

UNIVERSIDADE TÉCNICA DO ATLÂNTICO
INSTITUTO DE ENGENHARIA E CIÊNCIAS DO MAR

WEST AFRICAN SCIENCE SERVICE CENTRE ON CLIMATE CHANGE
AND ADAPTED LAND USE

Master Thesis

**INFLUENCE OF TEMPERATURE ON THE
SWIMMING PERFORMANCE AND SPATIAL
DISTRIBUTION OF BLUE SHARKS (*Prionace
glauca*)**

GILLES FLORENT SORO

Master Research Program on Climate Change and Marine Sciences

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Supervisor | Dr Nuno Queiroz
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Influence of temperature on swimming performance and spatial distribution of blue sharks

(*Prionace glauca*)

Gilles Florent Soro

Master's thesis presented to obtain the master's degree in Climate Change and Marine Sciences, by the Institute of Engineering and Marine Sciences, Atlantic Technical University in the framework of the West African Science Service Centre on Climate Change and Adapted Land Use

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Dedication

I dedicate this modest work to my father, Mr SORO Souleymane and my mother, Kehi Djié Nicole, for their prayers, love, patience, and confidence in me.

To my dear sisters for their constant encouragement and moral support,

To my beloved brothers, for their support and encouragement,

To all my family for their support throughout my university career,

May this work be the fulfilment of your long-standing wishes and the fruit of your unfailing support,

Thank you for always being there for me.

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Resumo

Os tubarões azuis são tubarões epipelágicos oceânicos em águas temperadas e tropicais. Encontram-se ao largo das costas de todos os continentes excepto a Antárctida, em águas que variam entre 12 a 20 °C e 7 a 25 °C. De facto, a temperatura da água é um dos factores mais influentes no desempenho fisiológico e comportamento dos tubarões ectotérmicos marinhos (por exemplo, tubarões azuis), que são organismos que não podem regular a temperatura do seu corpo internamente. Os efeitos das alterações na temperatura dos oceanos podem afectar as suas respostas fisiológicas, tais como crescimento, alimentação, equilíbrio ácido-base e metabolismo, com alterações significativas no seu orçamento energético e nos seus padrões de distribuição horizontal e vertical. Para alargar o estudo e fornecer uma visão do comportamento dos ectotérmicos marinhos em relação à temperatura do oceano, particularmente o comportamento do tubarão azul, a questão central abordada neste estudo é como o nicho térmico e a distribuição espacial do tubarão azul variam com a temperatura do oceano. Neste estudo, determinámos o nicho térmico do tubarão azul, incluindo a forma como a temperatura do oceano afecta o seu desempenho natatório e distribuição espacial. Para a montagem da experiência, foram utilizados dados da etiqueta do tubarão azul registados por acelerómetros e transmissores de satélite (PSAT- transmissores de satélite pop-up) no Oceano Atlântico Norte. Do extenso estudo realizado, os resultados mostraram que os tubarões azuis eram mais activos a temperaturas oceânicas de 21,86 °C com uma tolerância de temperatura de 10-22 °C; entretanto, passam a maior parte do seu tempo a temperaturas que vão de 13 °C a mais de 25 °C. A partir de estudos de curto e longo prazo, o nicho térmico foi estimado entre 18 °C a 21 °C. Por outro lado, o tempo gasto em cada faixa de profundidade mostrou que se encontravam principalmente nos 50 m superiores. O seu desempenho na natação mostrou que a sua distribuição horizontal seguia a temperatura do oceano, e tornar-se-ão mais concentrados em altas latitudes com o aquecimento global.

Palavras chaves: Desempenho de natação, nicho térmico, distribuição espacial, etiqueta de acelerómetros, PSAT, *Prionace glauca*.

Abstract

Blue sharks are oceanic epipelagic sharks in temperate and tropical waters. They are found off the coasts of all continents except Antarctica, in waters temperatures ranging from 12 to 20 °C and 7 to 25 °C. Indeed, water temperature is one of the most influential factors in the physiological performance and behaviour of marine ectothermic sharks (e.g. blue sharks), which are organisms that cannot regulate their body temperature internally. The effects of changes in ocean temperature can affect their physiological responses, such as growth, feeding, acid-base balance, and metabolism, with significant changes in their energy budget and their horizontal and vertical distribution patterns. To broaden the study and provide insight into the behaviour of marine ectotherms in relation to ocean temperature, particularly the behaviour of the blue shark, the central question addressed in this study is how the thermal niche and spatial distribution of blue sharks vary with ocean temperature. In this study, we determined the thermal niche of blue sharks, including how ocean temperature affects their swimming performance and spatial distribution. For the experiment setup, blue shark tag data recorded by accelerometers and satellite transmitters (PSAT- pop-up satellite transmitters) in the North Atlantic Ocean were used. From the extensive study carried out, the results showed that blue sharks were most active at ocean temperatures of 21.86 °C with a temperature tolerance of 10-22 °C; meanwhile, they spend most of their time at temperatures ranging from 13 °C to over 25 °C. From both short and long-term studies, the thermal niche was estimated to be between 18 °C to 21 °C. On the other hand, the time spent in each depth range showed that they were mainly in the upper 50 m. Their swimming performance showed that their horizontal distribution followed ocean temperature, and they will become more concentrated in high latitudes with global warming.

Keywords: Swimming performance, thermal niche, spatial distribution, accelerometers tag, PSAT, *Prionace glauca*.

