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Role of the wider Azores region as a nursery ground for North Atlantic blue shark (*Prionace glauca*)

By

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Abstract - Resumo

Abstract

In the North Atlantic, blue shark has become an important by-catch for the pelagic swordfish fisheries, and, in some cases, even the target species of the fishery when swordfish abundance is low. Still, their complex life cycle and population structure remain poorly understood, limiting current management and conservation efforts for this species. Particular concern exists regarding the possible overlap between pelagic longline fisheries and putative juvenile grounds, given that juvenile survival was shown to be essential for the maintenance of blue shark populations. The main goal of this dissertation was therefore to improve the knowledge on the spatial ecology of North Atlantic blue shark, particularly focussing on the juvenile segment of the population and the central area of the oceanic basin. This region in the central North Atlantic has been identified as a putative nursery area and is being heavily exploited by pelagic longline fleets from Spain and Portugal.

A detailed analysis of the demography and seasonal abundance of blue shark in the central North Atlantic based on detailed analyses of fishery independent and observer data, demonstrated the central role of the area for North Atlantic blue shark population. Catch rates varied greatly over the year, reflecting the changing presence of different sex and life stages in the area, and were strongly influenced by environmental factors, namely sea surface temperature, sea surface height anomalies and lunar cycle. In general, the catches were strongly dominated by juvenile blue sharks, with higher catch rates during winter months. Young-of-the-year juveniles of both sexes were present throughout the year, while the presence of older juveniles of both sexes alternated seasonally. The presence of mature females in advanced stages of pregnancy during spring further suggests that the area is used as a pupping ground. Mature males appear mainly during summer, probably for feeding. The periodic presence of all these life stages emphasises the central role of the area, as some of these population components are seasonally associated with one of either sides of the North Atlantic. This central role was corroborated by a satellite tagging experiment that was designed to investigate the long-term movements, distribution and habitat use of mainly juvenile blue shark. This experiment provided strong evidence for the existence of a year-round oceanic nursery for small juvenile blue shark in the central North Atlantic. Moreover, large scale patterns of sexual segregation and shifts in distribution and movements across the

Abstract

species' life history were revealed and discussed in light of the evolutionary adaptations of pelagic sharks to their oceanic environment. Finally, the pelagic habitats juvenile blue shark were inferred using a statistical modelling approach that was developed to quantify habitat preference based on both satellite telemetry data and fisheries data. The models demonstrated that the spatio-temporal distributions of juveniles and patterns of segregation are shaped to a large extent by differential habitat preferences and revealed the existence of different strategies to exploit some of the most productive habitats within their range. For the first time, predictions of essential pelagic habitats of juvenile blue shark in the North Atlantic provide a unifying framework to understand the dynamic spatial structuring of the juvenile blue shark population at the scale of entire ocean basin.

Resumo

O tubarão azul tornou-se uma importante captura acessória na pescaria de palangre do Atlântico norte ou até, nalguns casos, a espécie alvo da pescaria quando a abundância de espadarte é reduzida. Contudo, a sua complexa estrutura populacional e ciclo de vida permanecem largamente desconhecidos, limitando os actuais esforços de conservação e gestão desta espécie. Em particular, é preocupante a possível sobreposição da pescaria com zonas de maternidade, pois a sobrevivência juvenil foi demonstrada ser essencial para a manutenção das suas populações. O objectivo principal desta dissertação foi, assim, melhorar o conhecimento da ecologia espacial desta espécie no Atlântico norte, centrada no segmento juvenil e na área central desta bacia oceânica. Esta região foi identificada como possível maternidade e tem sido intensamente explorada pelas frentes palangreiras espanhola e portuguesa.

