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AGE AND GROWTH OF THE BLUE SHARK (*Prionace glauca*) IN THE INDIAN OCEAN

UNIVERSIDADE DO ALGARVE
Faculdade de Ciências e Tecnologia
2017

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MSc Marine Biology

Supervised by:
Rui Coelho, PhD (IPMA)
Karim Erzini, PhD (UAlg/CCMAR)

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Declaração de autoria de trabalho

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.

(Inês Andrade)

Agradecimentos

Obrigada ao Dr. Rui Coelho por ter aceite orientar este trabalho e por toda a ajuda imprescindível, assim como ao Dr. Karim Erzini. À Daniela Rosa, obrigada por toda a ajuda e pela paciência durante estes meses de trabalho, e também ao Rubén Muñoz-Lechuga pela sua disponibilidade.

Obrigada aos observadores do IPMA, Carlos Barbosa e Sérgio Goes, que recolheram as amostras sem as quais esta tese não seria possível, e também à restante equipa do IPMA por me terem feito sentir integrada.

Aos meus pais e à minha irmã, obrigada por terem estado sempre presentes mesmo quando eu não estava, e por todo o apoio incondicional. À minha restante família, um grande abraço e obrigada por tudo.

Obrigada à Inês por estares presente em tudo quase desde sempre, à Mariana que chegaste mais tarde, mas para ficar para sempre e ao Diogo que mesmo quando estiveste longe estiveste sempre perto.

To all the friends I met in Faro, but I feel like I have known for so long, thank you for making these two years so much fun even when times were harder. I wish you all the best.

UAlg
UNIVERSIDADE DO ALGARVE

IPMA
Instituto Português
do Mar e da Atmosfera

Abstract

The blue shark, *Prionace glauca*, is a cosmopolitan species considered to be the most abundant pelagic shark in the world. It is frequently caught in pelagic fisheries, being the most captured shark by the Portuguese pelagic longline fishery targeting swordfish. The biology of blue sharks has been relatively well studied in the Atlantic and Pacific oceans. However, high levels of uncertainty still persist regarding many of its biological aspects in the Indian Ocean, specifically in terms of age estimation and growth modelling. For this study, a total of 818 vertebral samples were collected from blue sharks captured by pelagic longliners in the Indian Ocean, between March 2013 and September 2016, with sizes ranging from 82 to 301 cm fork length (FL). The age of individuals was estimated through counting growth band pairs in sectioned vertebrae, assuming annual deposition. Two growth models were fitted to the age data, a three-parameter von Bertalanffy growth function (VBGF) re-parameterized to calculate L_0 (size at birth) and a two-parameter VBGF with a fixed L_0. The latter was considered the most adequate to describe the growth of the species, with the estimated parameters being L_{inf} = 272.2 cm FL, k = 0.15 $year^{-1}$ for males and L_{inf} = 283.2 cm FL, k = 0.13 $year^{-1}$ for females. These results suggest that females have a slower growth than males. The maximum age estimated was 25 years, representing the oldest attributed age to this species so far. Further work is needed regarding blue sharks in the Indian Ocean, but this study adds important life-history information that can contribute for the management and conservation of the species.

Keywords: elasmobranchs, bycatch, growth modelling, fisheries, pelagic longline

Resumo

Os tubarões oceânicos permanecem menos estudados que os tubarões costeiros, e estão entre os menos estudados de todos os elasmobrânquios, que incluem raias e tubarões. A sua natureza altamente migratória dificulta o estudo destes organismos, e a falta de fiabilidade por vezes existente em termos de registos de capturas e rejeições limita as projeções em termos dos impactos de atividades pesqueiras. No entanto, a biologia destes organismos, incluindo características como crescimento lento, ciclo de vida longo, maturação sexual tardia, entre outras, torna-os mais vulneráveis em termos de sobreexploração. Neste sentido, a importância destes predadores de topo nas cadeias alimentares oceânicas impõe a necessidade de aumentar o nível de conhecimento sobre os mesmos.

A tintureira, ou tubarão azul, como é conhecida a espécie *Prionace glauca*, é um tubarão pelágico e oceânico com uma distribuição cosmopolita, que inclui águas temperadas e tropicais. Além da distribuição abrangente, esta é considerada a espécie de tubarão pelágico mais abundante em todo o mundo, assumindo, portanto, grande importância nestes ecossistemas a nível global. Apesar de ser uma espécie oceânica, pode ser ocasionalmente encontrada em ambientes costeiros, nomeadamente no caso de juvenis. Grandes migrações são também uma característica desta espécie, podendo os seus movimentos migratórios estar relacionados com o seu ciclo reprodutor, distribuição de presas, correntes oceânicas ou mesmo com a temperatura da água. Relativamente à distribuição da tintureira no Oceano Índico, dados recentes apontam para uma maior abundância de tintureiras de maior dimensão em zonas equatoriais e tropicais, enquanto os indivíduos mais pequenos demonstram uma preferência por zonas temperadas nas latitudes mais altas. A nível de tamanhos, a tintureira ultrapassa os 300 cm, podendo chegar até aos 380 cm. São tubarões vivíparos, com um período de gestação que poderá prolongar-se por 9 ou 12 meses, após os quais as fêmeas dão à luz entre 4 a 135 crias, durante a Primavera e o Verão. Ambos os sexos atingem maturação com um comprimento corporal e idades semelhantes, sendo a idade de maturação para machos entre os 4 e 6 anos, e entre os 5 e 7 anos para fêmeas. Em termos de longevidade, pensa-se que esta espécie possa viver até aos 20 ou 23 anos de idade.

A tintureira é uma das espécies de tubarão pelágico mais frequentemente capturada como presa acessória (*bycatch*) pelas frotas pesqueiras em todo o mundo, principalmente por palangres de superfície. A nível de pesca desportiva, esta espécie é uma das preferidas por parte

de quem pratica esta atividade e frequentemente um dos alvos principais. Em termos de pesca comercial, a tintureira tradicionalmente era uma espécie de baixo valor comercial, no entanto o interesse nestes organismos tem vindo a aumentar. No Oceano Índico, esta é a espécie de tubarão mais capturada pela frota Portuguesa de palangre de superfície dirigida ao espadarte, sendo a segunda mais capturada além da espécie alvo. A tintureira encontra-se atualmente listada como uma espécie quase ameaçada (*Near Threatened*) pela IUCN a nível global, assim como no Nordeste Atlântico, sendo já considerada como criticamente ameaçada (*Critically Endangered*) no Mediterrâneo.

A idade de um organismo é considerada um dos parâmetros biológicos mais importantes, sendo que é necessário por exemplo para o cálculo de taxas de crescimento, taxas de mortalidade, produtividade e longevidade. Em termos de avaliação de stocks em biologia pesqueira, a idade e crescimento são muito relevantes, dado que são utilizados para calcular parâmetros como abundancia e mortalidade, que estão na base do estabelecimento de medidas reguladoras da atividade pesqueira. Os estudos de idade e crescimento em elasmobrânquios são feitos através da análise de deposição de bandas de crescimento em estruturas calcificadas destes organismos, sendo que as suas vértebras são as mais utilizadas para tal. Uma vez que a tintureira é uma espécie muito comum nos ecossistemas pelágicos de todo o mundo, a sua biologia tem sido muito estudada ao longo dos anos, incluindo estudos de idade e crescimento. No entanto, estes estudos têm-se focado em regiões dos Oceanos Atlântico e Pacífico, existindo atualmente apenas dois estudos de idade e crescimento desta espécie no Oceano Índico.

Dadas as lacunas no conhecimento da biologia de tintureira no Oceano Indico, especificamente em termos de idade e crescimento, este trabalho tem como objetivos: 1) estimar a idade de indivíduos da espécie em estudo através da leitura das bandas de crescimento depositadas nas vértebras dos mesmos; 2) obter modelos de crescimento para ambos os sexos na região do Índico Sul e finalmente 3) fornecer os dados de idade e crescimento obtidos à IOTC (*Indian Ocean Tuna Commission*), sendo esta a organização inter-governamental internacional responsável pela gestão desta espécie no Oceano Índico. Para tal, um total de 818 vértebras foram recolhidas por observadores de pesca do IPMA abordo de navios de pesca comercial dirigida ao espadarte, com arte de palangre de superfície. As amostras recolhidas foram submetidas a um processo de limpeza e posteriormente de seccionamento. Uma vez obtidas as secções das vértebras, estas foram utilizadas para a contagem de bandas de crescimento. Tendo como base estudos prévios de validação da idade desta espécie, uma

deposição anual das bandas de crescimento foi assumida. Após as leituras de idade efetuadas às amostras, foi atribuída uma idade final a um total de 679, tendo estas sido usadas para os modelos de crescimento. Dois modelos foram utilizados, a função de crescimento de von Bertalanffy com três parâmetros re-parametrizado para calcular L_0 (tamanho à nascença), e a função de crescimento de von Bertalanffy com dois parâmetros, mantendo o L_0 fixo. Ambos os modelos foram ajustados para machos e fêmeas em separado, e para ambos simultaneamente.

O modelo final recomendado por este estudo é o modelo com dois parâmetros, mantendo o L_0 fixo, para cada sexo separadamente visto que se verificaram diferenças significativas entre sexos. Os valores estimados para cada parâmetro com este modelo sugerem que as fêmeas atingem um tamanho máximo assimptótico maior e que os machos têm um coeficiente de crescimento mais elevado, o que indica que as fêmeas têm um crescimento mais lento (machos: L_{inf} = 272.2 cm FL, k = 0.15 $year^{-1}$; fêmeas: L_{inf} = 283.2 cm FL, k = 0.13 $year^{-1}$). A idade máxima atribuída foi 25 anos.

No geral, os resultados obtidos neste estudo enquadram-se nos intervalos de valores previamente obtidos por outros estudos. No entanto, a idade máxima estimada no presente estudo foi a maior até agora descrita para esta espécie. Estes resultados vão de encontro ao facto de a tintureira ser uma espécie com um crescimento lento e elevada longevidade, representado uma nova e importante fonte de informação acerca da biologia desta espécie no Oceano Índico. Mais concretamente, estes resultados foram já fornecidos à IOTC, para serem considerados aquando a próxima avaliação desta espécie em Setembro desde ano.

Palavras-chave: elasmobrânquios, capturas acessórias, modelação de crescimento, pescas, palangre de superfície

Index of Contents

Index of Figures

Index of tables

List of Abbreviations

AIC - Akaike Information Criteria
APE - Average percent error
BIC - Bayesian Information Criterion
BSSPM - Bayesian State-Space Production Model
CIs - Confidence intervals
CV - Coefficient of variation
ERA - Ecological risk assessment
FAO - Food and Agriculture Organization of the United Nations
FL - Fork length
IATTC - Inter-American Tropical Tuna Commission
ICCAT - International Commission for the Conservation of Atlantic Tunas
IOTC - Indian Ocean Tuna Commission
IPMA - Instituto Português do Mar e da Atmosfera
ISC - International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean
IUCN - International Union for Conservation of Nature
k - Growth coefficient
L_0 - Size at birth
L_{inf} - Maximum asymptotic size
LRT - Likelihood ratio test
L_t - Mean size at age t
MSY - Maximum Sustainable Yield
OTC - Oxytetracycline
PA - Percentage agreement
SD - Standard deviation
SE - Standard error
SRA - Stock reduction analysis
SS3 - Stock Synthesis III
t_0 - Theoretical age at which the expected length is zero
TL - Total length
VBGF - von Bertalanffy growth function
VR - Vertebral radius
WCPFC - Western and Central Pacific Fisheries Commission

1. Introduction

1.1. Elasmobranchs and oceanic pelagic shark exploitation

Elasmobranchs are organisms from the subclass Elasmobranchii, which along with the subclass Holocephali, belong to the Chondrichthyes class (Compagno *et al.*, 2005). Elasmobranchs include sharks, rays and skates, and can be distinguished from holocephalans by having 5 to 7 pairs of gill openings that are not covered (Bonfil, 1994; Compagno, 2001). They can be found throughout the world's oceans (Bonfil, 1994) and their habitats extent from coastal areas to the open ocean, and even the deep sea (Garcia *et al.*, 2008).

In the past, except for their fins, elasmobranchs had a low commercial value which did not promote research towards their management (Bonfil, 1994). They have been a target for commercial fisheries (Springer, 1952), as well as recreational fishing (Anderson, 1980; Casey & Hoey, 1985). However, elasmobranch exploitation has received more attention due to them being caught as bycatch of fisheries targeting other species (Anderson, 1980; Bailey *et al.*, 1996; Coelho *et al.*, 2012; Witzell, 1985).

In terms of what makes elasmobranchs more vulnerable to overexploitation, their life-history traits, such as reproduction and growth rates, which are also dependent on their habitat, seem to play a crucial role (Garcia *et al.*, 2008), therefore deserving particular attention. Holden (1973) previously stated that the capacity of elasmobranchs to withstand increasing levels of exploitation is directly dependent on the their reproductive biology. Their reproductive modes are variable, ranging from some species with oviparity, to others with aplacental or placental viviparity. All elasmobranchs have internal fertilization and, in general, a small number of offspring that are born at relatively large sizes (Conrath & Musick, 2012; Snelson *et al.*, 2008). Reproductive cycles can vary from months to years (Camhi *et al.,* 1998) and both reproduction rates and fecundity are typically low (Snelson *et al.*, 2008), especially when compared to teleost fish (Camhi *et al.*, 1998). Thus, the low reproductive potential of elasmobranchs (Vas, 1990), slow growth rates, late age of maturity and low fecundity (Camhi *et al.*, 1998; Coelho & Erzini, 2002, 2006; Smith *et al.*, 1998; Stevens, 2000), increases their susceptibility regarding overexploitation when compared with other marine organisms (Frisk *et al.*, 2001; Stevens, 1992). Also, elasmobranchs are predators and are therefore found in lower abundance than organisms belonging to lower trophic levels (Bonfil, 1994).

Within elasmobranchs, oceanic pelagic sharks are species that spend at least part of their lives away from continental shelves, in the open ocean, with pelagic meaning they are not associated to the bottom of the ocean (Compagno, 2008).

The distribution of pelagic sharks in the water column of every ocean basin, makes them easily accessible to high-technology fleets operating in the open ocean (Camhi *et al.*, 2008; Compagno, 2008). Thus, they are very often caught as bycatch, namely of longline pelagic fisheries targeting tuna and swordfish, with species such as the blue shark (*Prionace glauca*), silky shark (*Carcharhinus falciformis*), and shortfin mako (*Isurus oxyrinchus*) being the most commonly caught ones (Camhi *et al*., 2008; Clarke *et al*., 2014; Huang & Liu, 2010; Oliver *et al.*, 2015).

In the Indian Ocean, the estimation of total catches of pelagic sharks is compromised by the deficiency in accurate data, since catches of sharks are often not recorded at the species-specific level (Clarke *et al*., 2014; Herrera & Pierre, 2013). Nevertheless, the total catch of sharks between 1950 to 2012 is thought to have been 40 to 60% of the total catch with all the species combined for the fleets of longliners targeting swordfish (Herrera & Pierre, 2013).

Despite being highly impacted by fishing, oceanic sharks have been less studied than coastal sharks, and are amongst the least studied of all elasmobranchs in general (Pikitch *et al.*, 2008). Their highly migratory nature as well as wide distribution ranges (Kohler & Turner, 2008) creates difficulties in the research process (Bonfil, 1994), and the lack of reliability of landings and discards data (Clarke *et al*., 2014; Pikitch *et al*., 2008) also limits the prediction of fishing impacts. Thus, the importance of these organisms in oceanic pelagic food webs as apex predators (Bonfil, 1994; Camhi *et al*., 1998; Pikitch *et al*., 2008) imposes a need to further study them, fulfilling the gaps of knowledge regarding these organisms (White & Last, 2012).