Abbreviations and acronyms

| | |
|-----------------------|---|
| % | Percentage |
| App | Application |
| ATP | Adenosine triphosphate |
| cm | Centimeter |
| CMIP6 | The Sixth phase of the Coupled Model Intercomparison. Project |
| CO₂ | Carbon Dioxide. |
| COP12 | Twelfth session of the Conference of the Parties. |
| Ctmax | Critical maximum temperature |
| Ctmin | Critical minimum temperature |
| DLW | Double-labelled Water |
| Fig | Figure |
| FL | Folk Length |
| GPS | Global Positioning System |
| H | Hour |
| Hz | Hertz |
| ICCA | International Commission for the Conservation of Atlantic Tunas. |
| IUCN | International Union for the Conservation of Nature. |
| m | Meter |
| °C | Degree Celsius |
| ODBA | Overall Dynamic Body Acceleration |
| °N | Degree North |
| °S | Degree South |
| DO | Dissolved Oxygen |
| Pro | Professional |
| PSAT | Pop-up satellite archival tag |
| PSD | Power Spectral Density |
| Rtimer | Release timer |
| Shark Id | Shark Identification |
| SMS | Short Message Service |
| SST | Sea Surface Temperature |

| | |
|-------------|---------------------------|
| t/yr | Tonne per year |
| TAD | Time At Depth |
| TAT | Time At Temperature |
| TL | Total Length |
| TL | Total Length |
| Top | Optimal Temperature |
| TPc | Thermal Performance Curve |
| uSD | Micro Secure Digital card |
| ... | |

General index

| | |
|---|------|
| Financial support | vi |
| Dedication | vii |
| Acknowledgements | viii |
| Resumo | ix |
| Abstract | x |
| Abbreviations and acronyms | xi |
| General index | xiii |
| Figure index..... | xv |
| Table index..... | xvii |
| 1. Introduction | 1 |
| 1.1 Background and Context | 1 |
| 1.2 Problem Statement..... | 2 |
| 1.3 Research Questions..... | 2 |
| 1.4 Relevance and Importance of the Research..... | 3 |
| 1.5 Structure of the work | 3 |
| 2. Literature review | 5 |
| 2.1 Generality: blue sharks' biology and ecology..... | 5 |
| 2.2 Distribution and migration..... | 6 |
| 2.3 Sharks' conservation status | 8 |
| 2.3.1 Anthropogenic impact on blue sharks | 8 |
| 2.3.2 Environmental influence: the case of the temperature | 9 |
| 2.4 Overall body dynamic measurement | 10 |
| 2.5 Thermal performance curve..... | 11 |
| 3. Materials and Methods | 13 |
| 3.1 Materials | 13 |
| 3.1.1 <i>Prionace glauca</i> | 13 |
| 3.1.2 Equipment..... | 13 |
| 3.2 Methods..... | 16 |
| 3.2.1 Study area | 16 |
| 3.2.2 Shark tagging and tag recovery | 17 |
| 3.2.3 Data description..... | 18 |
| 3.2.4 Data processing..... | 20 |
| 4. Results | 22 |
| 4.1 Blue sharks' overall dynamic body acceleration and thermal performance curve | 22 |
| 4.2 Identification of the thermal preferences..... | 23 |

| | | |
|-----|---|----|
| 4.3 | Current swimming performance maps | 25 |
| 4.4 | Future swimming performance map..... | 27 |
| 5. | Discussion | 28 |
| 5.1 | Swimming activity performance | 28 |
| 5.2 | Temperature preference | 28 |
| 5.3 | Current and future swimming activity map..... | 30 |
| 6. | Conclusions and recommendations..... | 32 |
| 7. | References | 33 |
| | Appendix | 44 |

Figure index

| | |
|---|----|
| Figure 1: Blue sharks' reproductive cycle pathway in North Atlantic Ocean. Source: (Martin, 2003)..... | 5 |
| Figure 2: Blue shark seasonal migration. a) Blue shark migration models in the North Atlantic during autumn and winter. b) Blue shark migration models in the North Atlantic during spring and summer. Source: (Camhi et al., 2009)..... | 7 |
| Figure 3: General shape of a thermal performance curve. The relationship between environmental temperature and a physiological rate of an ectotherm is expressed as a thermal performance curve (grey line). The ecophysiological key characteristics of critical thermal minimum (CT _{min}) and maximum (CT _{max}) delimit an organism's thermal tolerance. The optimum temperature (T _{opt}) specifies the temperature at maximum performance. Source: (Gannon, et al., 2014)..... | 12 |
| Figure 4: Blue shark colour and morphological characteristics. a) blue shark (<i>Prionace glauca</i>) body colour. Source: (Marc, 2021). b) blue shark (<i>Prionace glauca</i>) morphology characteristics. 1. Body is slender, 2. The snout is long and rounded, 3. Caudal fin is heterocercal, 4. Pectoral fins are very long and pointed, 5. The first dorsal fin is closer to the pelvic fins than the pectoral fins. Source: (FAO, s.d.)..... | 13 |
| Figure 5: Pelagic longline. Source: (NOAA, 2019)..... | 14 |
| Figure 6: Accelerometer tag. A) Oxygen sensor; B) Depth/temperature sensor; C) GPS unit; D) Led. Source: CIBIO, MOVE group. | 15 |
| Figure 7: Pop-up satellite archival tag (MiniPAT tag). a) Argos antenna, b) temperature sensor, c) communications port with plug, d) light sensor, e) float, f) release pin, g) LED light, h) wet/dry sensor, i) ground plate, j) light sensor, k) pressure sensor. Source: (Wildlife Computers, 2019)..... | 15 |
| Figure 8: Area of the fine-scale study around Faial Island (Azores Archipelago – Portugal). | 16 |
| Figure 9: Map of tagging locations and area covered by the blue sharks during long-term monitoring (2010, 2011 and 2017) in the North Atlantic Ocean. | 17 |
| Figure 10: Accelerometer tag orientation on the dorsal fin of a blue shark. Source: Photo credit, Ivo da Costa..... | 18 |
| Figure 11: Thermal performance curve of blue sharks tagged fine-scale study around Faial Island (Azores Archipelago – Portugal)..... | 23 |