A análise detalhada da demografia e abundância sazonal de tubarão azul no Atlântico norte central baseada em dados independentes da pescaria e em dados de observadores demonstrou o papel central da área para a população norte Atlântica. As capturas variaram significativamente ao longo do ano, reflectindo a presença variável dos diferentes sexos e componentes etários da população na área, e foram fortemente influenciadas por factores ambientais como a temperatura de superfície, as anomalias de altura superficial, e o ciclo lunar. Em geral, as capturas foram dominadas por tubarão azul juvenil, sobretudo nos meses de inverno. Os juvenis de primeiro ano de ambos os sexos encontram-se na região durante todo o ano enquanto que os de maior idade alternam sazonalmente a sua presença. A presença de fêmeas maduras em estado de gravidez avançado sugere também que a área possa ser usada como zona de desova. Machos maduros aparecem sobretudo no verão, provavelmente para se alimentar. A presença periódica destas componentes populacionais enfatiza o papel central da área pois algumas estão também sazonalmente associadas a um dos lados do Atlântico.

Este papel central da área foi corroborado por uma experiência de telemetria de satélite desenhada para investigar os movimentos de longa duração, distribuição e uso do habitat dos juvenis. Desta experiência resultaram fortes evidências da existência de uma maternidade anual para os juvenis pequenos de tubarão azul no Atlântico norte central. Os padrões de larga escala de segregação sexual e as mudanças na distribuição e movimentos ao longo da vida da

espécie são revelados e discutidos à luz das adaptações evolutivas dos tubarões pelágicos no seu ambiente oceânico. Finalmente, o habitat pelágico dos juvenis de tubarão azul foi inferido usando uma modelação estatística ambiental desenvolvida para quantificar a preferência do habitat baseado em dados de telemetria e das pescarias.

Os modelos demonstraram que os padrões de distribuição espacio-temporal dos juvenis e de segregação são moldados, em larga medida, pelas diferentes preferências, e revelaram a existência de estratégias distintas para explorar alguns habitats mais produtivos dentro da área de distribuição. Pela primeira vez são feitas predicções do habitat essencial pelágico de juvenil de tubarão azul para o Atlântico norte, oferecendo um enquadramento unificador da dinâmica especial estruturadora da população juvenil à escala da bacia oceânica

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Chapter 1

Introduction

Chapter 1

Introduction

1. Context

The populations of many apex pelagic predators are under increasing threat due to climate variability and the high mortality induced by fishing, be it as a target in directed fisheries or as an incidental by-catch from non-directed fisheries (Myers and Worm, 2003; Sibert et al., 2006; Robinson et al., 2009). Pelagic shark populations, in particular, may have suffered severe declines (Baum et al., 2003; Ward and Myers, 2005; Dulvy et al., 2008, Ferretti et al., 2008) and the effect of their removal from oceanic ecosystems and food webs remains uncertain (Stevens et al., 2000; Kitchell et al., 2002; Ferretti et al., 2010). National and regional legislative efforts (e.g. United States, Canada, Australia, Europe) to control and ban certain practises related to the exploitation and trade of sharks and related products may regionally reduce mortality of certain shark species, particularly coastal sharks. Yet, for oceanic species this reduction is probably more modest as many fleets operating in international waters are not bound by such a legal framework (Kitchell et al., 2002).

This problem has long been recognised (Camhi et al., 1998) and led to several international initiatives. In 1999, the Food and Agriculture Organisation of the United Nations (FAO) launched its International Plan of Action for the Conservation and Management of Sharks (IPOA-sharks), a set of guidelines to ensure the conservation and management of sharks and their long term sustainable use. It encourages States that contribute to the fishing mortality of sharks to elaborate a national shark-plan and control fishing mortality by applying the precautionary approach while improving data collection and monitoring (FAO, 1999). Nonetheless, to date implementation of these guidelines at a national level remains largely unsatisfactory (Davis and Worm, 2012).