1.2. Blue shark, the studied species

The blue shark, *Prionace glauca* (**Figure 1.1**), is the only species belonging to the genus *Prionace,* first described by Linnaeus (1758), belonging to the Carcharhinidae Family (Order Carcharhiniformes) (Nakano & Seki, 2003). It is considered the most abundant species of pelagic sharks (McKenzie & Tibbo, 1964; Nakano & Seki, 2003; Nakano & Stevens, 2008), thus being an important component of pelagic ecosystems at a global level (IOTC, 2007).

Blue sharks have a slender and elongated body, and can be distinguished by their blue dorsal coloration as well as long pectoral fins, long snout, large eyes, absence of spiracles and the presence of gillrakers in the internal gill openings (Compagno, 1984; Nakano & Seki, 2003; Nakano & Stevens, 2008).

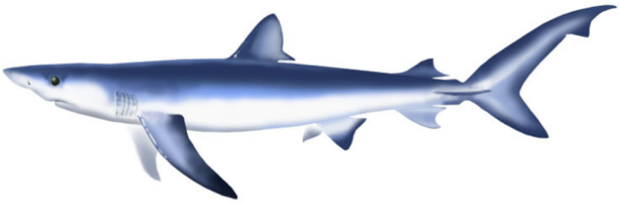

Figure 1.1. Drawing of a blue shark (*Prionace glauca*) by A. López, "Tokio", as seen in ICCAT Manual (Valeiras and Abad, 2009).

The blue shark is a pelagic species with a worldwide distribution (**Figure 1.2**), including both temperate and tropical waters (Compagno, 1984), from latitudes of 60º N to 50º S (Stevens, 2009). Kohler and Turner (2008) even mention that the blue shark is the chondrichthyan with the widest distribution range in the world. This species can usually be found from the surface until around 200 m (Froese, 2016), but its presence has already been recorded at depths greater than 1000 m (Queiroz *et al.,* 2012).

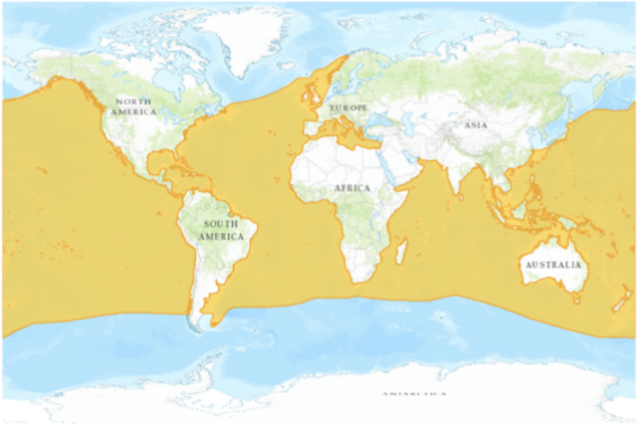

Figure 1.2. Global distribution of *Prionace glauca* with the color yellow representing the area of its extant range, as seen in The IUCN Red List of Threatened Species 2009 (Stevens, 2009).

In the Indian Ocean, blue sharks can be as far south as 40º S according to IOTC (2007), although other authors consider that their distribution goes to 50º S (Nakano & Stevens, 2008; Stevens, 2009). In the tropical waters of this ocean, blue sharks are found in higher abundance at depths of 80 to 220 m, with temperatures ranging from 12°C to 25°C (IOTC, 2007), but the preferred temperature interval mentioned for this species is from 7°C (Compagno, 1984) to

20ºC (Last & Stevens, 1994). According to Gubanov and Grigoryev (1975), the most favourable area in the Indian Ocean for the occurrence of blue sharks is in its western equatorial part, with the highest catches recorded at depths of 130 to 140 m. In the comprehensive study of Coelho *et al.* (in press), results suggest that larger blue shark individuals are found in equatorial and tropical parts of the Indian Ocean while smaller specimens preferred higher latitudes.

The fact that the blue shark is an oceanic species (Compagno, 1984) is supported by studies on its horizontal distribution, showing an increase in abundance in areas with greater bottom depths in contrast to shallower areas (Hazin *et al.*, 1994). However, they occasionally can be found closer to inshore waters (Compagno, 1984), particularly in the case of small juveniles (Litvinov, 2006; Vögler *et al.*, 2012) and in areas of narrower continental shelf (Nakano and Stevens, 2008). In fact, blue sharks form aggregations of juveniles in areas near the coast, and male aggregations are common in the open ocean (Litvinov, 2006; Vögler *et al.*, 2012). This species can exhibit high site fidelity in areas of high productivity as well as display differences in diel behaviour linked to foraging habits, undergoing either normal diel vertical movements (ascending to shallower waters at sunset and descending to greater depths at sunrise) or reverse diel vertical movements (ascending at sunrise and descending at sunset), depending on the prey type they are following (Queiroz *et al.*, 2012). Still regarding their distribution patterns, sexual segregation, both temporal and spatial, is also mentioned for blue sharks (Hazin *et al.*, 1994; Tavares, *et al.*, 2012; Vögler *et al.*, 2012).

Blue sharks are highly migratory (Kohler & Turner, 2008; Nakano & Stevens, 2008) and their movement patterns are often related to their reproduction cycles, the distribution of their prey or even temperature (Montealegre-Quijano & Vooren, 2010; Nakano, 1994; Tavares *et al.*, 2012). In the Pacific Ocean they tend to undergo yearly migrations; northwards in the Summer, and then towards lower latitudes in the Winter, while in the tropics their abundance tends to be uniform throughout the year (Compagno, 1984). In the Atlantic Ocean, tagging studies have revealed this species undergoes frequent trans-Atlantic migrations, which are mentioned as being related to current systems (Compagno, 1984; Kohler *et al.*, 2002; Kohler & Turner, 2008). The study of da Silva (2010) revealed movements of blue sharks from the South Atlantic Ocean to the Southwest Indian Ocean, but there is a lack of information regarding migrations of blue sharks in the Indian Ocean (IOTC, 2007). Overall, males and females seem to have different migratory movements (Hazin *et al.*, 1994), with females tending to be more abundant than males at higher latitudes (Compagno, 1984).

When it comes to the diet of blue sharks, cephalopods are their most important prey type, squid in particular (Compagno, 1984; Henderson *et al*., 2001; Mendonça, 2009; Nakano and Stevens, 2008). Pelagic teleost fish are also a very common prey (Lopez *et al.*, 2010; McCord & Campana, 2003). They can also feed on bottom fish (Nakano & Stevens, 2008), small sharks, invertebrates, mammals and even seabirds (Compagno, 1984).

Blue sharks can be longer than 300 cm in total length (TL) (Pratt, 1979) and have been reported to reach as much as 380 cm TL (Compagno, 1984). They are placental viviparous sharks (Compagno, 1984), with both sexes attaining sexual maturity at similar body lengths (Pratt, 1979). In the north-western Atlantic Ocean, Pratt (1979) found that males are sexually mature at an average size of 183 cm fork length (FL) (218 cm TL) and females at 185 cm FL (221 cm TL), with similar values mentioned for the western Atlantic (Castro and Mejuto, 1995) and for the Indian Ocean (Gubanov & Grigoryev, 1975; Gubanov, 1978). In the case of the Pacific Ocean, slightly smaller lengths are reported for sexual maturity (Nakano, 1994). Mature females have been hypothesized to breed every second year on average (Vas, 1990), but this is still uncertain and an annual cycle is also possible. The gestation period of the blue shark lasts from 9 to 12 months, and the young are born in the Spring and Summer (Compagno, 1984; Nakano, 1994; Pratt, 1979). Pups are born within a size range of 35 to 44 cm FL, reaching numbers of 4 to 135 pups per litter (Castro & Mejuto, 1995; Compagno, 1984; IOTC, 2007; Nakano, 1994; Pratt, 1979). Snelson *et al.* (2008) even mentioned blue sharks as the pelagic sharks with the largest litter size. The estimated age of maturity for male blue sharks is at about 4 to 6 years old, and at 5 to 7 years old for females (Cailliet *et al.,* 1983; Lessa *et al.,* 2004; Nakano, 1994; Pratt, 1979; Vas, 1990). According to age and growth studies, the longevity of this species is thought to be about 20 to 23 years (Cailliet *et a*l., 1983; Manning & Francis, 2005; Romanov *et al.*, 2011; Stevens, 2009).

1.2.1. Blue shark major threats

The blue shark is considered the most abundant species of pelagic sharks (McKenzie & Tibbo, 1964; Nakano & Seki, 2003; Nakano & Stevens, 2008). However, it still faces some threats that can compromise their current populations.

The threat concerning blue sharks that has been mentioned the most over the years is that it is one of the most frequent pelagic sharks caught as bycatch of fisheries worldwide (Campana *et al.*, 2009; Pratt, 1979). While it can be caught by hook-and-lines, pelagic trawls, and bottom trawls if near the coast, pelagic longlines are the most common fishing gear capturing blue sharks (Compagno, 1984; Diaz & Serafy, 2005; Stevens, 1992), more specifically pelagic longline fisheries targeting tuna and swordfish (Anderson, 1980; Bailey *et al.*, 1996; Campana *et al.*, 2009; Carruthers *et al.*, 2011; Francis *et al.*, 2001; IOTC, 2016; Pratt, 1979; Stevens, 1992).

Despite the typical characteristics of elasmobranchs that make them more susceptible to overexploitation, other specific factors also contribute to blue sharks being a major bycatch species. Blue sharks are a placental viviparous species, meaning they give birth to live young that are nourished by females during their development, thus being more prone to overfishing (Vas, 1990). A factor that can be considered is the dense aggregation pattern they reveal, namely of males and juveniles (Litvinov, 2006; Vögler *et al.*, 2012). Such aggregations mean they can be found in a much higher abundance than average, in those specific locations, thus being an easier target for fisheries (Litvinov, 2006). Since male blue sharks form these aggregations in open waters, outside zones of national jurisdiction, combined efforts of inter-governmental organizations such as FAO (Food and Agriculture Organization of the United Nations), ICCAT (*International Commission for the Conservation of Atlantic Tunas*), IOTC (*Indian Ocean Tuna Commission*) and others, are needed to implement international measures related to their management (Litvinov, 2006), which can complicate that process. Also contributing to high numbers of blue sharks caught as bycatch, is the fact that due to foraging habits they can spend the night close to the sea surface, leading to a spatial and temporal overlap of their habitat and pelagic longline fishing effort (Queiroz *et al.*, 2012).

Blue sharks have also been frequently caught in sports fisheries (Anderson, 1980; Compagno, 1984; Skomal & Natanson, 2003; Stevens, 1984, 2009; Vas, 1990), in fact being one of the preferred species for those practicing this activity, along with mako sharks (Casey & Hoey, 1985). Babcock (2008) mentioned blue shark as the pelagic shark species that is most caught by anglers. In the study of Stevens (1984), blue shark was also the most abundant species in the sport fishing catches.

When it comes to commercial fisheries, blue sharks were rarely a targeted species in the past (Nakano & Stevens, 2009; Stevens, 2009). However, there has been an increasing commercial interest in this species in the recent years, both as a food source and also for its fins (Dent & Clarke, 2015; Eriksson & Clarke, 2015). Markets where blue shark meat has been increasing include Japan, Spain, China, Uruguay, Indonesia and Singapore (Dent & Clarke, 2015). Thus, regardless of its low commercial value in the past decades, the exploitation of blue shark as a target species has been increasing in recent years (Aires-da-Silva *et al.*, 2008).

1.2.2. Blue shark stock status

Globally, blue sharks are considered as “Near Threatened” by the International Union for Conservation of Nature (IUCN) Red List (Stevens, 2009). Regionally, this species has been considered "Near Threatened" in the Northeast Atlantic (Sims *et al.*, 2015) and “Critically Endangered” in the Mediterranean (Sims *et al.,* 2016).

According to data from FAO FishStat available in FAO (2017), despite a slight decrease of 140 251 t to 121 208 t from 2013 to 2014 respectively, the global captures of blue sharks have been increasing considerably over the past decades (**Figure 1.3**). The first year considered in this dataset is 1950, in which the capture production reported specifically for this species was only 47 t, and the last year considered is 2014. However, it should be noted that in the earlier years, species-specific data was not usually recorded or reported for sharks, as well as other bycatch species, and therefore those statistics in the earlier years have very limited use. On the other hand, in the late 1990's and early 2000', collection of species-specific statistics and reporting started to increase, especially for the more industrial offshore fleets, therefore also influencing the trends as reported by the FAO production statistics. The maximum capture was registered for 2013 (with 140 251 t as mentioned above).

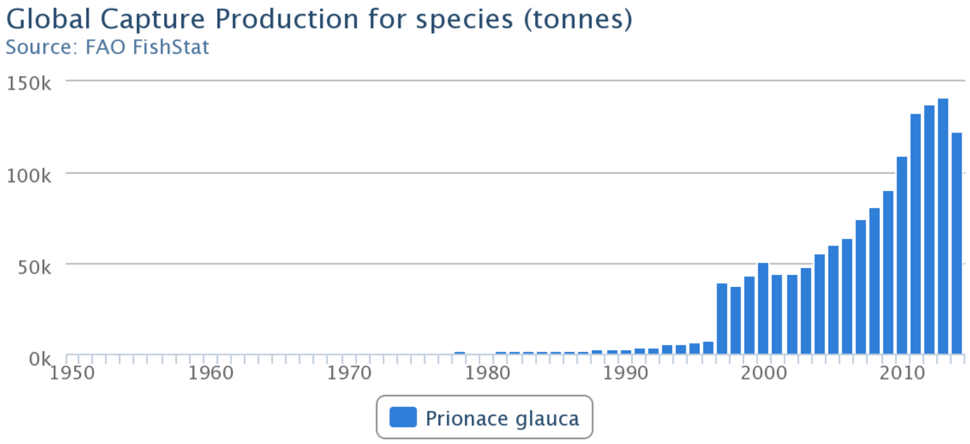

Figure 1.3. Global capture production of *Prionace glauca* in tonnes, from 1950 to 2014. Source: FAO (2017).

In the Indian Ocean, the inter-governmental organization responsible for the management of the blue shark is the *Indian Ocean Tuna Commission* (IOTC). This organization is in charge of the management of tuna and tuna-like species in the Indian Ocean, as well as non-target species associated to these fisheries, thus including pelagic sharks such as blue sharks. The responsibilities of IOTC include, amongst others, to accomplish the assessment of stocks, as well as adopting measures for both their management and conservation, based on scientific research and advice. The *Report of the 19th Session of the IOTC Scientific Committee* (IOTC, 2016) contains the latest stock information for the blue shark in the Indian Ocean, mentioning a reported catch of 30,054 t in 2015, and an average reported catch of 29,535 t between 2011 and 2015 for the species. The stock status for 2016 remains uncertain. The only stock assessment carried out so far for blue sharks in the Indian Ocean took place in 2015, with the next scheduled for September 2017. Three different stock assessment models were applied to blue sharks in 2015, namely the Stock reduction analysis (SRA), Bayesian State-Space Production Model (BSSPM) and Stock Synthesis III (SS3). Two of them (SRA and SS3) suggested that the stock is subject to overfishing at the moment, but still not overfished, and the other model (BSSPM) indicated that the stock was close to Maximum Sustainable Yield (MYS) levels, although not yet considered subject to overfishing. Therefore, the actual status of the stock in the Indian Ocean over the past decade remains uncertain, since the stock assessment models used obtained conflicting results so far.

The IOTC also conducted an ecological risk assessment (ERA) in 2012, which aimed to assess the resilience of the shark species in relation to the impacts of certain fisheries. From that assessment, blue sharks were ranked as “medium vulnerability” for longline fisheries in the ERA ranking, since they were the most productive but also second most susceptible species to this fishery (IOTC, 2016).