Figure 12: Percentage of time spent by blue sharks in the temperature range during the spring, summer, autumn and winter seasons..... 24

Figure 13: Percentage of average time spent by blue sharks in the temperature range in 2010, 2011 and 2017. 24

Figure 14: Average time spent by blue sharks at different depths in 2010, 2011 and 2017. .. 25

Figure 15: Present SST and swimming performance map. a) Mean SST (3 m) of 2010, 2011 and 2017; b) Area where blue sharks could be active at 3 m..... 26

Figure 16: Present SST and swimming performance map c) Mean SST (100 m) of 2010, 2011 and 2017; d) Area where blue sharks could be active at 100 m..... 26

Figure 17: Future SST and swimming performance map. a) Present mean SST; b) Future mean SST; c) Present mean swimming activities d) future swimming activities..... 27

Table index

| | |
|--|----|
| Table 1: Exemple of acceleration (accX, accY and accZ) and environmental (depth, temperature and oxygen) data from blue sharks tagged around Faial Island (Azores Archipelago – Portugal) during the fine-scale study. Shark_Id: shark Identification, accX: acceleration on X axis, accY: acceleration on Y axis, accZ: acceleration on Z axis. | 19 |
| Table 2: Exemple of time-at-temperature (TAT) data from the long-term study in the North Atlantic. DeployID: deployment identification. HistType: histogramme type..... | 19 |
| Table 3: Exemple of time-at-depth (TAD) data from the long-term study in the North Atlantic. DeployID: deployment identification. HistType: histogramme type..... | 19 |
| Table 4: Summary of the eleven blue sharks tracked. shark_Id: shark identification number, FL: folk length, TL: total length, Rtimer: Release timer. | 20 |
| Table 5: Statistic table of temperatures encountered and ODBA performed by the blue sharks during the fine-scale study. Island. Max_temp: maximum temperature, Min_temp: minimum temperature, Mean_temp: mean temperature, Max_odba: Maximum ODBA, Min_odba: minimum ODBA, Mean_odba: mean ODBA. | 22 |

1. Introduction

1.1 Background and Context

Blue sharks are oceanic epipelagic sharks occurring worldwide in temperate and tropical waters (Froese et al., 2006). They occur around the coasts of all continents except Antarctica (Compagno & Leonard, 1984). Their most significant concentrations with strong seasonal fluctuations mainly occur in the Pacific Ocean between 20 °N and 50 ° N. In the tropics, they can be found between 20 °N and 20 °S (Compagno & Leonard, 1984), within water temperatures between 7-25 °C (Compagno et al., 2004). In tropical waters, they live at greater depth; meanwhile, in temperate waters, they usually come close to the coast, where they can be observed by divers (Compagno & Leonard, 1984).

In general, sharks are high economic value species for fishing and tourism and play a key role in marine ecosystems as top predators (Clarke et al., 2007). Firstly, shark tourism is one of the most important aspects for humans because it generates significant economic value (Topelko & Dearden, 2005). Shark tourism is a form of ecotourism that allows people to dive with sharks in their natural environment (Shark tourism, 2020). This activity provides auxiliary income to destination countries and communities via tax revenues and expenditure on accommodation, food and transport (Vianna et al., 2012). A good example is the case of Indonesia, one of the world's major marine tourism destinations, with an annual market of at least 200 million international and domestic tourists per year, of which about 18 million are associated with marine and/or reef travel (Mustika et al., 2020). Besides their touristic values, sharks are harvested for their fin and meat, used as food by many people living near the seas and oceans in Asia, Africa, Latin America, Australia and Europe (Podarilove, 2022).

With over three hundred known species of shark, which differ in size, lifestyle, diet and behaviour, only a few are of commercial importance (Podarilove, 2022). In addition to their economic importance, sharks help preserve marine biodiversity and prevent the overpopulation of several fish species (Sheppard, 2015). Indeed, sharks occupy high trophic levels in most coastal, demersal and pelagic food webs (Compagno, 2001). They control the prey population not only through direct consumption but can also induce assertive avoidance behaviour, causing them to modify their use of the habitat according to the relative risk of predation, which in turn can change their trophic interactions (Heithaus et al., 2009). However, despite their advantages, sharks face several challenges (Speed et al., 2010), such as overfishing (Davis, 2021) and climate change effects (Natl. Res. Counc. 2011).