A persisting problem is the deficient reporting of shark catches to national and international management bodies (Worm et al., 2013), impeding thorough stock assessment of exploited or impacted populations. In their latest stock assessment of pelagic sharks, for instance, the

International Commission for the Conservation of Atlantic Tunas (ICCAT) stressed that notwithstanding recent improvements, the quality and quantity of data continued to be a constraint for the assessment (Anonymous, 2009).

A second impediment for managing pelagic sharks is the poor knowledge on their biology and ecology (Camhi et al. (Eds.), 2008). Sharks have complex life histories and an intricate spatial structuring of their populations resulting from segregation between sexes and life stages (Springer, 1967; Hoenig and Gruber, 1990). Additionally, pelagic shark redistribute over large distances in search of patchily distributed prey, resulting in a highly variable distribution of their populations.

Few current stock assessment models address spatial variability in both fishing pressure and populations (Goethel et al., 2011), but progress is being made to create spatially explicit assessment methods that incorporate parameters like individual movements (Cadrin and Secor, 2009; Goethel et al., 2011). At the same time, this spatial structuring can also represent an opportunity when safeguarding certain population components, like juveniles or reproductive females, is possible and can benefit an entire population. Pelagic marine protected areas are regarded as a useful addition to current fisheries management, but their implementation has been slow (Game et al., 2009; Kaplan et al., 2009). So far, pelagic MPAs have shown mixed success, but examples like the real time spatial management of southern blue fin tuna, *Thunnus maccoyii*, off Australia demonstrate their potential (Hobday and Hartmann, 2006; Game et al., 2009; Hobday et al., 2011). The spatio-temporal dimension of resource management is therefore becoming increasingly important. The rapid development and increased access to new technologies, like satellite telemetry and remote sensing of ocean processes, offer an opportunity, and at the same time a challenge, to investigate the spatial ecology of pelagic sharks.

2. Biology and life history of sharks

Together with skates, rays and chimaeras, sharks belong to the class chondrichthyes or cartilaginous fishes, one of the oldest living taxa of vertebrates. The term shark is often used for the subclass Elasmobranchii, encompassing skates and rays (Batoidea) as well as true sharks (Selachii), but for the purpose of this dissertation we will use the term sharks exclusively for the Selachii and elasmobranch for the subclass. Elasmobranchs form a diverse group with

approximately 1160 living species (Compagno, 2008), of which over 400 species belong to the Selachii. Elasmobranchs are found throughout all worlds' oceans and are mostly marine species. They can be found across trophic levels of the food web, from planktivores to apex predators, and display a wide range of reproductive modes, from oviparity to placental viviparity (Snelson et al., 2008).

Pelagic elasmobranchs form a small group of species, with the Squaliformes, Carcharhiniformes, Lamniformes and Rajiformes being the best represented orders. Compagno (2008) proposed the following definitions for pelagic, semipelagic and oceanic elasmobranchs. "Pelagic elasmobranchs" refers to highly mobile species that are not closely associated with the sea-bottom. "Oceanic" species include those pelagic elasmobranchs that live large part of their lives in the ocean basins, away from continental land masses, while "semipelagic" elasmobranchs enter oceanic waters but concentrate close to continental landmasses over the continental slopes and rises (Compagno, 2008). The species diversity of oceanic and semipelagic elasmobranchs is very low compared to other environments, with approximately 26-31 oceanic and 31-33 semipelagic species, and only 24-28 oceanic shark species (Compagno, 2008).