According to IOTC data (2016), the reported catches of blue shark have been increasing sharply since the 1970’s in the Indian Ocean, when the expansion of many pelagic longline fleets started in that Ocean. Between 2011 and 2015, the main fleets capturing this species in this region were Indonesia, Spain, China (Taiwan), Japan, and Portugal (IOTC, 2016). In the case of the Portuguese pelagic longline fleet targeting swordfish (*Xiphias gladius*), in the Indian Ocean, blue shark is the most captured species of shark (Muñoz-Lechuga *et al.*, 2016). The work of Muñoz-Lechuga *et al.* (2016) reveals that the blue shark catch was 28.9% of the total catch for this fishery in the period of 2011-2015, being the second most caught species following the main target, swordfish (**Figure 1.4**).

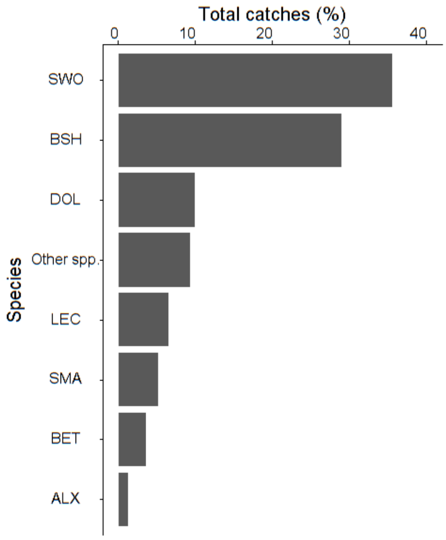

Figure 1.4. Total recorded catch (%) by species for the Portuguese pelagic longline fleet targeting swordfish in the Indian Ocean, from 2011 to 2015. SWO = swordfish, BSH = blue shark, DOL = common dolphinfish, LEC = escolar, SMA = shortfin mako, BET = bigeye tuna and ALX = long snouted lancetfish. Source: Muñoz-Lechuga *et al.* (2016).

Overall, and as the MSY estimate for the blue shark in the Indian Ocean still remains uncertain, IOTC suggests a "precautionary approach to the management" of this species, indicating that the tendency for an increase in fishing effort can lead to biomass declines of blue sharks.

In the Atlantic Ocean, blue sharks are managed by the *International Commission for the Conservation of Atlantic Tunas* (ICCAT). Despite an overall level of uncertainty in the results of their latest stock assessment, all models used suggested that the North Atlantic stock is not overfished and overfishing is not occurring (ICCAT, 2015). Regarding the South Atlantic stock, one of the models estimated the same scenario but another one indicates that the stock could be overfished and that overfishing could be occurring. Since 2016, ICCAT has implemented catch limits for blue shark in the North Atlantic (ICCAT Rec 16-12, 2016).

In the Pacific Ocean, there are two organisations responsible for the management of blue sharks, namely the *Western and Central Pacific Fisheries Commission* (WCPFC) in the western and central Pacific, and the *Inter-American Tropical Tuna Commission* (IATTC) in the eastern Pacific. The *International Scientific Committee for Tuna and Tuna-like Species in the North*

Pacific Ocean (ISC) carries out stock assessments in the Pacific Ocean, providing information to the previously mentioned institutions. In the ISC's report regarding their last stock assessment for blue sharks, considering the most reasonable parameter values, both models used suggest that the North Pacific stock is not overfished and overfishing is not occurring (ISC Shark Working Group, 2014).

1.2.3. Blue shark stock structure

When it comes to the management and conservation of a certain species, its stock structure is a crucial factor to take in consideration. Knowing if there is one global stock or several ones, and how many in each ocean, becomes extremely important since different inter-governmental organizations are responsible for managing a certain species and carrying out stock assessments at a population level in the respective oceans of their mandate.

In the case of the Atlantic Ocean, three different stocks are currently considered for blue sharks, the North Atlantic, South Atlantic and Mediterranean stocks (ICCAT, 2015). However, a new project mentioned in the latest ICCAT blue shark stock assessment report aims to investigate the population structure of blue sharks in the Mediterranean, exploring their connection with non-Mediterranean populations. Despite the existing South and North differentiation, studies such as the one by Veríssimo *et al.* (2017) and da Silva *et al.* (2010) suggest that the South Atlantic stock is at least continuous with the Western Indian Ocean, possibly with the North Atlantic too.

In the Pacific Ocean, different stocks of blue sharks are currently recognized by ISC, one in the South Pacific and another in the North Pacific (ISC Shark Working Group, 2014). The genetic study of Taguchi *et al.* (2015) reported significant but weak differences between populations of blue sharks in the South and North Pacific, thus supporting the separation currently assumed when it comes to management purposes. Additionally, the study of King (2015) confirms that the North Pacific as a whole is a single stock, but points to the need for investigation of the genetic structure of populations in the South Pacific. The ISC also mentions that blue sharks are rarely found in the tropical equatorial waters that separate the North and South stocks. In addition, the results obtained by Li *et al.* (2016) suggest that in the Central Pacific Ocean there is one single panmitic population of blue sharks.

The stock structure of blue sharks in the Indian Ocean still remains uncertain, as mentioned in the most recent IOTC report regarding this species (IOTC, 2016). However, studies such as the previously mentioned suggest that there is a single stock between the South Atlantic and the Indian Ocean (da Silva *et al*., 2010; Veríssimo *et al*., 2017). Overall, more studies on the population structure for blue sharks are needed since stock structure has high implications in terms of the management of the species, and there is a lack of biological information in the South Pacific and Indian Oceans (Taguchi *et al*., 2015).

1.3. Age and Growth studies in elasmobranchs

The age of an organism is considered one of the most important biological parameters, since it is a crucial component for estimating growth rates, mortality rates, productivity and longevity (Campana, 2014; Campana, 2001; Goldman *et al.,* 2012).

Overall, stock assessment is very important for fisheries management by providing information about the effects of fisheries on fish populations, through population modelling (Francis, 2016). Therefore, information about age and growth is essential to fisheries management because it is required to calculate parameters such as abundance and mortality (Campana, 2001) which are estimated from stock assessment and are the basis for establishing harvest control rules (Dichmont *et al*., 2016). Thus, errors when it comes to age estimation, especially underestimation of age, can result in inaccurate stock assessments (Goldman *et al*., 2012), possibly leading to the overexploitation of certain stocks (Campana, 2001).

The information obtained from stock assessment not only indicates the status of populations at that given period, but it also provides a mean to make predictions about their future condition. Furthermore, fisheries biologists often use age-based population models for which age structure data is essential, as well length and weight (Cailliet & Goldman, 2004).

Regardless of being commonly phrased together (Campana, 2001), age and growth have different meanings, that were stated by DeVries and Frie (1996) as age being a “quantitative description of the length of time that an organism has lived” and growth to “the change in body or body part size between two points in time”.

Age estimation in fish can be done through methods such as radiochemical decay rates, tag-recapture studies and others, but the most common is by counting periodic growth increments in hard structures (Bennett *et al*., 1982; Campana, 2001, 2014). In teleost fish, the estimation of age is mostly done by counting periodic growth increments in otoliths (Fablet & Le Josse, 2005). However, other calcified structures show these increments too, including scales and even opercular bones (Campana, 2001; Mahé *et al*., 2016). Elasmobranchs do not have otoliths and their modified scales (i.e., dermal denticles) do not reveal perceptible growth bands (Campana, 2014). Thus, age estimation in these organisms is usually done through vertebrae, spines, neural arches, caudal thorns and other structures, with vertebrae being the most commonly used (Goldman *et al.*, 2012). The vertebrae are removed from cervical or thoracic regions of the animals, or even other locations depending on the species (Campana, 2014). Nevertheless, as stated by Campana (2014), the application of age estimation techniques in elasmobranchs is still much behind that of teleost fish, which have been much more studied regarding this parameter, in part due to the absence of otoliths in elasmobranchs. In some species of elasmobranchs, namely deep water organisms, the structures such as vertebrae are poorly calcified, making age estimation more complex and difficult, and age determination is usually based on spines (Cailliet & Goldman, 2004).

As summarized first by Cailliet and Goldman (2004) and later by Goldman (2005), the process of estimating age is composed of five steps: collecting the hard part samples, their preparation for the age determination, age reading, assessing the validity and reliability of the results and finally data interpretation (modelling growth).

Regarding age estimation in elasmobranchs using vertebrae, transverse sections, longitudinal (sagittal) sections, or the whole vertebral centra have been used (**Figure 1.5**) (Goldman *et al.*, 2012). Although using the whole vertebral centra can lead to inaccurate results for most species because it becomes difficult to distinguish age bands in older mature organisms, as these bands get more tightly grouped (Campana, 2014). If the growth bands are illuminated from below, having transverse sections of the vertebrae can avoid obscuration of the bands on opposite halves. However, age estimation for older animals can still be difficult (Cailliet & Goldman, 2004; Goldman *et al.*, 2012). Thus, unless it is clearly demonstrated that the same age is estimated for a certain species through the whole vertebral central or transversal sections, sagittal sections of vertebrae should be used (Campana, 2001; Goldman, 2005). Also, these vertebral sections should be cut through the centre of the vertebral centra (Campana, 2014).

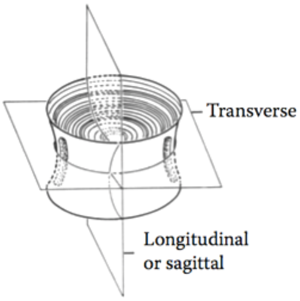

Figure 1.5. Representation of transverse and sagittal sections of the vertebral centra by G.M. Cailliet (Moss Landing Marine Laboratories, California State University), as seen in Goldman (2012).

Along the vertebrae, as with other structures used for age estimation, the calcified material is deposited forming opaque and translucent bands, according to the seasons (Cailliet *et al.,* 2006). Opaque/wide bands correspond to summer growth and translucent/narrow bands to winter growth (Cailliet & Goldman, 2004; Carlson & Baremore, 2005).

In 2004, Cailliet and Goldman (2004) and Goldman (2005) mentioned that the optical properties of age bands (opaque/translucent pattern) could be variable between species, as well as depending on the light source and methodology used, thus advising that the wide/narrow pattern should be used for ageing instead, stating that it tends to be consistent. However, Cailliet *et al.* (2006) updated the previous work, mentioning that the optical properties should be used rather than the wide/narrow pattern, since the width of bands can be variable, bands can be more exaggerated in the early years and get more similar to each other as individuals get older and consequently have slower growth. Therefore, according to these authors, the pattern of opaque/translucent bands is more seasonally consistent. However, Cailliet *et al.* (2006) indicated that the opaque/translucent pattern should still be used depending on the methodology applied, because the methods of preparation of the calcified structures can modify their optical properties, as previously mentioned. More recently, Goldman *et al.* (2012) went back to the initial idea by stating that the basis for elasmobranch age estimation should be the wide/narrow pattern. Campana (2014) also mentions the width of bands when it comes to the interpretation of the vertebral sections. Additionally, Goldman *et al.* (2012) indicate that the narrow bands are the ones used for counting, being referred to as *rings* or *annuli.*

An annual growth cycle in elasmobranchs is then represented by a pair of wide/narrow bands in a vertebral section, which extends from one arm of the *corpus calcareum* to the other arm, crossing the *intermedialia* (**Figure 1.6**) (Goldman *et al*., 2012). These authors also recommend a species-specific approach instead of relying on the assumption that the banding pattern is consistent for different species.

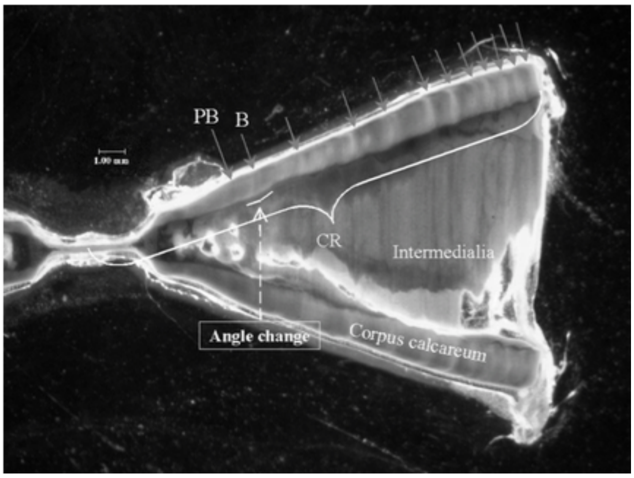

Figure 1.6. Sagittal section of *Lamna ditropis* where the *corpus calcareum* and the *intermedialia* are visible, as well the centrum radius (CR), pre-birth ring (PB) and birth ring (P). The arrows represent the age rings. Source: Goldman (2005).

The preparation of samples for the age readings is well described by Goldman (2005) and more recently by Goldman *et al.* (2012), basically including cleaning and sectioning the calcified structures. These can be stained by a variety of different methods before being mounted on microscope slides, including crystal violet and silver nitrate staining which are amongst the most simple ones, in order to enhance the visibility of age bands (Goldman, 2005).

The interpretation of age bands represents a source of error, often revealing substantial variability (Goldman *et al.*, 2012). However, accuracy in age estimations and therefore growth estimations is essential for the sustainable management of fisheries (Fernandez-Carvalho *et al.*, 2015). Thus, establishing ageing protocols and using methods to evaluate the precision of age readings becomes necessary (Goldman, 2005; Goldman *et al.*, 2012). Ageing protocols refer to the need of a consistent methodology when it comes to the estimation of age, highlighting the need for not one but at least two readers to independently interpret the age bands twice, and without previous knowledge of the size of individuals (Campana, 2014; Goldman, 2005; Goldman *et al.*, 2012). If there is a disagreement regarding some samples, those should be analysed again by the two readers together, although if they do not reach a consensus, then those should not be included in the study (Goldman *et al.*, 2012). The methods most often used for the evaluation of the precision of estimations are the average percent error (APE) technique (Beamish & Fournier, 1981), and the modification of this method by Chang (1982), the coefficient of variation (CV). Another method used is the percent reader agreement/percentage agreement (PA), mentioned as simple and accurate (Goldman, 2005), as well as the percent agreement plus or minus one year (PA ± 1 year). Additionally, age bias plots are also advised to use together with the previous statistical approaches (Campana, 2001).

In addition to the accuracy of age estimation by the readers, the assumption that the growth rings of the samples used are true indicators of the age of individuals should also be confirmed (Goldman *et al.*, 2012). Therefore, the terms validation or verification of age estimations are related to the evaluation of the periodicity of the growth bands deposition on the calcified structures (Cailliet, 1990). Cailliet (1990) defines verification as "the process of confirming an age estimate by comparison with other indeterminate methods" and validation as "proving the accuracy of an age estimate by comparison with a determinate method". Several methods can be used for age validation, namely mark-recapture studies of known-age organisms, bomb radiocarbon dating and most commonly in the case of elasmobranchs, chemically tagging wild individuals (Goldman *et al.*, 2012). Nevertheless, due to the difficulty of validation in elasmobranchs, verification methods are more frequently used, such as the relative marginal increment analysis and the centrum edge analysis (Goldman *et al.*, 2012), these being statistical approaches. Despite this separation, the same authors also state that some of these methods can be used either for verification or validation, particularly if used in combination with others.

When it comes to the estimation of growth parameters in fish, there are many growth models and variations of those models, but the von Bertalanffy and Gompertz are the most frequently used (Goldman *et al.*, 2012). However, in fisheries biology the most commonly used is the von Bertalanffy growth function (VBGF) (Cailliet *et al.*, 2006; Haddon, 2011), which derives from the original model defined by von Bertalanffy (1938).

1.3.1. Age and Growth of the blue shark

Along the years, several studies on the age and growth of blue sharks in various regions were carried out, using different methodologies to obtain growth models for this species in the various oceans. In addition, a few studies on age validation of this species have also been done.