1.2 Problem Statement

Growing human pressures, including climate change, have profound and diverse consequences for marine ecosystems (Doney *et al.*, 2012). In the case of the elasmobranch (sharks, rays, and skates), the rapid decline rates of their populations have led to concerns about their long-term survival and questions about how their disappearance might affect marine ecosystems (Pacoureau *et al.*, 2021). Today, many sharks and rays are listed on the Red List of threatened species by the International Union for the Conservation of Nature (IUCN) (Hannah *et al.*, 2007) due to overfishing and illegal fishing (Davis, 2021). The International Commission for the Conservation of Atlantic Tunas assessed Atlantic blue shark stocks and found that despite relatively high biomass, the possibility of overfishing of the population could not be ignored (ICCA, 2016). Similarly, the US National Marine Fisheries Service stock assessment suggests that the North Atlantic and North Pacific blue shark population is declining by more than 5% yearly (CoP12, 2012).

Secondly, climate change is another problem that marine ecosystems face (Doney *et al.*, 2012). The rising carbon dioxide (CO₂) in the atmosphere is one of the most severe problems causing climate change since its effects are widespread on a global scale and irreversible on ecological timescales (Natl. Res. Counc. 2011). The primary direct consequences are increasing ocean temperatures (Bindoff *et al.*, 2007) and acidity (Doney *et al.*, 2009). Indeed, the water temperature is one of the most influential drivers of the physiological performance and behaviour of marine ectotherms sharks (e.g. blue sharks) (Lear *et al.*, 2019), which are organisms that cannot internally regulate their body temperature (Payne *et al.*, 2018). The effects of changes in ocean temperature can affect their physiological responses, such as growth, feeding, acid-base balance and metabolism (Portner & Knust, 2007), with significant changes in horizontal and vertical distribution swimming patterns (McHenry *et al.*, 2019). However, little is known about how ectotherms regulate their metabolic performance and, thus, their distribution patterns according to the ocean temperature variation (Ferretti *et al.*, 2010).

1.3 Research Questions

To further study and provide information on the sharks with a particular focus on blue sharks' behaviour and swimming performance, the main question is to understand how their thermal niche, swimming activity and spatial distribution vary with ocean temperature.

1.4 Relevance and Importance of the Research

Ecosystem stability is vital as human welfare depends on the services ecosystems render, many of which are provided by marine ecosystems, including food production, climate regulation and nutrient cycling (Holmlund & Hammer, 1999). In terrestrial and aquatic ecosystems, predators can exert strong top-down forces that shape communities over large spatio-temporal scales and promote long-term stability (Estes *et al.*, 1998). Monitoring habitat use and movement of top predators, for instance, blue sharks, based on environmental conditions are critical since they significantly influence lower food chains and the functioning of ecosystems (Baum & Worm, 2009).

Furthermore, determining the scale of movements and their driving factors, alongside population structure, can be critical in developing effective management plans, including for marine protected areas and their strategic application (Queiroz *et al.*, 2016). Therefore, understanding blue sharks' thermal niche and spatial distribution could represent powerful tools for forecasting ecological consequences of range shifts with future warming and maximising the efficacy of bather protection programs (Payne *et al.*, 2018). It may also allow an understanding of the temperature sensitivity of blue sharks and whether it varies with the rate of warming, which will improve predictions of the organisms' vulnerability to environmental variation (Nguyen *et al.*, 2011).

Therefore, the main objective of this study is to understand the thermal niche of free-swimming blue sharks and how ocean temperature affects their swimming performance and spatial distribution. Specifically, it involved the following specific objectives:

- i. Determination of the overall dynamic body acceleration (ODBA) and creation of a thermal performance curve;
- ii. Identification of the thermal preference and the thermal niche;
- iii. Establishment of the swimming activity (performance) map for present and future scenarios.

1.5 Structure of the work

The structure of this work is divided into six sections. The introductory section presents the background to this study, including the relevance and questions that led to this research. The second section is the literature review, which overviews different researchers' most relevant work related to this thesis. Material and methods were described in the third section, which details the approaches used to achieve this study's objectives. Next, the results obtained from

the different analyses were presented and discussed in the fifth section. And the final section presents the conclusions and recommendations for improving this work.

2. Literature review

This section aims to provide a comprehensive overview of previously published work on shark movement, particularly the migration and distribution of the blue shark and will be divided into subsections. The main points reviewed are the general biology and ecology of blue sharks, their conservation status, the threats they face, and the evolution of methodology for studying the overall body dynamics acceleration and their limitations.

2.1 Generality: blue sharks' biology and ecology

Blue sharks reproduce by placental viviparity mode, with gestation lasting between 9–12 months (Castro & Mejuto, 1995). They can give birth to an average litter of about 30 puppies (up to 135 have been registered) ranging in size from 35 to 50 cm TL at birth (Castro & Mejuto, 1995). In the western Atlantic Ocean, approximately 50% of male blue sharks reach sexual maturity at 218 cm total length (TL), while some might reach maturity as early as 182 cm (Pratt, 1979). Females become sub-adult between 173 and 221 cm (TL) and mature at 221 cm (Pratt, 1979). There have been reports of seasonal reproduction in most areas, with young pups born in spring or summer (Pratt, 1979). However, it is unclear whether adult females breed yearly (Nakano & Stevens, 2008). Casey, 1985 explained that mature females, pregnant sharks, and new-borns are typical in the Eastern Atlantic Ocean during certain seasons, and a large proportion of the North Atlantic breeding population occurs in this region, as shown in Figure.1.



