also showed this strong diel movement pattern, with the majority of the nighttime spent closer to the surface and the most of the daytime spent bellow the thermocline in deeper waters (300-500m). In another study in the eastern tropical Pacific, Nakano et al. (2003) used acoustic telemetry to actively track two bigeye thresher specimens during 70 and 96 hour periods, and also detected this type of strong diel vertical behavior. Moreover, Nakano et al. (2003) also detected the occasional quick dives that we observed in our study, and reported a maximum depth of 723 m, which is less than the 954.5m recorded in our study. In the Central Pacific, Musyl et al. (2011) tagged eight bigeye threshers with satellite telemetry tags and analyzed data from three reporting tags, and also reported the same diel vertical movement pattern. Likewise, in Eastern Australia, Stevens et al. (2010) tagged one bigeye thresher (with an effective deployment period of 14 days), that also presented this type of behavior. By the contrary, Carlson and Gulak (2012) analyzed one bigeye thresher tagged in the Gulf of Mexico, in a location closer to the continental shelf of the USA, and reported that that particular specimen did not show evidences of these strong diel movement patterns. Carlson and Gulak (2012) hypothesized that the lack of the diel behavior in their tagged specimen might be related to the depth limitations of the shark location, given that it was moving closer to the continental shelf in shallower waters, while most of the other studies, like in our case, were conducted in oceanic waters.

Diel behavior has been suggested to be related with foraging ecology for other pelagic species like the swordfish, bigeye tuna (*Thunnus obesus*), blue shark, shortfin mako and common thresher (*Alopias vulpinus*) (Preti et al. 2008, Stevens et al. 2010, Musyl et al. 2011). The daytime vertical migrations of the bigeye thresher may therefore be described as a strategy to remain near prey organisms in the deep sound scattering layer (SSL), similarly to what has already been documented for swordfish and bigeye tuna, with possible vertical adjustments during the nighttime to lunar illumination

(Musyl et al. 2011). In addition, after analyzing stomach contents, it has been suggested that besides demonstrating the same general diel migrations as swordfish, the bigeye thresher also forages on many of the same prey (Preti et al. 2008). In fact, although both species are predominately deeper water species in the pelagic environment, they have a varied diet and may feed opportunistically across habitats in the mixed-surface layers, contrary to other pelagic sharks (Preti et al. 2008). Both species have been described as presenting similar physiological adaptations for extended foraging in dark cold waters, like the presence of large eyes and cranial endorthermy (Weng and Block 2004, Preti et al. 2008). In the particular case of the bigeye thresher a highly developed *rete mirabile* within the orbital sinus has been identified suggesting heat conservation in the eyes and brain which potentially enhances the physiological performance of the shark, by enabling a prolonged foraging time beneath the thermocline (Weng and Block 2004).

Of the 15 deployed tags only three failed to transmit, representing a success rate of 80%. Hence, the performance of the satellite tags used in our study can be considered high when compared to the reporting rates of 38% from Musyl et al. (2011) and 50% from Carlson and Gulak (2012). Several factors can be attributed to the failure of satellite tags namely, expiration of the battery, physical damage of the transmitter, detachment and sink of the transmitter, death of the animal or failure of the salt-water switch (Hays et al. 2007). Additionally, the success rate of satellite tags also seems to be species-specific. Hammerschlag et al. (2011) carried out a revision of 48 studies using satellite tagging on sharks and reported an average rate of 10% tag failure (90% success rate). However, it is worth noting that several studies on species that also make deep dives presented lower success/reporting rates that our study, specifically for the basking shark, *Cetorhinus maximus* (Sims et al. 2003) and shortfin mako (Musyl et al. 2011). On the other hand, in our study a 13% rate of premature releases was observed, which is a very low rate when compared with the average rate of 66% premature releases reported for other sharks studies by Hammerschlag et al. (2011).

Some difficulties arose when using the satellite technology to estimate the geo-locations for this species, as has also been described by other authors (e.g. Weng and Block 2004, Musyl et al. 2011). The fact that the bigeye thresher spends most of the daytime in deep waters poses a limitation to this study, as no geo-location could be obtained for this species (other than the deployment and pop-up locations). Further efforts should be made in the future to develop new approaches to attain geo-location for species with this kind of diel behavior, either technologically or mathematically, as the tags cannot record the daylight needed for the geo-location estimations.