In the Northern Hemisphere, age and growth of blue sharks is well documented both in the Atlantic Ocean (Aasen, 1966; Henderson, *et al.*, 2001; MacNeil & Campana, 2002; Skomal & Natanson, 2003; Stevens, 1975) and Pacific Ocean (Blanco-Parra *et al.*, 2008; Cailliet *et al.*, 1983; Nakano, 1994; Tanaka *et al.*, 1990). There is also the study of Megalofonou *et al.* (2009) in the Mediterranean. In his study, Stevens (1975) states that no growth curves exist for blue sharks prior to his work. He used the von Bertalanffy growth model for his samples and for the length-frequency data previously obtained by Aesen (1966), thus obtaining the first two growth curves for blue sharks. MacNeil and Campana (2002) compared age estimations using the whole vertebrae and sectioned vertebrae. Their results show similar growth curves for both methods, although they mention that age estimations with the whole vertebrae can underestimate the age of older blue sharks.

In the Southern Hemisphere, age and growth of blue sharks are not as extensively studied as in the Northern Hemisphere. Lessa *et al.* (2004) estimated age for blue sharks of the South Atlantic, and Manning and Francis (2005) of the South Pacific. The latter used the whole vertebral centra for individuals < 150 cm FL and sectioned vertebrae for individuals of 150 cm FL or more. In the South Atlantic there is also the study of Hsu *et al.* (2015). More recently, in the South Pacific, Francis and Maolagáin (2016) attempted to estimate the age of specimens caught in New Zealand using the same method as Manning and Francis (2005), and X-rays to visualise the bands. However, they were unable to estimate the age of blue sharks due to ambiguity in band pattern interpretation. There is a particular lack of information for the Indian Ocean. The study of Jolly *et al.* (2013) in South African waters includes a small part of the Southeast Atlantic as well as the Southwest Indian Ocean, obtaining growth models. Rabehagasoa *et al.* (2014) provide the only other published work with growth models for blue sharks in the Indian Ocean, this being a working document from IOTC and not published as a peer-review paper. Other than these, regarding this ocean, there is information about the size of individuals by Romanov and Romanova (2009), in their sample of 2842 animals ranging from 57 to 311 cm FL, and size distribution patterns and structure (Coelho *et al.*, in press). Also importantly, Romanov and Campana (2011) were able to age/validate the age of two sharks using bomb radiocarbon.

Regarding age validation studies for the blue shark, only one was done for the Indian Ocean by Romanov and Campana (2011), as mentioned above. Previous to that, Skomal and Natanson (2003) validated the age of two young sharks in the North Atlantic through the injection of oxytetracycline (OTC) and recapture of the injected animals. In the South Atlantic, Lessa *et al.,* (2004), tried to validate the periodicity of growth band deposition using Marginal Increment analysis. Despite the results not being conclusively supportive of an annual deposition, they still considered that growth bands are formed annually, but recommended more validation studies for this species, particularly with larger sample sizes. More recently in the South Atlantic, Hsu *et al.* (2015) concluded that band deposition is annual, through Marginal increment ratio and centrum edge analysis. In the North Pacific, results obtained by Wells (2016), also using OTC injections in a sample of 26 sharks (most of them being juvenile, and with a maximum time at liberty before recapture of 587 days) supported an annual deposition of band pairs for this species.

2. Objectives

The present work aims to fill the gap of knowledge about the biology and the population dynamics of blue sharks in the South Indian Ocean, which are crucial aspects for both the management of fisheries as well as for the conservation of the species. The specific objectives are:

1. estimating the age of individuals through the reading of growth bands in the vertebrae;
2. obtaining growth models for both sexes in the South Indian Ocean;
3. providing age and growth data of this species to IOTC for stock assessment purposes and management advice.

3. Materials and methods

3.1. Sampling

All the samples used in this study were collected by scientific fishery observers from the *Instituto Português do Mar e da Atmosfera* (IPMA) on board of Portuguese commercial longline vessels that target swordfish (*Xiphias gladius*) in the Indian Ocean. A total of 818 vertebrae were collected from March 2013 to September 2016. Vertebral samples were collected in the South Indian Ocean between 23.75°S and 34.85°S (latitude) and from 40.70°E to 92.97°E (longitude) (**Figure 3.1**).

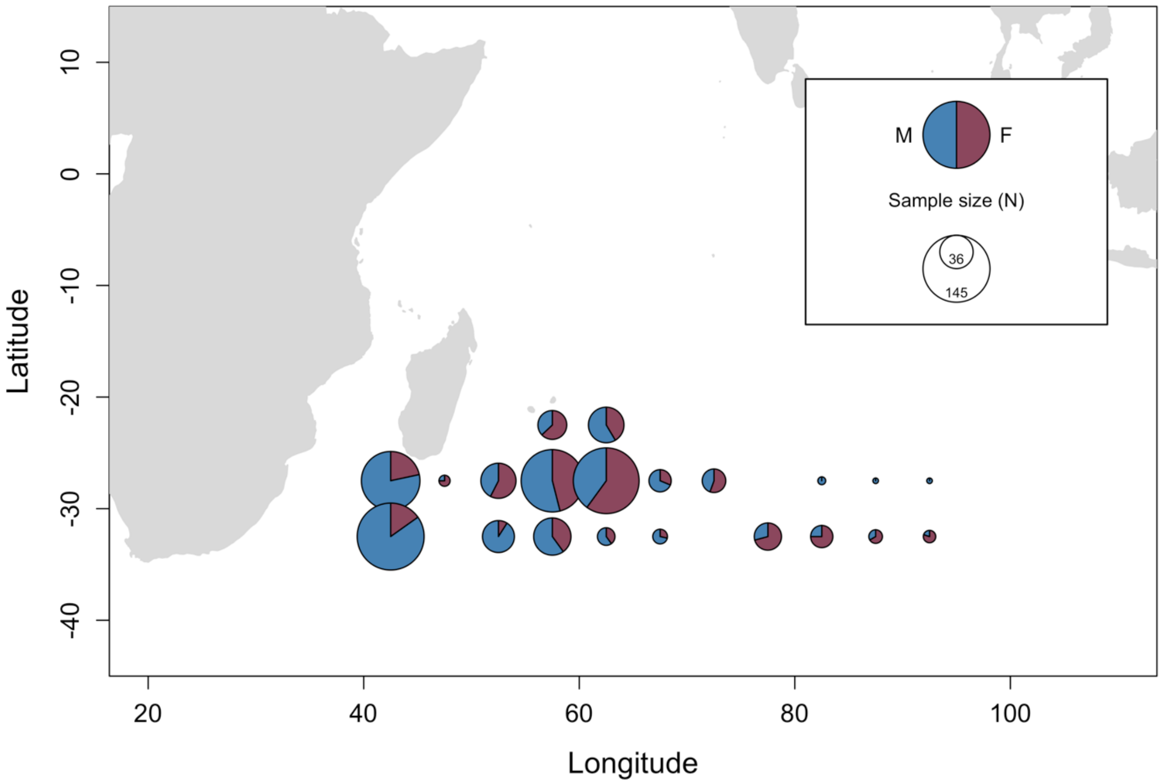

Figure 3.1 Map of the area of collection of *Prionace glauca* samples (females and males represented) in the South Indian Oceann. The plots are represented in 5x5 degree grids, with the sizes of the plots proportional to sample size (N).

Still on board of the fishing vessels, the sex of all individuals as well as the fork length (FL) were recorded. Fork lengths were measured in a straight line to the nearest lower cm. Vertebrae were removed from the region below the anterior part of the first dorsal fin of each individual. After extraction, all vertebral samples were kept frozen in the vessels, as well as during transportation to IPMA, and then stored frozen until being processed in the laboratory.

3.2. Sample processing

All vertebrae were first cleaned and then sectioned. The cleaning process started by manually removing all the organic tissues around each vertebra using scalpels and tweezers. After that, they were immersed in a solution of 4–6% sodium hypochlorite (commercial bleach) during approximately 5 to 10 minutes (depending on the size of each vertebra) to remove any remaining soft tissues, and finally placed in water for a few minutes to eliminate all the sodium hypochlorite. Once cleaned, all vertebrae were stored in ethanol at 70% until further use.

To prepare the vertebrae for the sectioning process, they were first air-dried from the storing ethanol during approximately 30 minutes and then mounted on microscope slides, using a synthetic polymer glue. The center of each vertebra was marked with a pencil to help making it more visible when placing them in the cutter. They were left during 24 hours for the glue to air dry completely. Once the glue was fully dried, each slide was placed in a sectioning cutter, a Buehler Isomet 1000 precision low-speed saw, with two diamond waffering blades, to produce 0.5 mm sagittal sections. The sections were cut through the center of the vertebrae and also through the rays, but avoiding the thicker ones.

To enhance the band pattern, the sections obtained were stained with Crystal Violet solution (Sigma-Aldrich Co., St. Louis, MO), previously used in other shark ageing studies (e.g., Coelho *et al.,* 2011; Fernandez-carvalho *et al.,* 2011; Fernandez-Carvalho *et al*., 2015; Rosa *et al*., 2017), during 2 (for small sections) or 3 minutes (for bigger sections) on each side. Only one of the two sections obtained from each vertebra was stained, to later compare the visibility of the stained versus the non stained bow-ties of the vertebrae. After staining, both sections of each sample were covered with paper and tightly wrapped between two microscope slides, in order to maintain the original shape once fully dried. They remained wrapped for 24h until completely dried.

Finally, the two sections of each vertebra were mounted onto microscope slides using Neo-Mount, and left to dry completely. Once dried, they were observed under a Nikon dissecting microscope with a mounted high resolution digital camera, using transmitted white light. Photos of each observed sample were recorded and then digitally enhanced using the ImageJ software (Schindelin *et al.*, 2015) by adjusting the contrast and brightness (**Figure 3.2**). The same software was then used to mark the growth bands, as well as the focus and the outer edge of the *corpus calcareum* of each vertebral sample.

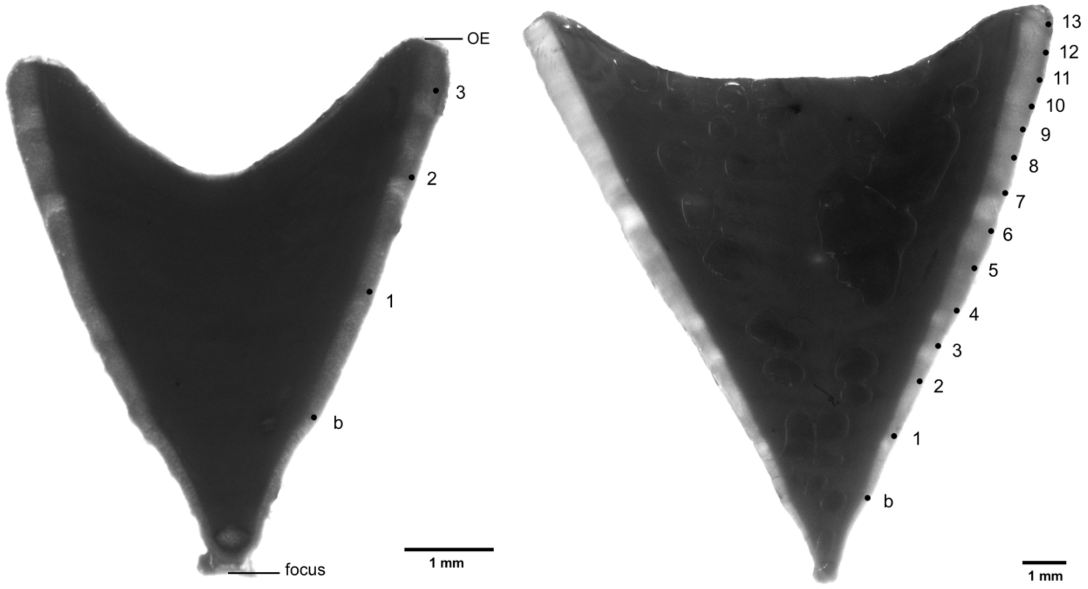

Figure 3.2 Microphotographs of two vertebral samples of *Prionace glauca* specimens collected for the present study with identification of the birthmark (b) and the growth bands (indicated by numbers), as well as the focus and the outer edge of the *corpus calcareum* (OE). The individual on the left has an estimated age of 3 years and the one on the right has an estimated age of 13 years.

3.3. Age estimation and precision analysis

Age was estimated by counting the number of wide/narrow pairs of bands in each sample, through the respective recorded photos. Annual deposition of growth bands was assumed and the first distinct band (usually associated to an angle change in the outer edge of the *corpus calcareum*) was considered to be the birthmark (Blanco-Parra *et al.*, 2008; Francis & Maolagáin, 2016; Hsu *et al.,* 2015; Jolly *et al.*, 2013; Lessa *et al.,* 2004; Megalofonou *et al.,* 2009; Rabehagasoa *et al.*, 2014; Skomal & Natanson, 2003; Wells *et al.,* 2016).

Prior to the start of the readings used to obtain the results, a reference set of 50 samples was selected, 25 being from female specimens and other 25 from males. These were selected containing approximately the same number of samples corresponding to individuals of each body length class (size classes of 10 cm), in order to be representative of the total sample size. Once the reference set was complete, growth bands in these 50 vertebrae were then read by the main reader and author of the present work, together with two researchers from IPMA, reaching a consensus for the age of all of them. Then each reader carried out an independent reading. When the results from the three readers had two or three readings differing from the initial agreed age for a certain sample, those vertebrae were analysed again by the three readers together to reach a new consensus/agreed age.

From the total sample size (n=818), 793 samples were used for age readings, with the remaining 25 being initially excluded since no obvious/consistent band pattern was visible. All 793 vertebrae were read three times and without previous knowledge of the length or sex of each specimen, in order to prevent bias while counting the growth bands. In order to calibrate the readings (i.e., making sure the same criteria were always used when marking the growth zones), a reading of the reference set was carried out before the start of each reading. Also, to prevent familiarity with any particular vertebra, each reading was finished before starting the following one. Additionally, a fourth reading was carried out for the samples whose first three readings produced three different attributed ages, but with two of the three differing only by one year. After all the readings, only vertebrae whose band pair counts obtained three or two out of three equal readings were considered for the age and growth analysis.

In order to compare the precision between the three initial readings, the coefficient of variation (CV) (Chang, 1982), the percentage of agreement (PA) (Beamish & Fournier, 1981) and percentage of agreement within one growth band, and two growth bands (PA ± 1 year, PA ± 2 years) were calculated and compared among the readings. Additionally, age bias plots were also used to graphically compare the accuracy of the three readings (Campana, 2001). Each of the three readings (with 95% CI) was plotted for the agreed age. This agreed age was attributed when between these three readings, at least two were identical. The precision analysis was carried out using the R statistical language (R Core Team, 2015).

3.4. Growth modelling

In order to obtain the vertebral radius (VR) of each vertebra, the distance between the focus of vertebrae and the outer edge of the *corpus calcareum* was digitally measured in the photos of each vertebral sample using the "Measure Cumulative Distances [1]" macro in the ImageJ software. This macro measures cumulative distances along a segmented line selection or between the points of a point selection. The distances were measured to the nearest 0.001 mm as according to the scale present in the dissecting microscope magnification used to take the photos. Three different scales were used when taking the photos, depending on the size of the vertebrae, and all of them were adjusted to pixels in ImageJ (resulting in 1 mm = 298 pixels, 1 mm = 157 pixels or 1 mm = 99 pixels). Since in some of the vertebral sections the tips were broken, thus not showing the focus or the complete outer edge of the *corpus calcareum*, those were not used to calculate VRs, only 727 out of the 818 were used. The relationship between the vertebral radius and fork length of each specimen was then obtained using a linear model following the equation below:

$$FL = a + b\text{VR}$$

where, b is the slope and a is the intercept.

To obtain growth curves for the studied species, two growth models were used, both of them applied to males and females separately and to the two sexes combined. The first model used was a three-parameter von Bertalanffy growth function (VBGF) re-parameterized to estimate L_0 (size at birth) instead of t_0 (theoretical age at which the expected length is zero) (Cailliet *et al*., 2006):

$$L_t = L_{inf} - (L_{inf} - L_0) \times e^{(-kt)},$$

where L_t = mean size (FL, cm) at age t (year);
L_{inf} = maximum asymptotic size (FL);
L_0 = size (FL, cm) at birth;
K = growth coefficient and t = age (year).