Figure 1: Blue sharks' reproductive cycle pathway in North Atlantic Ocean. Source: (Martin, 2003).

The blue shark migrates following oceanic features (e.g. temperature) and the animal they feed on (Campana *et al.*, 2011). Their diet consists principally of small pelagic fish and cephalopods, particularly squid, invertebrates (mainly pelagic crustaceans), small sharks, cetaceans (sometimes as carrion) and seabirds are also preyed upon (Compagno & Leonard, 1984). Blue sharks feed throughout the day but are most active at night, with the highest activity in the early evening (Sciarrotta & Nelson, 1977). Elliott *et al.* (2022), in their study on the diving behaviour of the blue shark in the southwest Pacific, have used SPLASH tags, designed to follow the vertical and horizontal movements of free-ranging marine animals and composed of depth, temperature, light and wet/dry sensors (Wildlife computers, 2022). They showed that the blue shark uses the vertical habitat between 0 and 1364 m below. Carey *et al.* (1990) associated these movements with a hunting tactic in response to prey distribution and related to behavioural thermoregulation.

2.2 Distribution and migration

Blue shark horizontal migration in the North Atlantic Ocean

Tagging studies on blue sharks have revealed that blue sharks travel extensively in the Atlantic Ocean and perform frequent transatlantic migrations (Kohler & Turner, 2008), which is probably achieved through a combination of slow swimming and the use of major current systems (Stevens, 1976). For instance, in late autumn and winter in the western Atlantic, most of the blue shark population is composed of juveniles of both sexes, sub-adult females, and adult males and move offshore into the Gulf Stream or south along the margins of the Gulf Stream (Fig.2a), with some of them making their way to the Caribbean, South America and the Eastern Atlantic Ocean (Casey, 1985).

Although, during spring and summer (Fig.2b), the adult males and females occur around 32-35 °N, where they mate (Pratt, 1979); meanwhile, immature females move to Northern Europe, where they occur commonly in summer, particularly around the southwest coast of England (Stevens, 1976). On the other hand, in the eastern Atlantic, during the winter, female adults are found in the Canary Islands area and the African coast around 27-32 °N (Muñoz-Chápuli, 1984), during which many of them are pregnant (Casey, 1985). Tagging studies in the North Atlantic have revealed that blue sharks are the champion migrators among sharks (Last & Stevens, 1994). They can migrate up to 1,200 to 1,700 miles (Last & Stevens, 1994), with a record of 3,740 miles from New York to Brazil (Martin, 2003) and dive from the water surface to a depth of 1400 m (Vedor *et al.*, 2021).