The main conclusions of our study are that the bigeye thresher is using the habitat in terms of depth with a very specific and constant diel movement pattern, with the specimens spending most of the daytime in deeper waters and the nighttime periods closer to the surface at shallower depths. Additionally, we were also able to find differences in the utilization of the habitat when comparing adults and juveniles, with both maturity stages making the diel movements but staying at different depth classes. Consequently, the maturity stages are being affected in different ways by the pelagic longline fisheries. For the specific case of the shallow pelagic longline fisheries that typically deploy night sets targeting swordfish, the impacts on the bigeye thresher are potentially higher for juveniles than for adults, as the percentage of overlapped time is higher for the younger specimens.

The results presented in this work are novel and substantially increase the knowledge on this species biology, ecology and habitat utilization in the pelagic environment, as well as the overlapping and potential impacts with pelagic longline fishing gear. The results now presented can be used in the future as inputs for ongoing and future Ecological Risk Assessments for pelagic sharks captured in oceanic tuna fisheries, and serve as a basis for the provision of more efficient management advice aiming the conservation of this species. Moreover, this information can now be used to establish more efficient bycatch mitigation measures, particularly in hot spot areas for this vulnerable species, such as those with high rates of bycatch and/or concentration of juveniles.

VI.5. Acknowledgments

This study was supported by Fundação para a Ciência e Tecnologia (FCT, *Portuguese Foundation for Science and Technology*) through Project THRESHER (PTDC/MAR/109915/2009). Thanks are due to the technicians S. Amorim and S. Goes, and the crew of the fishing vessel *Príncipe das Marés*, for their cooperation and careful handling of the sharks during the tagging operations. The authors wish to thank the skipper of the fishing vessel *Amencer* for returning the tag from the recaptured specimen, and to Kim and Jeff Kuehl for returning the tag that was found stranded in a beach in the Bahamas. J. Fernandez-Carvalho was supported by a PhD grant from FCT (BD 60624 /2009) and R. Coelho was supported by a Post-Doc grant from FCT (BPD/93936/2013).

CHAPTER VII. FINAL REMARKS AND CONCLUSIONS

This thesis was included in the most comprehensive study ever carried out for this vulnerable shark species in the Atlantic Ocean (Project THRESHER, funded by FCT). The results presented herein provide novel and important information for this species, filling knowledge gaps on the biology, ecology and the fishery impacts of the bigeye thresher shark in the Atlantic Ocean.

All the information and results obtained by this thesis were presented to the scientific community with scientific papers in scientific journals and presentations in international conferences. Additionally, the most relevant results as regards management were also presented to the Scientific Committee of Research and Statstics of ICCAT, the management body responsible for pelagic sharks in the Atlantic, including the bigeye thresher shark. In that way, the results obtained were presented both to the scientific community to increase the knowledge of the species, but were also used to directly provide better and more efficient management advice for the conservation of this species in the Atlantic.

This final chapter presents a general discussion and a summary of the key findings and conclusions presented in the various sections of this thesis.

VII.1. Major conclusions and practical applications of this study

After analyzing the hooking mortalities of the pelagic sharks caught by the Portuguese pelagic longline fishery, the main conclusion was that the bigeye thresher is amongst the shark species with the highest hooking mortality rates (around 50%). This high mortality implies that the current ICCAT recommendation prohibiting the retension of the species onboard and therefore requiring mandatory discarding is not entirely efficient, as around 50% of the specimens are being discarded already dead. As such, alternative management regulations should be considered for decreasing the bycatches of the species, such as gear modifications and spatial and/or temporal closure of areas where juveniles are more likely to be captured.

When testing the effects of hook style and bait type on the bigeye thresher bycatch rates in the northeast tropical Atlantic, namely in the Cape Verde Archipelago Islands region (one of the species critical habitat areas proposed within the distributional study carried out within this thesis), no significant effects of hook style or of bait type were found. In fact, those modifications increased at-haulback mortalities of the bigeye thresher shark. Therefore the use of circle hooks or mackerel bait (instead of J-style hook and squid bait) does not seem an effective gear modification to reduce the bycatch of this species in the pelagic longline fishery targeting swordfish in the region.