The second model used was a two-parameter von Bertalanffy growth function (VBGF) where L_0 was fixed:

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

where b was calculated with the following equation:

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

For the latter model, L_0 was fixed to the maximum size at birth described for this species by Pratt (1979) and also by IOTC (2007) in the Indian Ocean, which is 44 cm (FL).

Both of the previous models were fitted to the age data using nonlinear least squares (nls function in R) and all plots were created with the package "ggplot2" (Wickham, 2009) in R (R Core Team, 2015). For each of the fitted models, the growth parameters were estimated, along with standard error (SE) and 95% confidence intervals (CIs).

In order to test the null hypothesis that there was no difference in growth parameters between both sexes, a likelihood ratio test (LRT) (Kimura, 1980) was performed, using the "fishmethods" package (Nelson, 2017) in R (R Core Team, 2015). Additionally, the model goodness-of-fit was compared with the Akaike Information Criteria (AIC), as well as with the Bayesian Information Criterion (BIC) values. The model with the smallest AIC and BIC values is considered the best fit to the data.

4. Results

4.1. Sample characteristics

A total of 818 shark vertebrae were collected for the present study, of which 491 (60%) were from male sharks and 327 (40%) were from females. The size distribution ranged from 93 to 301 cm FL for males (mean ± SD: 203 ± 50.2 cm) and the females ranged from 82 to 284 cm FL (mean ± SD: 204 ± 40.9 cm) (**Figure 4.1**).

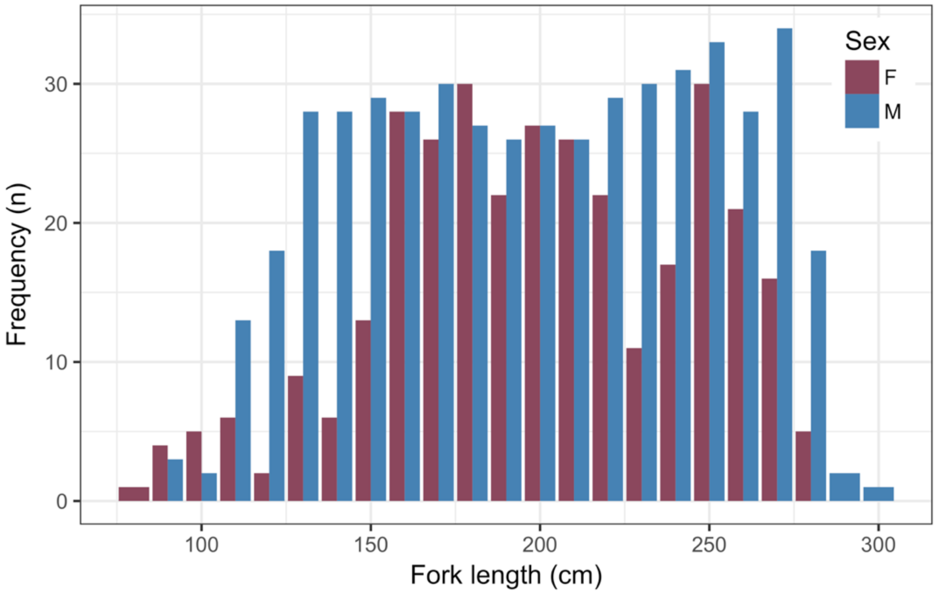

Figure 4.1. Size (FL, cm) frequency distribution of males (n=491) and females (n=327) vertebral samples of *Prionace glauca* individuals collected in the South Indian Ocean between March 2013 and September 2016 (n=818).

Of the 818 samples, 793 were used for age readings, with 133 of these having three different readings but at least two of them differing only by 1 year, thus a fourth reading was carried out for these 133 samples. After all readings were completed, 679 (85.6%) vertebrae (421 males and 267 females) were considered to have a valid estimated age (at least two identical readings) and were thus considered for the age and growth analysis.

4.2. Age estimation and precision analysis

The percentage agreement between the three readings, first and the second, first and third and the second and third was 29%, 37%, 44% and 54%, respectively, suggesting a progressive improvement in the consistency of readings. PA ± 1 year between the first and second, first and third, and second and third readings was 67%, 71% and 78%, respectively. PA ± 2 years between the first and second, first and third, and second and third readings was 83%, 85% and 89%, respectively. The CV between the three readings, the first and second, first and third, and second and third was 8.95%, 9.15%, 8.05% and 5.65%, respectively, and APE between the three readings, the first and second, first and third, and second and third was 6.72%, 6,42%, 5.69% and 3,99%. The age bias plots (**Figure 4.2**) between each reading and the agreed age between the three reveal a high agreement with no systematic bias.

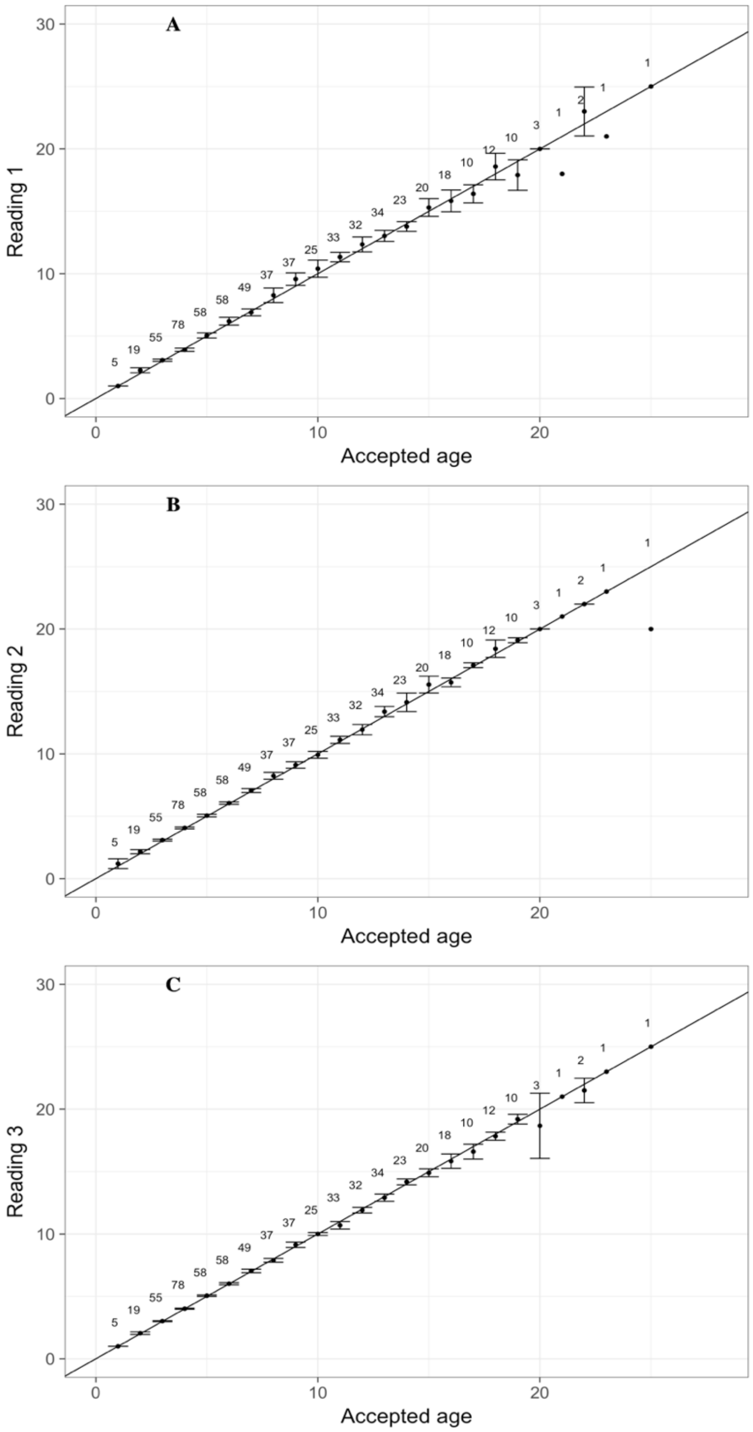

Figure 4.2. Age-bias plots of pairwise age comparisons between reading 1 (A), reading 2 (B), reading 3 (C) and the accepted band pair count, for vertebral samples from *Prionace glauca* collected from the South Indian Ocean.

4.3. Growth modelling

Regarding the relationship between vertebral radius (mm) of each vertebra and the fork length (cm) of the respective specimen (**Figure 4.3**), significant differences were found between sexes ($P < 0.05$). Therefore, the regression equations between VR and FL were calculated for females (FL = 17.45 VR + 13.26; $r^2 = 0.91$) and males (FL = 15.82 VR + 29.82; $r^2 = 0.95$) separately.

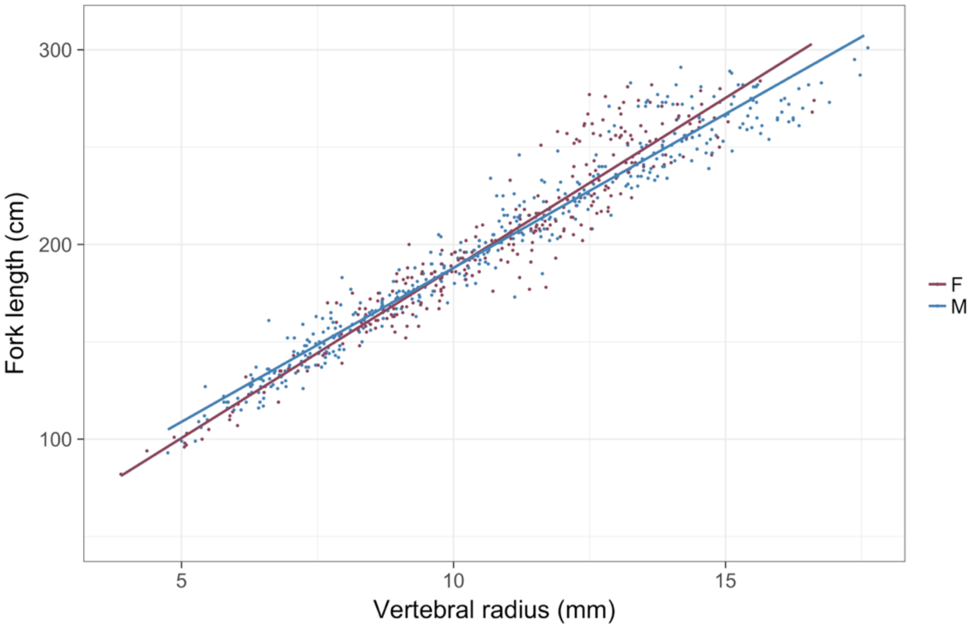

Figure 4.3. Relationship between the fork length (cm) and the vertebral centrum radius (mm) for *Prionace glauca* males (M) and females (F) from the South Indian Ocean. Dots represent individual observations and the solid lines represent the linear regressions where FL = 15.82 VR + 29.82 for males and FL = 17.45 VR + 13.26 for females. FL = fork length and VR = vertebral radius.

A total of 679 blue shark specimens were given a final agreed estimated age, with ages ranging between 1 to 20 years old for females and between 1 to 25 years old for males. The LRT test (Kimura, 1980) results did not reveal differences between males and females for each parameter individually (L_{inf} LRT: $X^2 = 0.07$, $P > 0.05$; k LRT: $X^2 = 0.29$, $P > 0.05$; t_0 LRT: $X^2 = 2.73$, $P > 0.05$). However, for all parameters combined the test indicated significant differences between sexes (LRT: $X^2 = 10.25$, $P < 0.05$). Therefore, both growth models used, the three-parameter VBGF and the VBGF with a fixed L_0, were fitted for females and males separately (**Figure 4.4**).

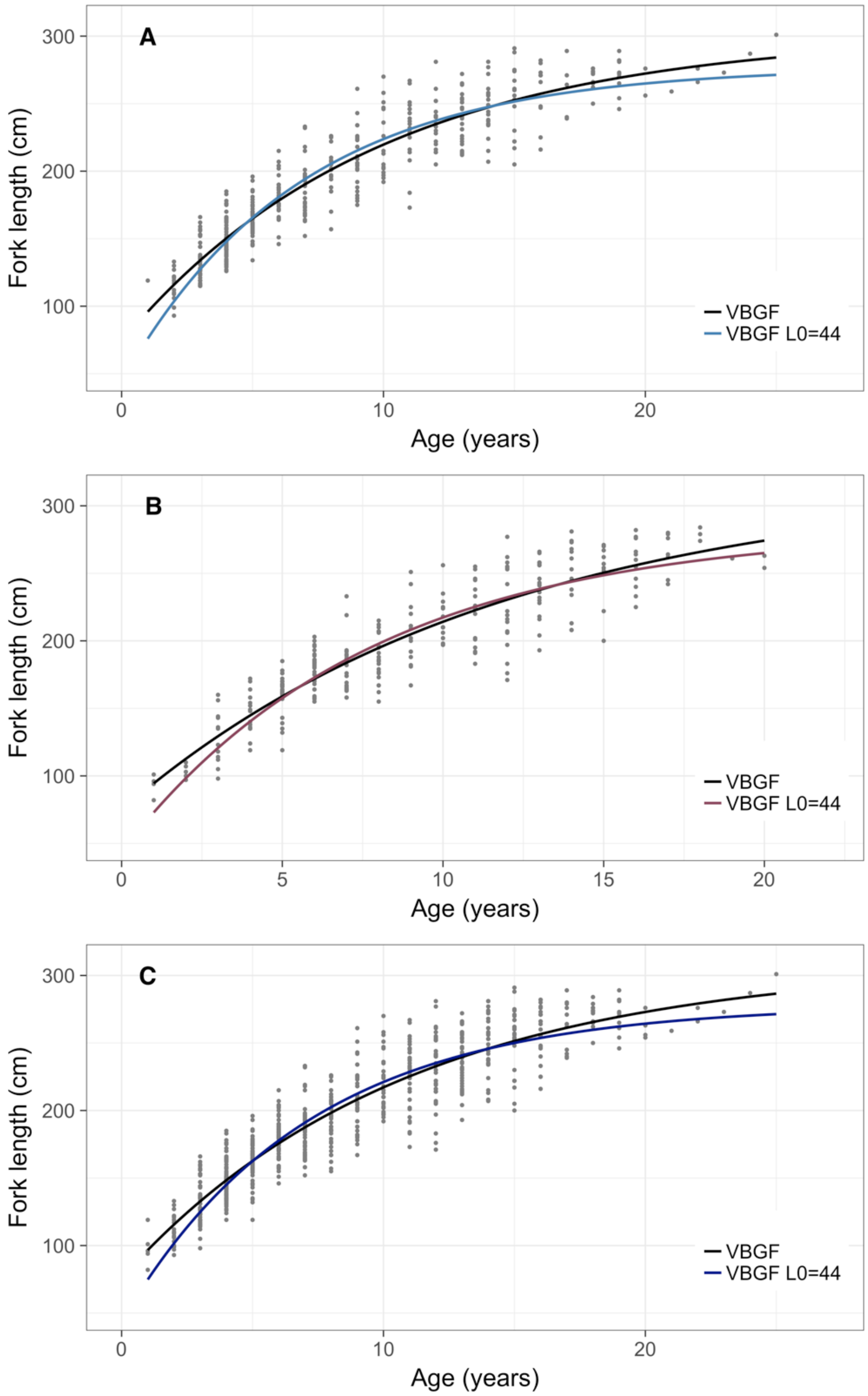

Figure 4.4. The von Bertalanffy growth function (VBGF) for *Prionace glauca* based on age estimations through counting of vertebrae growth bands. Circles represent observed data and the lines represent the VBGF (three-parameters VBGF and VBGF with fixed L_0) for males (A), females (B) and combined sexes (C).