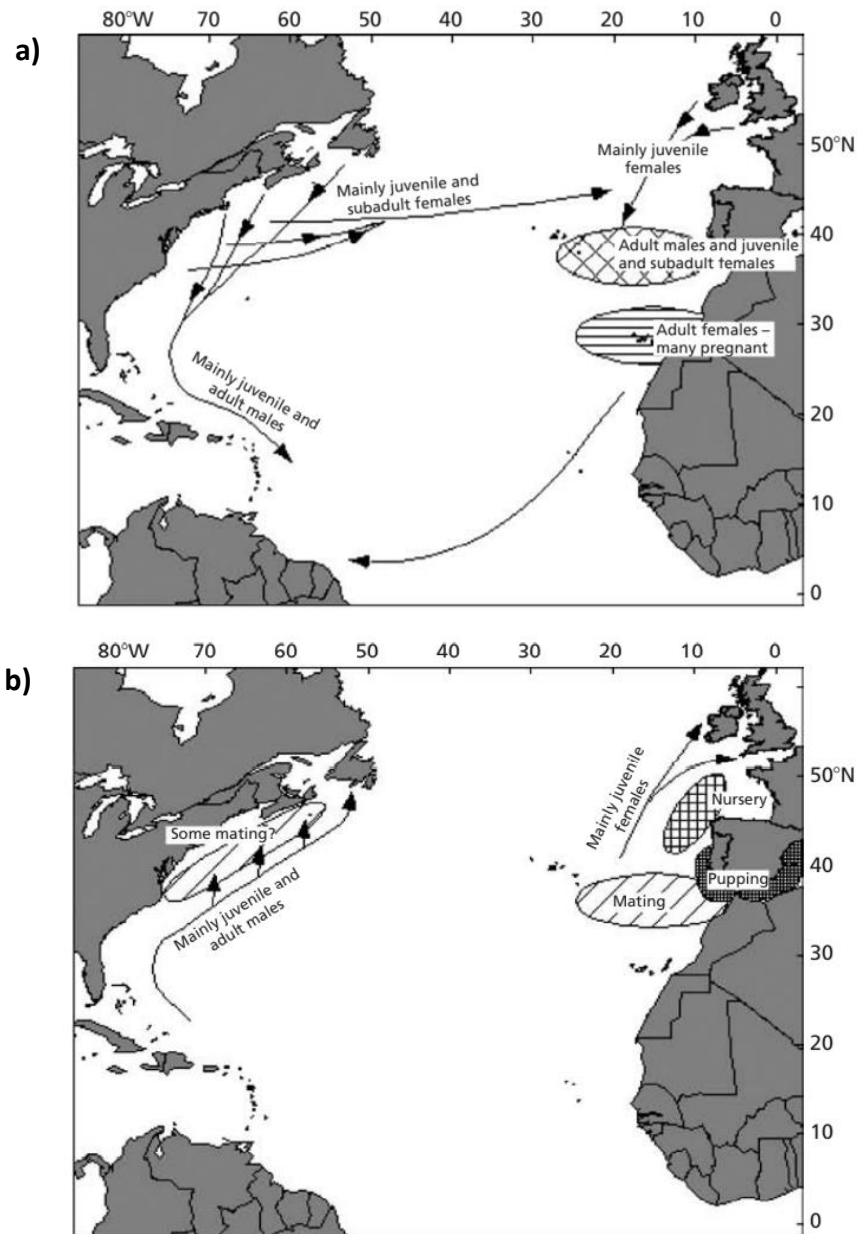


Figure 2: Blue shark seasonal migration. a) Blue shark migration models in the North Atlantic during autumn and winter. b) Blue shark migration models in the North Atlantic during spring and summer. Source: (Camhi *et al.*, 2009).

Blue shark Vertical migration

The investigation of the vertical movement of the blue shark using PSAT tags (Vandepierre *et al.*, 2014) showed that blue sharks demonstrate a wide vertical distribution, inhabiting depths from the surface to a maximum of 1160 m. To elucidate that observation, West & Stevens (2001) explained that large predators, such as sharks and tuna, change their diving behaviour in response to the diurnal migration of their prey by moving up and down within the water column. In the case of blue sharks and down movement may help them scan potential prey visually (Martin, 2003).

In addition, (Vedor *et al.*, 2021) examine the time spent by the blue shark during its up and down movement at various depths and times of the day, using a total of 22 adult blue sharks tagged in the mid-Atlantic and the North-Western Atlantic regions, between June 2010 and August 2011. They found that blue sharks use surface waters and have cyclical diurnal behaviours, with 95% of time spent above 250 m at night, with variable depth during the day. Queiroz *et al.* (2012) explain that the space-use patterns of blue sharks indicate that they spend much time in areas where pelagic longline activity is generally high and at depths where fisheries particularly target species, which may explain the recent rapid declines reported for blue sharks in many parts of the world's oceans.

2.3 Sharks' conservation status

Chondrichthyan fishes (sharks, rays and chimaeras) constitute one of the most endangered and least documented aquatic vertebrate taxa (Dulvy *et al.*, 2014). Despite their characteristics and life-history traits (Cortés, 2000), it is essential to note that throughout their evolutionary history, many species of sharks, rays and chimaeras face particular challenges, such as delayed maturation, prolonged gestation, production of few offspring and lack of parental care (Carrier *et al.*, 2004). Together, these life-history traits make many species highly susceptible to population decline (Kindsvater *et al.*, 2016).

The most important and modern threat to chondrichthyan fish is directed and incidental overfishing (Dulvy *et al.*, 2014), already causing a more significant conservation challenge and extinction risk than most other vertebrates taxa (Dulvy *et al.*, 2017). In that sense, five stock assessments have been conducted by (Rigby *et al.*, 2019) in the Atlantic, Pacific, and Indian Oceans to investigate the current status of blue sharks. This population assessment showed that blue sharks are in decline and have therefore been classified as Near Threatened (IUCN, 2018).

2.3.1 Anthropogenic impact on blue sharks

Humans are the most significant threat to blue sharks (Joseph, 2022). According to Walker (1998), blue sharks are frequently caught due to intentional harvest, sport fishing, and by-catch, killed by humans fishing for another species (Joseph, 2022) and fished for their fins and meat (Podarilove, 2022). However, sport fishing is probably the least of these threats; catch and release survival rates are over 90%. To reduce blue sharks' anthropogenic threat, restrictions have been placed on their harvesting (Joseph, 2022). However, they are still being harvested in most parts of the world for their meat, mostly their fins (Joseph, 2022), with an estimation of 200,000-500,000 t/yr for the early/mid-2000 s (COSEWIC, 2017). Additionally, despite blue

sharks' evident ecological and economic value, the sustainability of their ecosystem services is also globally threatened by environmental conditions (Speed *et al.*, 2010), such as pollution and habitat degradation (Ferretti *et al.*, 2010).

2.3.2 Environmental influence: the case of the temperature

Effect of Ocean temperature on the spatial distribution of ectotherms predators

Marine fish, seabirds, and mammals experience significant environmental threats, such as high mortality rates, loss of breeding sites, and massive species displacement in search of favourable ecological conditions in response to ocean surface temperatures increase (IUCN, Ocean warming, 2021). This situation may indirectly impact ectotherm predators like sharks by disturbing their prey's location (Climate, 2015). Indeed, many shark preys are more easily affected by ambient water temperature. As the waters warm, these fish may move poleward, causing the sharks to follow (Climate, 2015). As a consequence, blue sharks that are known to live in both temperate and tropical waters, which range from 12-20 °C (Untamedscience, 2021), could be in lack of prey and then decline and/or a shift in their vertical or horizontal migration (Masson *et al.*, 2001). Similarly, during their studies on the movements of blue sharks, Carey *et al.* (1990) found irregular diving behaviour probably related, directly (physiological responses) or indirectly (changes in their prey availability), to changes in the thermal structure of the water column.