Notwithstanding the small species diversity, the oceanic elasmobranchs are composed of the typical apex predators (e.g. mako shark, *Isurus oxyrinchus*), as well as large filter feeders (e.g. whale shark, *Rhincodon typus*, and devil rays, Mobulidae), a few moderate (e.g. pelagic stingray, *Pteroplatytrygon violacea*) and small sized species (e.g. pygmy sharks) (Compagno, 2008). Reproduction in pelagic elasmobranchs is strictly viviparous, with differences among species in the way the young are nourished during the second stage of gestation (Snelson et al., 2008). Lamniform sharks (genus Alopiidae and Lamnidae) exhibit aplacental viviparity with oophagy, in which the embryos feed firstly on the yolk sac inside their capsule and afterwards on unfertilized oocytes produced by the mother. Requiem sharks (Carcharhinidae), with the exception of the tiger shark (*Galeocerdo cuvier*), are placental viviparous. After the yolk sac is exhausted, embryos of requiem sharks are fed through a placenta-like connection that has formed between the mother and the embryo. In pelagic sting ray and mobulid rays (Myliobatiformes), after depletion of the yolk sac, the embryos are fed through trophonemata, i.e. fingerlike projections from the uterus that secrete a nutritional rich fluid (White et al., 2006; Snelson et al., 2008).

Sharks have generally low reproductive rates, with long gestation periods and a small number of precocious offspring when compared to other fish, locating them on the K-side of the classic r/K selection theory spectrum (Hoenig and Gruber, 1990; Cortés, 2000). Still, sharks display significant variation in these traits and developed a wide range of life-history strategies as an evolutionary response to their environment. Life history strategies can be perceived as the counter-balancing of interrelated anatomical, physiological and behavioural adaptive traits that control the investment in reproduction and self-maintenance. Hoenig and Gruber (1990) describe it as a set of traits brought about by natural selection to solve particular ecological problems. It encompasses interrelated physiological factors like reproductive periodicity, litter size, size at birth, growth rate, time to maturity, but also prey interactions, social and sexual relationships, movements, migrations and the use of nursery areas (Branstetter, 1990; Hoenig and Gruber, 1990; Heupel et al., 2007).

One aspect of the life history strategy of sharks that received relatively little attention is the segregation by sex and size (Wearmouth and Sims, 2008). Sexual segregation is said to be a universal trait of sharks (Springer, 1967), yet Sims (2005) found evidence for only 38 out of the approximately 400 living shark species, illustrating how little is known about the biology of the majority of the species (Wearmouth and Sims, 2008). Segregation can be geographical, resulting from sex or size differences in habitat preference, but also behavioural, for example, to avoid inter-specific aggression or predation (Branstetter, 1990; Sims et al., 2001; Sims, 2005; Wearmouth and Sims, 2008). The selective pressures behind sexual and size segregation, however, are not yet fully understood (Sims, 2005; Wearmouth and Sims, 2008).

The concept of nursery areas as a component of a shark's life history was introduced by Branstetter (1990). He suggested the existence of trade-offs between nursery areas and other life history components like size at birth, litter size, growth rate, reproductive periodicity and time to maturity (Branstetter, 1990). In his view, predation is probably the most important limiting factor on juvenile growth, whereas food availability is less important as juveniles are generally born in prey rich habitat. He therefore differentiated between two strategies aimed at maximizing the survival of shark pups: slow growing species are either born at large sizes or rely on protected nursery areas, while fast growing species rely more on growth rates. Heupel et al. (2007) elaborated on these views and suggested that other attributes than predation risk, like factors that increase growth rates, could contribute to the existence of unprotected nursery areas.

Much of this theory is based on evidence of coastal sharks, but much less is known about the biology of oceanic species. Compared to their coastal family members, pelagic sharks have slightly larger litters of smaller young, probably as an adaptation to their oceanic habitat (Snelson et al., 2008). Compared to coastal habitats, predation risk in an oceanic environment will be generally lower, while the availability of food will be more patchy and scarce. This evolutionary adaptation may therefore be advantageous because of the necessity to disperse and thrive on these limited resources (Snelson et al., 2008). How these differences in reproductive strategies and habitat between coastal and oceanic sharks translate in terms their distribution, patterns of segregation and movements, i.e. the spatio-temporal structure of their populations, remains largely unknown (see Camhi et al. (Eds.), 2008 for a review).