The estimates for growth parameters are displayed in **Table 4.1**. The estimated values of L_{inf} were higher for both sexes when using the three-parameter VBGF instead of VBGF with fixed L_0. For both models, L_{inf} was higher for females. The values for k were slightly higher when using VBGF with a fixed L_0. The estimates for L_0 with the three-parameter VBGF were similar for males (L_0 = 73,8 cm FL) and females (L_0 = 74,99 cm FL) (**Table 4.1**). The three-parameter model presented a lower AIC and BIC then the model with a fixed L_0, suggesting that the first model represents a better fit to the data. However, more biologically reasonable values are likely produced with the two-parameter model with fixed L_0 *(see discussion section for details*). The results obtained with the recommended final model suggest females reach a higher asymptotic length (L_{inf}) than males, and males have a higher growth coefficient (k), indicating a slower growth for females (males: L_{inf} = 272.2 cm FL, k = 0.15 year^{-1}; females: L_{inf} = 283.2 cm FL, k = 0.13 year^{-1}).

Table 4-1. Growth parameters estimated for *Prionace glauca* (males, females and combined sexes) in the South Indian Ocean with the three-parameter von Bertalanffy growth function (VBGF) and VBGF with fixed L_0 at 44 cm fork length (FL). All parameter estimates for both models are presented with standard error (SE) and 95% confidence levels (95% CI). L_{inf} = maximum asymptotic length, k = growth coefficient (year^{-1}), L_0 = size at birth (cm FL). Final parameters recommended to be used are represented in bold (*see discussion section for details*).

Sex	Model	AIC	BIC	Parameter	Estimate	SE	95% CI	
							Lower	Upper
Males	VBGF	3543	3559	L_{inf}	302.0	8.3	287.6	321.2
				k	0.102	0.009	0.084	0.121
				L_0	73.8	5.1	63.3	83.6
	VBGF L0=44	3567	3579	**L_{inf}**	**277.2**	**3.4**	**270.6**	**284.2**
				k	**0.147**	**0.005**	**0.138**	**0.157**
Females	VBGF	2350	2364	L_{inf}	319.7	18.4	291.1	371.8
				k	0.084	0.013	0.058	0.111
				L_0	74.7	7.4	59.3	88.9
	VBGF L0=44	2362	2373	**L_{inf}**	**283.2**	**6.2**	**271.6**	**284.8**
				k	**0.129**	**0.007**	**0.115**	**0.143**
Combined	VBGF	5900	5918	L_{inf}	309.5	8.4	295.0	328.6
				k	0.093	0.007	0.078	0.108
				L_0	75.9	4.2	67.6	83.9
	VBGF L0=44	5944	5958	L_{inf}	278.3	3.0	272.3	284.6
				k	0.141	0.004	0.133	0.149

5. Discussion

Blue sharks are considered the most abundant pelagic sharks (McKenzie & Tibbo, 1964; Nakano & Seki, 2003; Nakano & Stevens, 2008), as well as one of the most frequently caught bycatch species of fisheries and by sports fishing worldwide (Campana *et al*., 2009; Casey & Hoey, 1985; Pratt, 1979). Thus, they have been extensively studied, this including age and growth studies. However, age and growth studies of blue sharks in Southern Hemisphere are lacking considerably when compared to the Northern Hemisphere, in particular for the case of the Indian Ocean in which this topic has barely been explored for this species. Therefore, the present study presents important new age and growth data for blue sharks in the South Indian Ocean.

Vertebrae of blue sharks are known to be difficult to read, due to a poor contrast of the bands (Manning & Francis, 2005; Rabehagasoa *et al*., 2014; Skomal & Natanson, 2003). In the present study, 25 vertebral samples of the total 818 that were collected were initially excluded, not being used for age readings since no band pattern was visible or was extremely diffuse. This could be due to the preparation of such samples, or simply their quality prior to sample processing. Nevertheless, this is an interesting fact since 25 represents a small percentage of the total sample size of 818 of the present study, thus not compromising age and growth estimations. However, in studies with much smaller sample sizes, discarding considerable amounts of samples can represent significant problems.

Age estimation using whole vertebrae instead of sections is an easier and less expensive approach, since it is less time consuming and does not require specific sectioning equipment (MacNeil & Campana, 2002). However, different studies report that whole vertebrae tend to under-estimate the age of older sharks, since they do not provide an adequate visualization of the growth bands in these specimens, when they start to group, and being more diffuse, thus more difficult to interpret (MacNeil & Campana, 2002; Tanaka *et al*., 1990). On the other hand, Jolly *et al.* (2013) prepared whole centra unstained and also stained sections, mentioning that the latter ones were unsuccessful to read. Nonetheless, all vertebral samples used in the present study were sectioned, and although difficult to read as it is known for this species, such sections allowed readings to be made for all age groups, from 1 year old sharks to as old as 25 years. Regarding the staining method used, in which sections were stained with Crystal Violet solution, this stain had been successfully used in other shark species (e.g., Coelho *et al.,* 2011; Fernandez-carvalho *et al.,* 2011; Fernandez-Carvalho *et al*., 2015; Rosa *et al*., 2017), but never before used with blue sharks. For each vertebral sample one section was stained and the other was left unstained for comparison purposes, and it was concluded that the stained sections provided a higher contrast in the growth bands for the vast majority of the samples. Thus, the stained sections were preferred overall, with the unstained being used on rare occasions for confirmation purposes. Another factor that helped with band visualization in this study was the digital enhancement of the section's photos. A slight adjustment of contrast and brightness made a considerable improvement in the contrast between the bands, however such adjustment should be slight since overdoing it can create the opposite effect.

In the present study, age validation was not carried out. However, other studies such as those of Hsu *et al.* (2015), Lessa *et al.* (2004), Romanov *et al.* (2011), Skomal and Natanson (2003) and Wells *et al.* (2016) have verified or validated the age of blue sharks, with all of them supporting an annual periodicity of growth band deposition for this species. Thus, previous age and growth studies for blue sharks (**Table 5.1**) have considered that growth bands are formed once a year with the first one being the birthmark (age 0). The same assumptions were considered in the present study. However, more work needs to be done regarding age validation for blue sharks. Studies already done are not only few, but also use very small sample sizes, covering small age ranges and not leaving animals in liberty long enough before recapture, in case of validation through tag-recapture. For instance, Skomal and Natanson (2003) validated the age of only two specimens around the age of 4, and Romanov *et al.* (2011) validated the age of only two sharks as well, these being much older (19 and 23). Therefore, the absence of more comprehensive age validation studies (with greater sample sizes, wider age ranges and longer liberty periods) for this species, all over the world, can compromise the objectivity of age and growth estimation studies.

In terms of precision analysis of the age estimates, several approaches were used in the present study, namely the percentage agreement, the coefficient of variation, the average percent error and age bias plots. The PA was progressively higher between the first and second, first and third and second and third readings, revealing a gradual improvement in the consistency of age readings. CV and APE are both widely used for precision analysis of ageing studies, with Campana (2001, 2014) suggesting a value of less then 7.6% for CV and 5.5% for APE, although mentioning most shark age studies have a CV exceeding 10%. In this study, all values of CV were below the usual 10% found in many shark studies, one of them even being below the suggested 7.6% level. Regarding APE, two of them exceed the suggested value of

5.5%, but only for around a unit maximum, and a third value exceeds it by 0.10%. Therefore, and considering these are suggested values and not a set level for precision analysis (Campana, 2001), the CV and APE results together with the age bias plots obtained for this study support the consistency of age estimations and their adequacy for the studied species.

When it came to choosing a growth model to fit to the age data, the von Bertalanffy growth function, that derives from the original model defined by von Bertalanffy (1938) was chosen because it is the most commonly used in fisheries biology for stock assessment purposes (Cailliet *et al*., 2006; Haddon, 2011), which is the end goal for the results of the present study. Also, since it is the most used in previous age and growth studies for blue sharks (**Table 5.1**), it is beneficial to use it when it comes to making comparisons. In the present study, two approaches of this model were used, namely a three-parameter VBGF, and a two-parameter VBGF with a fixed L_0. Unlike in the previous studies for this species, in which the three parameter VBGF estimated t_0 (theoretical age at which the expected length is zero), in this study this model was re-parameterized to estimate L_0 (size at birth) instead. Even though it may be the same using one or the other from a mathematical point of view, t_0 lacks biological meaning, making L_0 a more robust approach with an immediate interpretation (Cailliet *et al*., 2006; Carlson *et al.,* 2003; Goldman *et al*., 2012; Goosen & Smale, 1997). This is particularly relevant in the case of elasmobranchs, since size at birth for these organisms is usually well defined (Goldman et al., 2012).

When calculating the AIC and BIC values for both models, the three-parameter VBGF seems to be a better fit to the age data (*see Table 4.1 in the Results section*). However, while the fits are better from a purely statistical perspective, in biological terms it might be more adequate to use the two-parameter VBGF with a fixed L_0, since the birth size of the studied species is already known (IOTC, 2007; Pratt, 1979). As such, the inclusion of a well-known parameter in the model as a fixed value, rather than allowing for its estimation with the associated uncertainties, might be more adequate even at the expense of a somewhat poorer overall fit to the data. Therefore, the VBGF with fixed L_0 is the model recommended by this study, more specifically with a growth curve for each sex separately since significant differences were found between sexes.

When comparing the results obtained by the present study with the ones obtained by others in the Indian Ocean, namely Jolly *et al.* (2013) and Rabehagasoa *et al.* (2014) (**Table 5.1**), the maximum asymptotic length estimates are slightly higher in the present study than in the other two. In terms of k, the values here obtained are around the ones estimated by the previous authors. In this study, results suggest that females reach a higher asymptotic length than males, and males have a higher growth coefficient, indicating a slower growth for females. The same was found in some of the previous studies done all over the world, while in others the opposite results were obtained. The maximum size reported for blue sharks by Compagno (1984) is of 380 cm TL (317.3 cm FL*[1]) which is higher than both L_{inf} values estimated in this study. However, when considering the previous age and growth studies of blue sharks made all over the world that are summarized in Table 5.1, the estimates for L_{inf} here obtained are within the range of values of those studies, which range from 198.8 cm FL* to 353 cm FL* (Blanco-Parra *et al.,* 2008; Stevens, 1975). The same happens for the k estimates of the present study which are between the range of 0.10 $year^{-1}$ to 0.68 $year^{-1}$ observed in the other studies. Nevertheless, it is relevant to point out that the 0.68 $year^{-1}$ value for k obtained by MacNeil and Campana (2002) is much higher than all other studies here presented, where values vary mostly between 0.10 and 0.18 $year^{-1}$.

Regardless of the VBGF with a fixed L_0 being the model recommended to use, it is still interesting to look at the values estimated for L_0 using the three-parameter VBGF, and compare those with the known size at birth. The results obtained for L_0 were 73.8 cm FL for males, 74.65 cm FL for females and 76 cm FL for the combined sexes. These values are higher than the 35-44 cm FL size at birth range described by Pratt (1979), and also by IOTC (2007) in the Indian Ocean. Estimates in other blue shark studies fall in this range, such as the L_0 obtained by Cailliet *et al*. (1983) of 37.6 cm FL* and 47.1 cm FL obtained by Henderson *et al*. (2001). Megalofonou *et al*. (2009) and Rabehagasoa (2014) estimated slightly lower values of 26.8 cm FL* and 30.2 cm FL*, respectively, with the latter one corresponding to a study in the Indian Ocean. In the present study, the higher results for size at birth can be explained by the lack of samples of younger ages when comparing with the remaining ages within the total sample size.

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[1] **Note:** All FL* measures were obtained by converting original TL measures using the equation by Kohler *et al.* (1995) for blue sharks: FL = 0.8313 x TL + 1.39.

Tabela 5-1 Summary of previous age and growth studies of *Prionace glauca* in various regions of the world. C = combined sexes, F = female, M = male, TL = total length, PCL = precaudal length, FL = Fork length, VBGF = von Bertalanffy growth function, L_{inf} = maximum asymptotic size (in cm) and k = growth coefficient. Spaces filled with "-" refer to information that is not available.

Study	**Ocean**	**Vertebrae condition**	**Band Visualisation**	**n**	**Measure**	**Sample size (cm)**	**Sex**	**VBGF parameters**		**Max attributed age**
								L_{inf}	**k**	
Aasen (1966)	N Atlantic	Whole centra	Silver nitrate staining	268	TL	-	C	394	0.133	8
Stevens (1975)	N Atlantic	Whole centra and sections	Silver nitrate staining, transmitted polarized light	82	TL	42 – 272.5	C	423	0.110	7
Cailliet *et al.* (1983)	N Pacific	Whole centra	Silver nitrate staining, X-ray	130	TL	28-252.1	C M F	265.5 295.3 241.9	0.223 0.175 0.251	9
Tanaka *et al.* (1990)	N Pacific	Whole (w) centra and sections (s)	Haematoxylin staining (s), silver nitrate staining (w)	195	TL	110 - 280	M F	369 304	0.10 0.16	11
Nakano (1994)	N Pacific	Whole centra	Silver nitrate staining	271	PCL	-	M F	289.7 243.3	0.129 0.144	10
Henderson *et al.* (2001)	N Atlantic	Whole centra	Unstained, silver nitrate stained and alizarin red S stained; white light	159	TL	64 - 228	C	376.5	0.12	6
MacNeil & Campana (2002)	N Atlantic	Whole (w) centra and sections (s)	Unstained, reflected white light	185	FL	147 - 282	C	300 w 302 s	0.68 w 0.58 s	8
Skomal and Natanson (2003)	N Atlantic	Sections	Reflected white light	411	FL	49 - 312	C M F	285.4 282.3 286.8	0.17 0.18 0.16	16
Lessa *et al.* (2004)	S Atlantic	Sections	White light	236	TL	173.8 - 310	C	352.1	0.157	12
Blanco-Parra *et al.* (2008)	N Pacific	Whole centra	Silver nitrate staining	184	TL	90 - 253	C M F	303.4 299.9 237.5	0.10 0.10 0.15	16
Megalofonou *et al.* (2009)	Mediterranean	Whole centra	Digital enhancement, reflected light	54	TL	81.7 - 315	C	401.55	0.13	12
Jolly *et al.* (2013)	S Atlantic/ S Indian	Whole centra	No staining, white light	197	TL	72 - 313	C M F	311.6 294.6 334.7	0.12 0.14 0.11	16
Rabehagasoa *et al.* (2014)	S Indian	Sections	No staining, transmitted white light	188	FL	36 - 276	C	258	0.16	15
Hsu *et al.* (2015)	S Pacific	Whole centra	X-ray	742	TL	-	C	352.1	0.13	15
Francis and Maolagáin (2016)	S Pacific	Whole centra and sections	No staining, white light and X-ray	232	FL	Readers in this study were unable to age the samples				
Present study	S Indian	Sections	Crystal Nitrate staining, white light	679	FL	82 - 301	C M F	278.3 277.2 283.2	0.14 0.15 0.13	25

The maximum estimated ages obtained in this study were 20 and 25, for females and males, respectively. The oldest individual was a 25 year old male with 301 cm FL. The estimates for both sexes are older than any of the previously estimated ages in previous studies, as summarized in Table 5.1. However, the longevity of this species is thought to be of about 20 to 23 years (Cailliet *et al.*, 1983; Manning & Francis, 2005; Romanov *et al.*, 2011; Stevens, 2009). In their age validation study for the Indian Ocean, Romanov *et al.* (2011) obtained the ages of 19 and 23 for male specimens with 273 cm FL and 270 cm FL, respectively. Therefore, the estimates of the present study are close to those of Romanov *et al.* (2011). Nevertheless, in that study both specimens were the same sex, and despite having almost the same size still presented different ages and growth rates. This supports the need for more age and growth studies of blue sharks in the Indian Ocean, and of their biology in general.

When looking at all previous studies mentioned as well as this study (**Table 5.1**), there are no evident trends in growth between the Atlantic, the Pacific and the Indian oceans, suggesting a similar growth for blue sharks among different world regions. The same idea was previously mentioned by Nakano and Seki (2003), and Tanaka *et al.* (1990), who reported that variations in the estimates between different studies are most likely due to differences in techniques used to prepare the samples, different criteria for growth zones ageing and reader precision and bias, which compromises a realistic comparison of growth between different areas.