In order to determine the size structure of the species and possible mating and nursery areas along the Atlantic, an integrated large scale collaborative study of all fishing fleets was carried out for the first time. The most significantly different region was the tropical northeastern Atlantic (closer to the Cape Verde Islands region) where specimens tended to be smaller and the proportion of juveniles higher than in other regions. Three nursery areas were proposed in the Atlantic Ocean, specifically in the tropical northeast Atlantic and equatorial waters closer to the African continent, in the tropical northwestern Atlantic in areas closer to the Caribbean Sea and Florida, and in the southwest Atlantic close to the Rio Grande Rise. In this study, a model was also created to calculate the odds-ratios of capturing more juveniles in the various regions/seasons combinations, and the results can now be used to provide management advice on bycatch mitigation in these critical habitats for the species.

Life history parameters of the bigeye thresher for the Atlantic were calculated herein given that these are the basic data needed for population modeling purposes. Only with this data can further population dynamics assessments be carried out in order to determine, for example, if the current fishing pressures are sustainable. This was the largest age and growth study ever carried out for this species in the Atlantic Ocean and allowed, for the first time, a comparison of the growth patterns between the northern and southern hemispheres. The main conclusions were that the bigeye thresher has a very slow growth rate, even lower than other thresher shark species, and that females have lower growth rates and larger asymptotic sizes than males. Comparing the two hemispheres, the growth rates are slower in the south Atlantic compared to the north Atlantic. Though these differences could be the related with the existence of different stocks or populations between the north and south Atlantic, they can also be the result of the relatively smaller sample size for the southern region, but also to the fact that most samples from the north Atlantic were collected around the Cape Verde Archipelago, where the majority of the specimens tended to be smaller. In fact, a parallel study within the THRESHER project focusing on population genetics concluded that the bigeye thresher consists likely of only one population in the Atlantic, with some genetic differentiation in areas closer to the African continent.

Important reproductive parameters such as the median size-at-maturity were also estimated in this thesis, and it was determined that this is occurring at approximately 79% of the maximum observed size for females and 61% for males. It was also possible to confirm the very low fecundity of the species of only two pups per reproductive cycle, making the bigeye thresher one of the least fecund of all shark species, with significant conservation implications. The results of these two components (age and growth and maturity) were used in a stochastic population dynamics model developed within the THRESHER project during the course of this thesis. It was possible to conclude that the bigeye thresher shark has one of the lowest intrinsic growth rates of any pelagic shark, with annual population increases of only around 1%. Therefore this species is extremely vulnerable to fishing pressure, with population collapses tending to occur even at relatively low levels of fishing mortality. Additionally, with the calculated model elasticities, it was concluded that conservation efforts should be focused mainly on the survival of the juveniles, as those are the stages that can contribute more for the increase in the population growth rates.

Finally, satellite telemetry was used to study habitat use and vertical migrations of this species. Again, this study was the most comprehensive study ever carried out for this species worldwide and allowed, for the first time, a comparison on how the two sexes and the different maturity stages (adults and juveniles) are using the habitat. The main conclusions were that the species presents a strong diel movement pattern, with most of the daytime spent at considerable depths and the night time period spent closer to the surface in shallower waters. Also, the maximum depth ever registered for this species was recorded (954.5 m). Additionally, differences were also detected on how the adults and juveniles distribute and use the habitat along this diel movement pattern. This information has significant implication for the conservation of the species, as it is now possible to infer on how the various fishing gears/métiers impact the different population stages. For example, within longline fisheries there are two main fishing métiers, specifically one métier targeting tunas that deploy deeper sets during the day and one métier targeting swordfish that operate shallower sets during the night. Therefore, it is now possible to calculate the overlaps of those various fishing métiers with each of the population stages (juveniles vs. adults) and calculate therefore the impact of the fisheries, using the probabilities of overlapping between the specimens and the fishing gear.