3. Movements of oceanic predators

Oceanic predators display large scale movements, generally related to feeding and reproduction, which are closely linked with their life history and environment. The open ocean forms an oligotrophic environment characterised by localised areas of increased productivity and diversity (Sydeman et al., 2006; Wingfield et al., 2011). These hotspots are generally associated with seamounts or oceanographic phenomena like eddies or fronts where primary productivity is enhanced through physical process like upwelling or mixing. These areas can shift with time depending on the season or oceanographic conditions, forcing large oceanic predators like tuna, billfishes, cetaceans, seabirds, sharks and turtles to move sometimes long distances in search of food (Block et al., 2011). Associations of species, with seamounts and oceanographic features have received much attention in scientific literature (e.g. Sydeman et al., 2006; Morato et al., 2008), in particular for commercial species due to the importance of such associations for fisheries.

Studies from fisheries data, field observations and more recently from satellite telemetry allowed characterising some of these associations and revealed their complexity. It was found that these associations depend on factors such as the area, the season, the physiology and feeding ecology of the species (Block et al., 2011). For example, Morato et al. (2008) found an aggregating effect for some seamounts near the Azores for skipjack (*Katsuwonus pelamis*), bigeye tuna (*Thunnus obesus*), common dolphin (*Delphinus delphis*) and Cory's shearwater (*Calonectris diomedea borealis*), but not for other species like loggerhead sea turtles (*Caretta caretta*), spotted (*Stenella frontalis*) or bottle nose dolphins (*Tursiops truncatus*). Similarly,

species explore different features of meso-scale eddies, from cores (anticyclonic and cyclonic) and peripheral edges to transition zones between eddies as a response to the distribution of their prey (e.g. Davis et al., 2002; Polovina et al., 2004; Hyrenbach et al., 2006; Kai and Marsac, 2010).

In order to optimize their success in finding prey, pelagic predators are thought exhibit search behaviour that is adapted to their environment (Humphries et al., 2010). This behaviour can rely on previous knowledge of good feeding areas (“directed” walks) (Papastamatiou et al., 2011) or some kind of optimal search strategy (“random” walks) (Sims et al., 2008; Humphries et al., 2010). In prey rich habitat, correlated random walks or Brownian movements appear more appropriate to describe the observed movement patterns (Reynolds and Rhodes, 2009; Humphries et al., 2010). In the open ocean the optimal search strategy is thought to be best described by “Lévy flight behaviour” due to the patchiness of the resources (Sims et al., 2008; Humphries et al., 2010). These are nomadic movements consisting of random, long distance movements punctuated by small-displacements during foraging (Sims et al., 2008; Humphries et al., 2010). Many species, including pelagic sharks, also display philopatric behaviour, returning to specific localities during part of their life cycles, for feeding, but also as part of their reproductive cycle (Hueter et al., 2004; Papastamatiou et al., 2011). Additionally, considerable individual variability in movement patterns can also exist between individuals of the same age group within a given population (Secor, 1999). Such behavioural polymorphism can manifest itself for instance in populations where a fraction of the adult population is relatively site-attached, while others show typical nomadic behaviour, like for example in tiger shark (*Galeocerdo cuvier*) (Meyer et al., 2010). The full extent of individual movements is still difficult to assess and will probably require continuous observation of movements of a sufficient number of individuals over long time periods (Grüss et al., 2011). A better understanding of the individual movements of pelagic predators and the relationship with their physical habitat is important because they will largely influence their distribution and accessibility to fisheries (Secor, 1999), while their predictability can be an important tool for fisheries management (Hobday and Hartmann, 2006; Game et al., 2009; Hobday and Evans, 2013).