Effect of Ocean temperature on the metabolism of ectotherms predators

Ectothermic organisms are affected by changes in water temperature due to the direct effect of this abiotic factor on their metabolic rates and biochemical reactions (A. Clarke & Fraser, 2004). The body temperature of ectotherms fluctuates with environmental temperatures, and the rates of most biochemical reactions and biological processes increase approximately exponentially with temperature (Zuo *et al.*, 2012). This link between ectothermic organisms and the water temperature poses a serious concern since many species may have limited capacity to acclimate to rising temperatures as the climate changes (Pörtner & Gutt, 2016). Thermal fluctuations are challenging for ectotherms because of the non-linear relationship between temperature and physiological processes, as the metabolic demands for cell maintenance increase at high temperatures (Ruel & Ayres, 1999). Thermal fluctuations increase metabolic demands compared with constant temperature conditions, causing energy trade-offs that can affect growth and development (Colinet *et al.*, 2015).

Furthermore, as temperature changes, ectotherm animals may be unable to maintain critical physiological and performance traits such as growth, foraging and predator avoidance (Dhillon & Fox, 2007). During development, thermal fluctuations can increase energetic demands, resulting in decreased development rates (Dhillon & Fox, 2007) and reduced body size at maturity compared with animals developing at the equivalent mean temperature (Dhillon & Fox, 2007). In contrast, some species' thermal fluctuations can increase body size and rate of development (Dong *et al.*, 2006). An elevated body temperature increases metabolic rates in ectotherms (Hochscheid *et al.*, 2004), possibly impacting an individual's energy balance. Let's note that the energy expenditure these ectotherms may face can be determined using the overall body dynamic acceleration (ODBA) method (Wilson *et al.*, 2006).

2.4 Overall body dynamic measurement

Quantifying energy expenditure is essential to understanding questions such as the history of life (Hall *et al.*, 2001), trophic flow (Lowe, 2002), biogeography (McNab, 2002) and animals' behavioural strategies (Hinch & Rand, 1998). Initially, energy expenditure was only approximated by direct and indirect calorimetry (respirometry) in the laboratory (Frappell *et al.*, 1989), which often has little to do with the metabolic rate in the field of wild animals (Tang *et al.*, 2000). One method commonly used for determining the rate of energy expenditure of animals in the field is the double-labelled water (DLW) method (Speakman & Racey, 1988), which indicates the total amount of energy expended over an integrated period. Although attempts have been made to estimate the costs of specific behaviours by analysing time-energy budgets in the DLW studies (Nagy *et al.*, 1984), such calculations suffer from biases (Wilson & Boris, 2010). They are challenging to carry out because of the difficulties in defining the conditions to which wild animals have been exposed (Furness & Bryant, 1996), and this technique is not appropriate for all taxa (Sparling *et al.*, 2008).

Apart from those methods, a new approach to approximate energy expenditure uses the overall dynamic body acceleration (ODBA) as an indicator (Wilson *et al.*, 2006) and appears less subject to time limitations. ODBA can be measured by attaching an electronic data logger with a tri-axial acceleration sensor to an animal's trunk so that the acceleration is recorded close to the animal, resulting from limb movement (Shepard *et al.*, 2010). The ODBA method proposes that since the most (and in many cases) variable factor in modulating energy expenditure in many vertebrates is movement (Karasov, 2008), the measurement of body acceleration should be correlated with energy expenditure (Wilson *et al.*, 2006). The overall dynamic body acceleration can be quantified by the use of the thermal performance

curve (Sinclair et al., 2016). However, the application of ODBA as a measure of energy expenditure is new, and assumptions have not been studied in detail, maybe due to the difficulty of linking the physics of acceleration movement with the chemistry of energy expenditure based on adenosine triphosphate (ATP) (Gleiss, Wilson, & Shepard, 2011).

2.5 Thermal performance curve

The thermal performance curve is often used to predict organism responses to climate change (Sinclair et al., 2016). Since all major ectotherm physiological processes are sensitive to temperature changes (Michael & Angilletta, 2009), the thermal performance curve (Fig.3) allows quantifying how ectotherm body temperature may affect their performances (e.g. ODBA) or fitness. It is advantageous to illustrate the effects of temperature on the behavioural or physiological performance of these predators (Gannon, et al., 2014), where the maximum performance (e.g. ODBA) is achieved at the optimal temperature (T_{opt}), with temperatures below T_{opt} representing a gradual decline in performance, and temperatures above T_{opt} result in a rapid decline until a critical temperature is reached (Gannon, et al., 2014).

However, there is a controversy about using thermal temperature curves to predict temperature effects on the ectotherm behavioural or physiological performance (Sinclair et al., 2016). During the investigation of the question, "Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures?", Sinclair et al. (2016) explained that thermal performance curves constructed based on a particular life stage of an organism are limited in terms of information. They do not represent the general thermal performance of organisms from birth to adulthood and do not consider previously experienced body temperatures. Therefore, they are unrepresentative of the thermal performance of organisms throughout their lives. They also stated that rather than assuming that thermal performance curves are fixed during ontogeny, they could be measured for each major life stage and incorporated into stage-specific ecological models to reveal the life stage most likely vulnerable to climate change.