VII.2. Future research

This study has presented comprehensive life history parameters along with size and sex distribution, habitat use and vertical movements of the bigeye thresher shark in the Atlantic, data which prior to this study was especially scarce for the Atlantic.

Nevertheless, some issues have remained unsolved in this PhD and these may be addressed by further research in the near future. During the present study the age of the bigeye thresher was verified by the use of centrum edge analysis but validation was not possible. One way of attempting to validate annual growth for this species (which has never been done) would be to inject with tetracycline and tag with external tags specimens that would be released back to the sea. Eventually, future catches returned by fishermen, even if only a few, could validate the ages estimated and verified at this stage. In fact, during the course of this work one specimen tagged with a satellite tag was captured a second time by a different commercial vessel. Thus, if it had been injected with tetracycline, the periodicity of band pair formation could have been validated for this species. In addition, analytical methods have been developed that could be further explored to verify the periodicity of band formation (e.g. Okamura and Semba 2009).

Given the vulnerable life cycle of the bigeye thresher and the fact that commercial fisheries are most probably having detrimental impacts on this species, further research should be conducted in order to successfully protect this species. It is crucial to continue to monitor its catches in the future as well as the fishing effort at areas and depths that we now know are important habitats for these species. Therefore, since this species is discarded, it is vital to maintain logbooks and the presence of regular fishing observers aboard pelagic longliners in order to monitor the fished quantities and discarded condition (alive or dead). Still, efforts should be made to ensure that in the logbooks the thresher species are differentiated and ideally the cover percentage of the fishery observers should be increased, since currently merely 5% of the fleet is covered by such program.

Other management measures that should be further explored are testing of by-catch reduction devices or strategies that might reduce the by-catch of the species and decrease the fishery impacts that are currently affecting these shark populations. Though circle hooks and bait type showed no efficiency in reducing the by-catch of the bigeye thresher, other gear modifications can be further explored. While developing this study it was clear that testing the effect of the leader material (monofilament vs. wire) in the catches of this species should be the next step, since for other pelagic shark species this factor has proved to be significant (Afonso et al. 2012, Ward et al. 2008).

Another aspect that should be a research priority is the species' post-hook mortality. During this thesis it was discovered that the immediate at-haulback mortality of the species is relatively high (around 50%). However, the fate of the discarded sharks that are released back to the sea alive is still unknown, as those can die after some hours or even days due to the trauma and stress caused by the fishing process. Thus the true mortality of this species (immediate at-haulback plus post-release) can be very high, and as such, the fishery impacts higher than expected. Campana et al. (2009) used archival satellite pop-up tags to assess the discard mortality of commercially caught blue sharks (*Prionace glauca*). A similar study should urgently be made for bigeye thresher sharks to calculate their post-hook mortality and further access the efficiency of the current ICCAT regulation on the no-retention (mandatory discards) of this species.

Other suggested future research includes the use of the biological parameters and fishing impacts that have been described herein to revisit risk analysis on these species. Also, predict population declines or even extinction probabilities in the future in light of the current fishing activities that are impacting these populations. In addition, demographic analysis should continue to be further explored to determine mortality and demographic parameters of the bigeye thresher and assess if the current levels of fishing mortality are sustainable.

Finally, it should be mentioned that more comprehensive studies which integrate life history, fishery impacts and mitigation and habitat use should be encouraged for other vulnerable pelagic sharks. While developing this study it was noted that protected species like the smooth hammerhead (*Sphyrna zygaena*), present very high hooking mortality but there is currently not much information available. Thus, their study in a similar integrated approach should be a priority since current management measures are probably not being efficient. Other pelagic shark species that should be studied in a comprehensive way with urgency are the oceanic whitetip (*Carcharhinus longimanus*) and the shortfin mako (*Isurus oxyrinchus*) due to their classification of highly vulnerable by the latest ecological risk assessment of pelagic sharks caught in Atlantic pelagic longline fisheries (Cortés et al. 2010). Finally, multidisciplinary studies and cooperation between scientists from different countries, as was partially done in this thesis (i.e chapter IV on the species distribution), needs to be further promoted in order to efficiently protect pelagic shark species that migrate through both national and international waters.

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