4. Fisheries

Their life history characteristics make sharks highly vulnerable to overfishing (Hoenig and Gruber, 1990). From this life history perspective, sharks could be compared to marine mammals, many of which continue under conservation threat decades after their commercial exploitation was ceased (Hoenig and Gruber, 1990). This general vulnerability of sharks is illustrated by historical examples of directed shark fisheries that are characterised by a highly productive initial phase followed by a rapid decline and occasionally a collapse of the fisheries (Bonfil, 1994). Examples of such fisheries include the northwest Atlantic fisheries for porbeagle, *Lamna nasus* (Campana et al., 2002), the Australian school shark (*Galeorhinus galeus*) fishery (Olsen, 1954) and the English basking shark (*Cetorhinus maximus*) fishery (Parker and Stott, 1965). There is also anecdotal evidence that, due to sexual segregation, the unequal exploitation of one sex, i.e. mature females, may have been responsible for the rapid collapses of the fisheries for spurdog (*Squalus acanthias*) in the English Channel (Steven, 1933) and basking shark off Ireland and Scotland (Anderson, 1990).

More broadly, important declines of the populations of pelagic sharks have been reported worldwide (Baum et al., 2003; Dulvy et al., 2008, Ferretti et al., 2008). These declines have been chiefly attributed to intense industrial fishing that capture these species either purposely or as an incidental by-catch. The main fisheries impacting oceanic sharks are industrial fisheries for tuna and bill fish, i.e. the pelagic longline fishery for swordfish or tuna and the purse-seine fishery for tropical tunas. In the North Atlantic (NA), the main threat to pelagic shark populations is the pelagic longline fishery (Bonfil, 1994).

Pelagic longlining in the NA started in mid-1950s with Japanese longliners targeting tuna in equatorial waters of the western Atlantic (Bonfil, 1994). Over the next decades, the high seas longline fisheries expanded and by the late 1970s the fleets extended their operational range throughout the entire ocean basin. Besides the Japanese fleet, the most important include tuna fleets from Taiwan and Korea and longline fleets targeting swordfish from Spain, United States, Canada and later also Portugal (Bonfil, 1994). Up to the late 1980s, the majority of the sharks were discarded at sea, but the removal of their fins, so-called “finning”, was probably common practise (Bonfil, 1994).

National legal restrictions and ICCAT resolutions and recommendations have been adopted to reduce the impact of longline fisheries on pelagic sharks. These generally aim to ban the

practise of finning (e.g. United States, European Union, ICCAT) and the landing and trade of endangered species (e.g. hammerhead sharks, family Sphyrnidae, and bigeye thresher shark, *Alopias superciliosus*). Nonetheless, it is likely that these restrictions will be insufficient, and that additional measures to reduce hooking mortality will be necessary, given the low population numbers and slow recovery rates (Camhi et al., 2008).

5. Blue shark

Blue shark (*Prionace glauca*) is a member of the family of requiem sharks (Carcharhinidae). It is the most abundant and probably the best studied oceanic shark (Nakano and Stevens, 2008). It has a circum global distribution and can be found from tropical to temperate latitudes. Maximum length of blue shark is 383 cm TL and is similar for both males and females (Compagno, 1984). It is a predator that feeds mainly on small pelagic prey, like bony fishes and squids, although other prey like invertebrates, seabirds, bottom fishes or mammalian carrion may be opportunistically taken (Compagno, 1984; Clarke et al., 1996; Henderson et al., 2001). It occupies a vertical niche that extends hundreds of meters, generally up to approximately 700m during daytime, but with occasional dives up to 1160 m (Carey and Scharold, 1990; Klimley et al., 2002; Queiroz et al., 2010; 2012; Campana et al., 2011). Compared to other pelagic sharks, blue sharks have a very productive life history, characterised by fast growth and the frequent production of numerous small offspring (Cortés, 2000; Frisk et al., 2001; Aires-da-Silva and Gallucci, 2007; Snelson et al., 2008; Anonymous, 2009).