Overall, the results obtained in this study are mostly within the ranges obtained in previous studies for other oceans. However, it should be noted that we estimated a higher maximum observed age compared to what was previously described. These results now presented support the fact that the blue shark is a long-lived, slow growth species, and provide important additional knowledge to the biology of blue sharks in the Indian Ocean.

6. Conclusion and remarks for future research

As a conclusion, we believe the present work provides relevant data about the biology, namely age and growth, of blue sharks in the Indian Ocean, filling the considerable lack of information regarding this species in this Ocean. Therefore, data here obtained can be used for stock assessment of blue sharks, contributing for the management and conservation of this species. That is of particular importance considering the stock status of blue sharks in the Indian Ocean still remains uncertain. In fact, the results obtained in this study were already provided to the *Indian Ocean Tuna Commission*, to be considered in the next meeting for stock assessment of this species that will take place in September 2017 (Andrade *et al*., 2017).

In terms of recommendations for future research, more work regarding age and growth of blue sharks in the Indian Ocean should be carried out, since even with the addition of the present study there are still significant information gaps, especially when comparing with the Atlantic and Pacific Oceans. However, even these oceans where age and growth of blue sharks have been more extensively studied would benefit from more studies, since in most of the previous works sample sizes were small and the size ranges of the collected specimens tended to be narrow. Thus, the estimated parameters may not be very representative of the overall populations, including all age classes. International collaborations between several fishing nations to obtain results covering entire ocean basins or even more, as opposed to studies at local scales, would be most useful. Particularly, if pursued with a standardized methodology, in order to minimize variation due to preparation techniques and age reading bias, thus providing a mean for objective comparisons between different areas. In addition, only a few age validation studies for blue sharks have been carried out. Thus, this is an area that should be more explored in order to improve the robustness of results obtained in all age and growth studies.

7. References

Aasen, O. (1966). Blåhaien, *Prionace glauca* (Linnaeus), 1758. *Fiskeridirektoratets Havforskningsinstitutt*, *1*, 1–15.

Aires-da-Silva, Alexandre Ferreira, R. L., & Pereira, J. G. (2008). Case Study: Blue Shark Catch-Rate Patterns from the Portuguese Swordfish Longline Fishery in the Azores. In *Sharks of the Open Ocean: Biology, Fisheries and Conservation* (p. 502).

Anderson, E. D. (1980). Analysis of Various Sources of Pelagic Shark Catches in the Northwest and Western Central Atlantic Ocean and Gulf of Mexico. *NOAA Technical Report*, *31*(79), 1–14.

Andrade, I., Rosa, D., Lechuga, R., & Coelho, R. (2017). Age and growth of the blue shark (*Prionace glauca*) in the Indian Ocean. *Indian Ocean Tuna Commission Technical Document. Ref: IOTC–2017–WPEB13–20. 18pp.*

Babcock, E. A. (2008). Recreational fishing for pelagic sharks worldwide. In *Sharks of the open ocean: biology, fisheries and conservation* (pp. 193–204).

Bailey, K., Williams, P. G., Itano, D., Williams, & South Pacific Commission. (1996). Programme, Oceanic Fisheries: By-catch and discards in western Pacific tuna fisheries: a review of SPC data holdings and literature. *Oceanic Fisheries Programme Technical Report*.

Beamish, R. J., & Fournier, D. a. (1981). A Method for Comparing the Precision of a Set of Age Determinations. *Canadian Journal of Fisheries and Aquatic Sciences*, *38*(8), 982–983. https://doi.org/10.1139/f81-132

Bennett, J. T., Boehlert, G. W., & Turekian, K. K. (1982). Confirmation of longevity in *Sebastes diploproa* (Pisces: Scorpaenidae) from 210Pb/226Ra measurements in otoliths. *Marine Biology*, *71*(2), 209–215. https://doi.org/10.1007/BF00394632

Blanco-Parra, M. D. P., Galvan-Magana, F., Marquez-Farias, F., Galván-Magaña, F., & Márquez-Farías, F. (2008). Age and growth of the blue shark, *Prionace glauca* Linnaeus, 1758, in the Northwest coast off Mexico. *Revista de Biología Marina Y Oceanografía*, *43*(3), 513–520. https://doi.org/10.4067/S0718-19572008000300010

Bonfil, R. (1994). Overview of world elasmobranch fisheries. *FAO Fisheries Technical Paper, 341*. FAO, Rome.

Cailliet, G. M. (1990). Elasmobranch age determination and verification: An updated review. *Elasmobranchs as Living Resources*, *90*, 157–165.

Cailliet, G. M., & Goldman, K. J. (2004). Age Determination and Validation in Chondichthyan Fishes. In *Biology of Sharks and Their Relatives* (pp. 399–447).

Cailliet, G. M., Martin, L. K., Harvey, J. T., Kusher, D., & Welden, B. A. (1983). Preliminary studies on the age and growth of the blue, *Prionace glauca*, common thresher, *Alopias vulpinus*, and shortfin mako, *Isurus oxyrinchus*, sharks from California waters. *Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks. NOAA Technical Report NMFS*, *8*, 179–188.

Cailliet, G. M., Smith, W. D., Mollet, H. F., & Goldman, K. J. (2006). Age and growth studies of chondrichthyan fishes: The need for consistency in terminology, verification, validation, and growth function fitting. *Environmental Biology of Fishes*, *77*(3–4), 211–228. https://doi.org/10.1007/s10641-006-9105-5

Camhi, M., Fowler, S., Musick, J., Bräutigam, A., & Fordham, S. (1998). Sharks and their Relatives: Ecology and Conservation. *IUCN/SSC Shark Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK* (Vol. 3). https://doi.org/10.1016/j.wear.2011.03.022

Camhi, M., Lauck, E., Pikitch, E. K., & Babcock, E. A. (2008). A Global Overview of Commercial Fisheries for Open Ocean Sharks. In *Sharks of the Open Ocean: Biology,* *Fisheries and Conservation* (pp. 1–502).

Campana, S. E. (2001). Accuracy , precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology*, *59*, 197–242. https://doi.org/10.1006/jfbi.2001.1668

Campana, S. E. (2014). Age determination of elasmobranchs, with special reference to Mediterranean species: a technical manual. Studies and Reviews. *General Fisheries Commission for the Mediterranean.* Rome, FAO.

Campana, S. E., Joyce, W., & Manning, M. J. (2009). Bycatch and discard mortality in commercially caught blue sharks *Prionace glauca* assessed using archival satellite pop-up tags. *Marine Ecology Progress Series*, *387*, 241–253. https://doi.org/10.3354/meps08109

Carlson, J. K., & Baremore, I. E. (2005). Growth dynamics of the spinner shark (*Carcharhinus brevipinna*) off the United States southeast and Gulf of Mexico coasts: a comparison of methods. *Fishery Bulletin*, *103*(2), 280–291.

Carlson, J. K., Cortés, E., & Bethea, D. M. (2003). Life history and population dynamics of the finetooth shark (*Carcharhinus isodon*) in the northeastern Gulf of Mexico. *Fishery Bulletin*, *101*(2), 281–292.

Carruthers, E. H., Neilson, J. D., & Smith, S. C. (2011). Overlooked bycatch mitigation opportunities in pelagic longline fisheries: Soak time and temperature effects on swordfish (*Xiphias gladius*) and blue shark (*Prionace glauca*) catch. *Fisheries Research*, *108*(1), 112–120. https://doi.org/10.1016/j.fishres.2010.12.008

Casey, J. G., & Hoey, J. J. (1985). Estimated catches of large sharks by US recreational fishermen in the Atlantic and Gulf of Mexico. *NOAA Technical Report NMFS*, *31*, 35–19.

Castro, J. A., & Mejuto, J. (1995). Reproductive parameters of blue shark, *Prionace glauca*, and other sharks in the Gulf of Guinea. *Marine and Freshwater Research*, *46*(6), 967–973. https://doi.org/10.1071/MF9950967

Chang, W. Y. B. (1982). A Statistical Method for Evaluating the Reproducibility of Age Determination. *Canadian Journal of Fisheries and Aquatic Sciences*, *39*, 1208–1210. https://doi.org/10.1139/f82-158

Clarke, S., Sato, M., Small, C., Sullivan, B., Inoue, Y., & Ochi, D. (2014). Bycatch in longline fisheries for tuna and tuna-like species: a global review of status and mitigation measures. *FAO Fisheries and Aquaculture Technical Paper No. 588*. Rome, FAO.

Coelho, R., & Erzini, K. (2002). Age and growth of the undulate ray, *Raja undulata*, in the Algarve (southern Portugal). *Journal of the Marine Biological Association of the UK*, *82*(6), 987–990. https://doi.org/10.1017/S0025315402006495

Coelho, R., & Erzini, K. (2006). Reproductive aspects of the undulate ray, *Raja undulata*, from the south coast of Portugal. *Fisheries Research*, *81*(1), 80–85. https://doi.org/10.1016/j.fishres.2006.05.017

Coelho, R., Fernandez-carvalho, J., Amorim, S., & Santos, M. N. (2011). Age and growth of the smooth hammerhead shark, *Sphyrna zygaena*, in the Eastern Equatorial Atlantic Ocean, using vertebral sections. *Aquatic Living resources*, *24*(4), 351–357. https://doi.org/10.1051/alr/2011145

Coelho, R., Fernandez-Carvalho, J., Lino, P. G., & Santos, M. N. (2012). An overview of the hooking mortality of elasmobranchs caught in a swordfish pelagic longline fishery in the Atlantic Ocean. *Aquatic Living Resources*, *25*(4), 311–319. https://doi.org/10.1051/alr/2012030

Coelho, R., Mejuto, J., Domingo, A., Yokawa, K., Liu, K., Romanov, E. V., Cortés, K. L. E., da Silva, C., Hazin, F., Arocha, F., Mwilima, A. M., Bach, P., de Zárate, V. O., Roche, W., Lino, P. G., García-Cortés, B., Ramos-Cartelle, A. M., Forselledo, R., Mas, F., Ohshimo, S., Courtney, D., Sabarros, P. S., Perez, B., Wogerbuer, C., Tsai, W., Carvalho, F., & Santos, M. N. (n.d.). Distribution patterns and population structure of the blue shark (*Prionace glauca*) in the Atlantic and Indian Oceans. *Fish and Fisheries*, 2017; 00:1–17. https://doi.org/10.1111/faf.12238

Compagno, L. J. V. (1984). *FAO Species Catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2 - Carcharhiniformes. FAO Fisheries Synopsis* (Vol. Vol.4). FAO, Rome.

Compagno, L. J. V. (2001). *Sharks of the World. An annotated and illustrated catalogue of shark species known to date. Volume 2. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO Species Catalogue for Fishery Purposes*. FAO, Rome.

Compagno, L. J. V. (2008). Pelagic Elasmobranch Diversity. In *Sharks of the Open Ocean: Biology, Fisheries and Conservation* (pp. 1–502).

Compagno, L. J. V., Dando, M., & Fowler, S. (2005). *Sharks of the World*. Collins, London.

Conrath, C. L., & Musick, J. A. (2012). Reproductive biology of elasmobranchs. In *Biology of Sharks and their Relatives* (pp. 291–312).

da Silva, C., Kerwath, S. E., Wilke, C. G., Meÿer, M., & Lamberth, S. J. (2010). First documented southern transatlantic migration of a blue shark *Prionace glauca* tagged off South Africa. *African Journal of Marine Science*, *32*(3), 639–642. https://doi.org/10.2989/1814232X.2010.540777

Dent, F., & Clarke, S. (2015). State of the global market for shark products. *FAO Technical Paper*, 196.

DeVries, D. R., & Frie, R. V. (1996). Determination of age and growth. In *Fisheries Techniques* (2nd ed, pp. 483–512). Bethesda, Maryland: American Fisheries Society.

Diaz, & Serafy, J. E. (2005). Longline-caught blue shark (*Prionace glauca*): factors affecting the numbers available for release. *Fishery Bulletin*, *103*(4), 720–724.

Dichmont, C. M., Deng, R. A., Punt, A. E., Brodziak, J., Chang, Y. J., Cope, J. M., Ianelli, J. N., Legault, C. M., Methot Jr, R. D., Porch, C. E., Prager, M. H., & Shertzer, K. W. (2016). A review of stock assessment packages in the United States. *Fisheries Research*, *183*, 447–460. https://doi.org/10.1016/j.fishres.2016.07.001

Eriksson, H., & Clarke, S. (2015). Chinese market responses to overexploitation of sharks and sea cucumbers. *Biological Conservation*, *184*, 163–173. https://doi.org/10.1016/j.biocon.2015.01.018

Fablet, R., & Le Josse, N. (2005). Automated fish age estimation from otolith images using statistical learning. *Fisheries Research*, *72*(2–3), 279–290. https://doi.org/10.1016/j.fishres.2004.10.008

FAO. (2017). Species Fact Sheets, *Prionace glauca*. Retrieved 11 January 2017, from http://www.fao.org/fishery/species/2018/en

Fernandez-carvalho, J., Coelho, R., Erzini, K., & Santos, M. N. (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. *Aquatic Living Resources*, *24*(4), 359–368. https://doi.org/10.1051/alr/2011046

Fernandez-Carvalho, J., Coelho, R., Erzini, K., & Santos, M. N. (2015). Modeling age and growth of the bigeye thresher (*Alopias superciliosus*) in the Atlantic Ocean. *Fishery Bulletin*, *113*(4), 468–481. https://doi.org/10.7755/FB.113.9

Francis, C. (2016). Growth in age-structured stock assessment models. *Fisheries Research*, *180*, 77–86. https://doi.org/10.1016/j.fishres.2015.02.018

Francis, M. P., Griggs, L. H., & Baird, S. J. (2001). Pelagic shark bycatch in the New Zealand tuna longline fishery. *Marine And Freshwater Research*, *52*(2), 165–178. https://doi.org/10.1071/MF00086

Francis, M. P., & Maolagáin, C. Ó. (2016). Size, maturity and length composition of blue sharks observed in New Zealand tuna longline fisheries. *New Zealand Fisheries Assessment Report* (Vol. 60).

Frisk, M. G., Miller, T. J., & Fogarty, M. J. (2001). Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(5), 969–981. https://doi.org/10.1139/cjfas-58-5-969

Froese, R. and D. P. (2016). FishBase. World Wide Web electronic publication. (10/2016). Retrieved from www.fishbase.org

Garcia, V. B., Lucifora, L. O., & Myers, R. A. (2008). The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. *Proceedings of the Royal Society B*, *275*(1630), 83–89. https://doi.org/10.1098/rspb.2007.1295

Goldman, K. J. (2005). 6. Age and growth of elasmobranch fishes. In *Management Techniques for Elasmobranch Fisheries*, *474*(76), 97–132.

Goldman, K. J., Cailliet, G. M., Andrews, A. H., & Natanson, L. J. (2012). Assessing the Age and Growth of Chondrichthyan Fishes. In *Biology of Sharks and Their Relatives* (pp. 423–451). https://doi.org/10.1017/CBO9781107415324.004

Goosen, A. J. J., & Smale, M. J. (1997). A preliminary study of age and growth of the smoothhound shark *Mustelus mustelus* (Triakidae). *South African Journal of Marine Science*, *18*(1), 85–91. https://doi.org/10.2989/025776197784161072

Gubanov, U. P., & Grigoryev, V. N. (1975). Observations on the distribution and biology of the blue shark *Prionace glauca* (Carcharhinidae) of the Indian Ocean. *Voprosy Ikhtiologii*, *15*, 43–50.

Gubanov, Y. P. (1978). The reproduction of some species of pelagic sharks from the equatorial zone of the Indian Ocean. *Journal of Ichthyology*, *18*(5), 781–782.

Haddon, M. (2011). *Modelling and Quantitative Methods in Fisheries* (2nd ed.). CRC Press, Taylor & Francis Group.