Blue sharks segregate by sex and size and display extensive movements related to reproduction and foraging resulting in a complex spatio-temporal structure of their populations (Nakano and Stevens, 2008). Most information on the population structure and movements comes from conventional tagging studies and data on fisheries catches. In the NA some extensive long term tagging programs were set up with the help of recreational and commercial fishermen, e.g. in the United States (National Marine Fisheries Service (NMFS) Cooperative Shark Tagging Program) (Kohler et al., 1998), Ireland (Central Fisheries Board Marine Sportfish Tagging Programme) (Fitzmaurice, 2005), Spain (Instituto Espanol de Oceanografia tagging program) (Mejuto et al., 2004) and the United Kingdom (Stevens et al., 1990). Within the NFMS program, the largest program in the NA, a total of 91450 blue sharks was tagged from 1962-2000, resulting in 5410 recaptures (Kohler et al., 2002). Recapture information from these programs formed the basis to classify the NA blue shark as a single

stock, with numerous recaptures across the NA basin and only few trans-equatorial migrations (Kohler et al., 2002). Together with catch and reproductive data it also led to the common idea of a clockwise, largely passive, migration cycle along the major NA current systems (Stevens, 1976; Casey, 1985; Stevens, 1990; Kohler et al., 2002; Fitzmaurice et al., 2005). Pupping areas are generally thought to be located at intermediate latitudes in the eastern NA (Stevens, 1976; Stevens, 1990; Buencuerpo et al., 1998). The eastern NA is dominated mainly by juvenile females (Stevens, 1990; Aires-da-Silva et al., 2008a), while the western NA is dominated mainly by males (Pratt, 1979; Simpfendorfer et al., 2002; Campana et al., 2006). Adult males and females generally display a more southern distribution than the juveniles (Castro and Mejuto, 1995; Tavares et al., 2012). Still, the information on the spatio-temporal structure of the NA blue shark population remains very patchy and incomplete (Fig. 11), as the tagging data are restricted to a few tag release sites (Nakano and Stevens, 2008), while catch data usually do not include information on sex and size and are inevitably constraint by the activity of the fishing fleets.

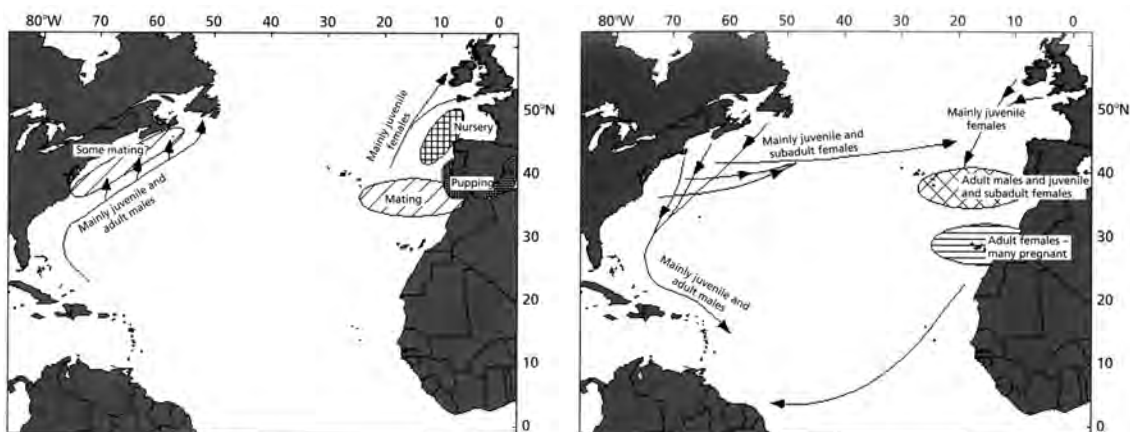


Figure 1.1 – Blue shark migration model for the North Atlantic Ocean. Left panel: spring – summer. Right panel: autumn – winter. (From Nakano and Stevens, 2008)

Blue shark is usually reported as the major constituent of the by-catch from the longline fisheries (Mejuto, 1985; Hurley, 1998; Castro et al., 2000; Mejuto et al., 2009). Their fins dominate the international shark fin trade, as shown from trade records from the world's largest Hong Kong shark fin market (Clarke et al., 2006). In the European NA swordfish fisheries, blue shark constitutes 60-80% of the catch (Aires-da-Silva et al., 2008a; Mejuto et al., 2009; Oceana, 2009). This fishery was traditionally directed at swordfish, but as a response to reduced swordfish quota and increased market demand for shark products, the fishery de

facto converted into a mixed fishery during the 1990s (Mejuto et al., 2002; Aires-da-Silva et al., 2008a).

The population status of blue shark in the NA is ambiguous. Recent stock assessments by ICCAT found no indications of overexploitation of the NA stocks, but remain constrained by poor data quality (Anonymous, 2005; 2009). Other studies reported very contrasting trends, for example in the western and north-western NA (Simpfendorfer et al., 2002; Baum et al., 2003; Aires-da-Silva et al., 2008b). Clarke et al. (2006) suggested that blue sharks are globally being exploited at levels close to or possibly exceeding maximum sustainable yield. These conflicting assessments challenge the idea that the productive life history parameters of blue shark allow the species to withstand heavy fishing pressure. A yield analysis carried out by West et al. (2004) suggests that the maximum sustainable yield of blue shark is likely only a few percent of the unexploited stock biomass. Similarly, a demographic analysis carried out by Aires-da-Silva and Galluci (2007) suggests that this concept of high productivity could be misleading as population growth is strongly dependent on the survival of juveniles (0-4 years). This is of special concern as there are indications of overlap between the fisheries and juvenile areas (Aires-da-Silva et al., 2009). The activities of the Portuguese and Spanish fleet in particular exhibit a strong overlap with putative pupping and nursery areas off the Iberian Peninsula, Northern Africa and the Azores (Mejuto et al., 2008; Aires-da-Silva et al., 2008a; 2009). In this context, the identification of juvenile areas and the assessment of their extent, temporal stability, connectivity and overlap with adult areas are essential to inform fisheries management as their protection could be the key to achieve a sustainable exploitation of NA blue shark.

6. Outline and objectives

The dissertation consists of three chapters that build up sequentially. Each chapter was prepared for direct submission as articles to peer review scientific journals. Supplemental information (tables and figures) not to be published are presented in the appendices.

Chapter 2 characterises the population structure and seasonal abundance of blue shark around the Azores Archipelago based on detailed analyses of fishery independent and observer data for the area. Different population components are identified and the relationship between the catches and environmental variables are established. This study demonstrates the central role

of the area, as it is periodically visited by different juvenile and adult life stages of blue shark. It identifies the area as an important juvenile ground and presents evidence that the area is used as a pupping ground. The results are discussed in light of the existing knowledge on the population structure of NA blue shark and form the basis for the design of the satellite tagging experiment in chapter 3.

Chapter 3 reports the results of a long-term electronic tagging experiment to gain insights in the spatial dynamics of the NA blue shark population. Blue shark ($n=37$) belonging to different life stages were equipped with satellite linked tags programmed for long-lasting deployments. The objectives were to characterise the long-term migratory pathways across different life stages of blue shark, investigate how these movements patterns change across life stages and assess the connectivity between the different areas used by blue sharks in the NA. The second goal was to verify the existence of a nursery area for blue shark in the central NA, and to determine its boundaries and stability over time.

Chapter 4 presents the outcome of a habitat modelling approach that was developed to investigate the interaction between the distribution of juvenile blue shark and their physical environment, using both fisheries and satellite telemetry data. Based on their habitat preference derived from telemetry data, suitable juvenile habitats are predicted and mapped for the entire NA and their location is discussed in the light of present knowledge of their distribution.

In a final chapter the findings are synthesised and contextualised, and an updated migration model for NA blue shark is proposed. In addition, implications for the management and conservation of NA blue shark are discussed and priorities for future research are proposed.