Hazin, F., Boeckmann, C., Leal, E., Lessa, R., Kihara, K. and Otsuka, K. (1994). Distribution and relative abundance of the blue shark, *Prionace glauca*, in the Southwestern Equatorial Atlantic Ocean. *Fishery Bulletin*, 92, 474–480. http://doi.org/10.2331/fishsci.60.487

Henderson, A., Flannery, K., & Dunne, J. (2001). Observations on the biology and ecology of the blue shark in the North-east Atlantic. *Journal of Fish Biology*, *58*(5), 1347–1358. https://doi.org/10.1006/jfbi.2000.1547

Herrera, M., & Pierre, L. (2013). *Review of the Statistical Data Available for Neritic Tuna Species*. *IOTC–2013–WPEB09–08*.

Holden, M. J. (1973). Are long-term sustainable fisheries for elasmobranchs possible. *Fish Stocks and Recruitment. Rapports et Proces-Verbaux Des Reunions Conseil International Pour l'Exploration de La Mer*, *164*, 360–367.

Hsu, H. H., Lyu, G. T., Joung, S. J., & Liu, K. M. (2015). Age and growth of the blue shark (*Prionace glauca*) in the South Atlantic Ocean. *Collect. Vol. Sci. Pap. ICCAT, 71(6): 2573-2584*.

Huang, H. W., & Liu, K. M. (2010). Bycatch and discards by Taiwanese large-scale tuna longline fleets in the Indian Ocean. *Fisheries Research*, *106*(3), 261–270. https://doi.org/10.1016/j.fishres.2010.08.005

ICCAT. (2015). *Report of the 2015 ICCAT Blue Shark stock assessment session*. Lisbon, Portugal.

ICCAT Rec 16-12. (2016). Recommendations by ICCAT on management measures for the conervation of Atlantic blue shark caught in association with ICCAT fisheries. Retrieved 21 August 2017, from https://www.iccat.int/Documents/Recs/compendiopdf-e/2016-12-e.pdf%0D

IOTC. (2007). Compilation of information on blue shark (*Prionace glauca*), silky shark (*Carcharhinus falciformis*), oceanic whitetip shark (*Carcharhinus longimanus*), scalloped hammerhead (*Sphyrna lewini*) and shortfin mako (*Isurus oxyrinchus*) in the Indian Ocean. *IOTC-2007-WPEB-INF01*, 1–18.

IOTC. (2016). *Report of the 6 th Session of the IOTC Working Party on Neritic Tunas*. Seychelles.

ISC Shark Working Group. (2014). *Stock assessment and future projections of blue shark in the north pacific ocean.* Taipei, Chinese-Taipei.

Jolly, K. A., da Silva, C., & Attwood, C. G. (2013). Age, growth and reproductive biology of the blue shark *Prionace glauca* in South African waters. *African Journal of Marine Science*, *35*(1), 99–109. https://doi.org/Doi 10.2989/1814232x.2013.783233

Kimura, D. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin*, *77*, 765–776.

King, J. R., Wetklo, M., Supernault, J., Taguchi, M., Yokawa, K., Sosa-Nishizaki, O., & Withler, R. E. (2015). Genetic analysis of stock structure of blue shark (*Prionace glauca*) in the north Pacific Ocean. *Fisheries Research*, *172*, 181–189. https://doi.org/10.1016/j.fishres.2015.06.029

Kohler, N. E., Casey, J. G., & Turner, P. A. (1995). Length-weight relationships for 13 species of sharks from the western North Atlantic. *Fishery Bulletin*, *93*(2), 412–418.

Kohler, N. E., & Turner, P. A. (2008). Stock Structure of the Blue Shark (*Prionace glauca*) in the North Atlantic Ocean Based on Tagging Data. In *Sharks of the Open Ocean: Biology, Fisheries and Conservation* (pp. 1–502).

Kohler, N. E., Turner, P. a, Hoey, J. J., Natanson, L. J., & Briggs, R. (2002). Tag and recapture data for three pelagic shark species: blue shark (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*) and porbeagle (*Lamna nasus*) in the North Atlantic Ocean. *International Commission for the Conservation of Atlantic Tunas, Collective Volume of Scientific Papers SCRS/2001/64*, *54*(4), 1231–1260.

Last, P. L., & Stevens, J. D. (1994). *Sharks and Rays of Australia*. CSIRO, Collingwood, Victoria, Australia.

Lessa, R., Santana, F. M., & Hazin, F. H. (2004). Age and growth of the blue shark *Prionace glauca* (Linnaeus, 1758) off northeastern Brazil. *Fisheries Research*, *66*(1), 19–30. https://doi.org/10.1016/S0165-7836(03)00193-0

Li, W., Dai, X., Zhu, J., Tian, S., He, S., & Wu, F. (2016). Genetic differentiation in blue shark, *Prionace glauca,* from the central Pacific Ocean, as inferred by mitochondrial cytochrome b region. *Mitochondrial DNA Part A*, *28*(4), 575–578. https://doi.org/10.3109/19401736.2015.1137903

Litvinov, F. F. (2006). On the role of dense aggregations of males and juveniles in the functional structure of the range of the blue shark *Prionace glauca*. *Journal of Ichthyology*, *46*(8), 613–624. https://doi.org/10.1134/S0032945206080091

Lopez, S., Meléndez, R., & Barría, P. (2010). Preliminary diet analysis of the blue shark *Prionace glauca* in the eastern South Pacific. *Revista de Biología Marina Y Oceanografía, 45*(1997), 745–749. http://dx.doi.org/10.4067/S0718-19572010000400017

MacNeil, M. A., & Campana, S. E. (2002). Comparison of whole and sectioned vertebrae for determining the age of young blue shark (*Prionace glauca*). *Journal of Northwest Atlantic Fishery Science*, *22*, 77–82. https://doi.org/10.2960/J.v30.a5

Mahé, K., Rabhi, K., Bellamy, E., Elleboode, R., Aumond, Y., Huet, J., & Roos, D. (2016). Comparison between the opercular bones, the scales and the otoliths to investigate the growth of the brilliant pomfret (*Eumegistus illustris*) off the coast of Reunion Island (SW Indian Ocean). *International Journal of Fisheries and Aquatic Studies*, *4*(1), 176–179.

Manning, M. J., & Francis, M. P. (2005). Age and growth of blue shark (*Prionace glauca*) from the New Zealand Exclusive Economic Zone. *New Zealand Fisheries Assessment Report*, *26*, 52.

McCord, M. E., & Campana, S. E. (2003). A quantitative assessment of the diet of the blue shark (*Prionace glauca*) off Nova Scotia, Canada. *Journal of Northwest Atlantic Fishery Science*, *32*, 57–63. https://doi.org/10.2960/J.v32.a4

McKenzie, R. A., & Tibbo, S. N. (1964). A morphometric description of blue shark (*Prionace glauca*) from Canadian Atlantic waters. *Journal of the Fisheries Research Board of Canada*, *21*(4), 865–866.

Megalofonou, P., Damalas, D., & De Metrio, G. (2009). Biological characteristics of blue shark, *Prionace glauca*, in the Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom*, *89*(6), 1233–1242. https://doi.org/Doi 10.1017/S0025315409000216

Mendonça, A. (2009). *Diet of the blue shark, Prionace glauca, in the Northeast Atlantic*. Faculdade de Ciências da Universidade do Porto.

Montealegre-Quijano, S., & Vooren, C. M. (2010). Distribution and abundance of the life stages of the blue shark *Prionace glauca* in the Southwest Atlantic. *Fisheries Research*, *101*(3), 168–179. https://doi.org/10.1016/j.fishres.2009.10.001

Muñoz-Lechuga, R., Rosa, D., & Coelho, R. (2016). Depredation in the Portuguese pelagic longline fleet in the Indian Ocean. *IOTC–2016–WPEB12-35*, 1–14.

Nakano, H. (1994). Age, reproduction and migration of blue shark in the North Pacific Ocean. *Bulletin of the Natural Research Institute of Far Seas Fisheries*, *31*, 141-256.

Nakano, H., & Seki, M. (2003). Synopsis of biological data on the blue shark, *Prionace glauca* Linnaeus. *Bulletin of Fisheries Research Agency*, *6*, 18–55.

Nakano, H., & Stevens, J. (2008). The Biology and Ecology of the Blue Shark, *Prionace glauca*. In *Sharks of the Open Ocean: Biology, Fisheries and Conservation* (p. 502). https://doi.org/10.1002/9781444302516

Nelson, G. (2017). Fishmethods: Fishery Science Methods and Models in R. R package version 1.10-3.

Oliver, S., Braccini, M., Newman, S. J., & Harvey, E. S. (2015). Global patterns in the bycatch of sharks and rays. *Marine Policy*, *54*, 86–97. https://doi.org/10.1016/j.marpol.2014.12.017

Pikitch, E. K., Camhi, M. D., & Babcock, E. A. (2008). Introduction to Sharks of the Open Ocean. In *Sharks of the Open Ocean: Biology, Fisheries and Conservation* (pp. 1–502).

Pratt, H. L. (1979). Reproduction in the Blue Shark, *Prionace glauca*. *Fishery Bulletin*, *77*(2), 445–470.

Queiroz, N., Humphries, N. E., Noble, L. R., Santos, A. M., & Sims, D. W. (2012). Spatial dynamics and expanded vertical niche of blue sharks in oceanographic fronts reveal habitat targets for conservation. *PLoS ONE*, *7*(2). https://doi.org/10.1371/journal.pone.0032374

Rabehagasoa, N., Vigliola, L., Lorrain, A., Sabarros, P. S., Romanov, E., & Bach, P. (2014). Modelling growth of blue shark (*Prionace glauca*) and silky shark (*Carcharhinus falciformis*) in the southwest Indian Ocean assessed by back-calculated length from vertebrae. *IOTC–2014–WPEB10–22*, 1–23.

R Core Team. (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Retrieved 20 July 2006, from https://www.r-project.org/

Romanov, E., Campana, S., & Rabehagasoa, N. (2011). Bomb radiocarbon dating of the Indian Ocean blue shark *Prionace glauca*: a preliminary test of ageing accuracy. *IOTC–2011–WPEB07–INF33*.

Romanov, E., & Romanova, N. (2009). Size distribution and length-weight relationships for some large pelagic sharks in the Indian Ocean. *IOTC–2009–WPEB–06.* (Vol. 33).

Rosa, D., Coelho, R., Fernandez-carvalho, J., Santos, M. N., (2017). Age and growth of the smooth hammerhead, *Sphyrna zygaena*, in the Atlantic Ocean: comparison with other hammerhead species. *Marine Biology Research*, *0*(0), 1–14. https://doi.org/10.1080/17451000.2016.1267366

Schindelin, J., Rueden, C. T., Hiner, M. C., & Eliceiri, K. W. (2015). The ImageJ ecosystem: An open platform for biomedical image analysis. *Molecular Reproduction and Development*. PMID 26153368.

Sims, D., Fowler, S. L., Ferretti, F., & Stevens, J. (2016). *Prionace glauca. The IUCN Red List of Threatened Species 2016: e.T39381A16553182.*

Sims, D., Fowler, S. L., Ferretti, F., & Stevens, J. D. (2015). *Prionace glauca. The IUCN Red List of Threatened Species 2015: e.T39381A48924261.*

Skomal, G., & Natanson, L. (2003). Age and growth of the blue shark (*Prionace glauca*) in the North Atlantic Ocean. *Fishery Bulletin*, *101*(3), 627–639.

Smith, S. E., Au, D. W., & Show, C. (1998). Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine And Freshwater Research*, *49*(7), 663–678. https://doi.org/10.1071/MF00020

Snelson Jr, F. F., Roman, B. L., & Burgess, G. H. (2008). The Reproductive Biology of Pelagic Elasmobranchs. In *Sharks of the Open Ocean: Biology, Fisheries and Conservation* (p. 502).

Springer, S. (1952). The effect of fluctuations in the availability of sharks on a shark fishery. *Proceedings of the Fourth Annual Gulf and Caribbean Fisheries Institute*, *4*, 140–145.

Stevens, J. (1975). Vertebral rings as a means of age determination in the blue shark (*Prionace glauca* L.). *Journal of the Marine Biological Association of the United Kingdom*, *55*(3), 657–665. https://doi.org/10.1017/S0025315400017318

Stevens, J. (1984). Biological observations of sharks caught by sportfishermen off New South Wales. *Australian Journal of Marine and Freshwater Research*, *35*(5), 573–590. https://doi.org/10.1071/MF9840573

Stevens, J. (1992). Blue and mako shark by-catch in the japanese longline fishery off South-eastern Australia. *Marine and Freshwater Research*, *43*(1), 227–236. https://doi.org/10.1071/MF9920227

Stevens, J. (2000). The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science*, *57*(3), 476–494. https://doi.org/10.1006/jmsc.2000.0724

Stevens, J. (2009). *Prionace glauca*, Blue Shark. *The IUCN Red List of Threatened Species 2009*, *8235*. https://doi.org/http://dx.doi.org/10.2305/IUCN.UK.2009-2.RLTS.T39381A10222811.en

Taguchi, M., King, J. R., Wetklo, M., Withler, R. E., & Yokawa, K. (2015). Population genetic structure and demographic history of Pacific blue sharks (*Prionace glauca*) inferred from mitochondrial DNA analysis. *Marine and Freshwater Research*, *66*(3), 267–275. https://doi.org/10.1071/MF14075

Tanaka, S. H. O., Cailliet, G. M., & Yudin, K. G. (1990). Age and Growth Differences in Growth of the Blue Shark, *Prionace glauca*: Technique or Population? *NOAA Tech. Rep.*

NMFS, *90*, 177–187.

Tavares, R., Ortiz, M., & Arocha, F. (2012). Population structure, distribution and relative abundance of the blue shark (*Prionace glauca*) in the Caribbean Sea and adjacent waters of the North Atlantic. *Fisheries Research*, *129*, 137–152. https://doi.org/10.1016/j.fishres.2012.06.018

Valeiras, J., & Abad, E. (2009). Description of Blue Shark (BSH). *ICCAT Manual*, 249–259.

Vas, P. (1990). The abundance of the blue shark, *Prionace glauca*, in the western English Channel. *Environmental Biology of Fishes*, *29*(3), 209–225. https://doi.org/10.1007/BF00002221

Veríssimo, A., Noble, L. R., Sampaio, Í., Mcdowell, J. R., Alexandrino, P., Mucientes, G., Queiroz, N., da Silva, C., & Jones, C. S. (2017). World without borders — genetic population structure of a highly migratory marine predator, the blue shark (*Prionace glauca*). *Ecology and Evolution*. https://doi.org/10.1002/ece3.2987

Vögler, R., Beier, E., Ortega-García, S., Santana-Hernández, H., & Valdez-Flores, J. J. (2012). Ecological patterns, distribution and population structure of Prionace glauca (Chondrichthyes: Carcharhinidae) in the tropical-subtropical transition zone of the north-eastern Pacific. *Marine Environmental Research*, *73*, 37–52. https://doi.org/10.1016/j.marenvres.2011.10.009

von Bertalanffy, L. (1938). A quantitative theory of organic growth. *Human Biology*, *10*, 181–213.

Wells, R. J. D., Spear, N., & Kohin, S. (2016). Age validation of the blue shark (*Prionace glauca*) in the eastern Pacific Ocean. *Marine and Freshwater Research*, *68*(6), 1130–1136. https://doi.org/10.1071/MF16054

White, W. T., & Last, P. R. (2012). A review of the taxonomy of chondrichthyan fishes: A modern perspective. *Journal of Fish Biology*, *80*(5), 901–917. https://doi.org/10.1111/j.1095-8649.2011.03192.x

Wickham, H. (2009). Ggplot2: Elegant Graphics for Data Analysis. Retrieved from http://ggplot2.org

Witzell, W. N. (1985). The incidental capture of sharks in the Atlantic United States Fishery Conservation Zone by the Japanese tuna longline fleet. *NOAA Technical Report NMFS*, *31*, 21–22.