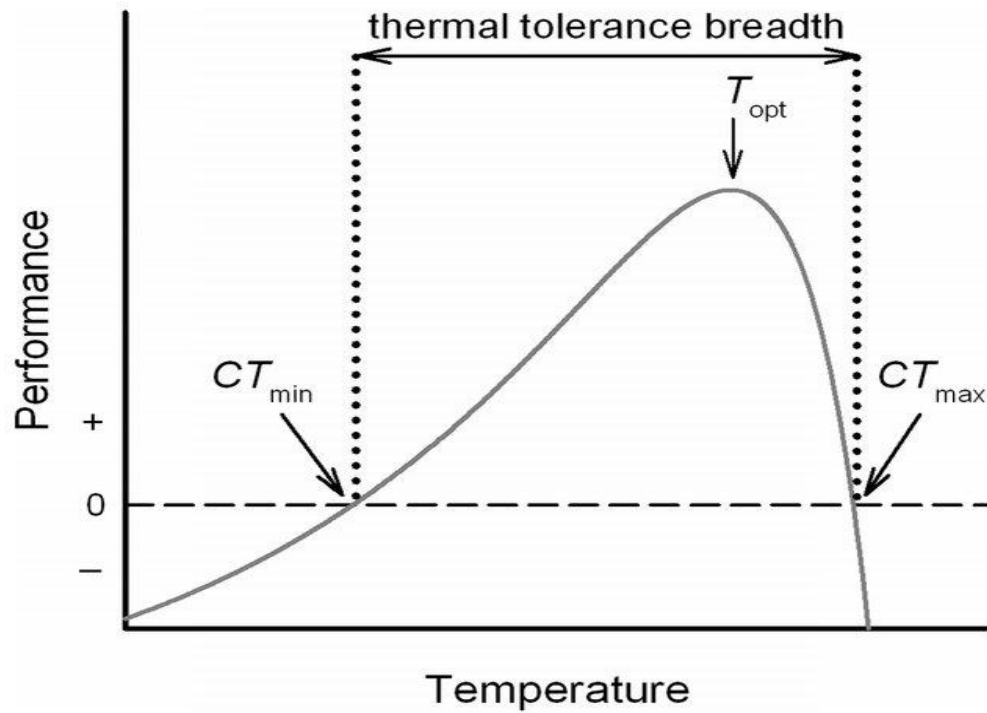


Figure 3: General shape of a thermal performance curve. The relationship between environmental temperature and a physiological rate of an ectotherm is expressed as a thermal performance curve (grey line). The ecophysiological key characteristics of critical thermal minimum (CT_{min}) and maximum (CT_{max}) delimit an organism's thermal tolerance. The optimum temperature (T_{opt}) specifies the temperature at maximum performance. Source: (Gannon, et al., 2014).

3. Materials and Methods

Various materials and methods were used to achieve this study's objectives. This section aims to provide details of all the materials used in the study, give a clear and brief description of the research procedures, and explain the data collection and analysis procedure.

3.1 Materials

3.1.1 *Prionace glauca*

The species to be studied is the blue shark, *Prionace glauca* (Linnaeus, 1758). The blue shark is distinguished from other sharks by the blue colouration of its body (Fig.4a) and its morphologically distinctive characteristics (Fig.4b). It has a slender body with a large eye and a long conical snout that is longer than the width of its mouth. It has extremely long, pointed pectoral fins, typically as long as the distance from its snout to the posterior gill slit (Compagno et al. 2005). The blue shark's name comes from its distinct dark blue dorsal surface. The dorsal fin is moderate in size and set back where it is closer to the pelvic fin insertion than the pectoral insertion point. There is a slight keel on the caudal peduncle, and the tail is narrowly lobed with a long ventral lobe. The ventral surface is a well-defined, crisp white colour (Compagno et al. 2005). These contrasting colours are counter-shading and provide camouflage for the open Ocean sharks (French & Naylor, 2018).

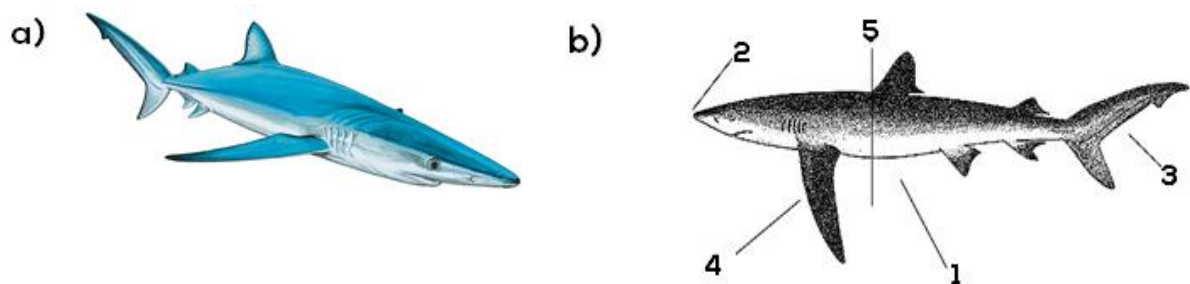


Figure 4: Blue shark colour and morphological characteristics. a) blue shark (*Prionace glauca*) body colour. Source: (Marc, 2021). b) blue shark (*Prionace glauca*) morphology characteristics. 1. Body is slender, 2. The snout is long and rounded, 3. Caudal fin is heterocercal, 4. Pectoral fins are very long and pointed, 5. The first dorsal fin is closer to the pelvic fins than the pectoral fins. Source: (FAO, s.d.).

3.1.2 Equipment

Diverse equipment was used to conduct the study process, from data collection to analysis. These included fishing gears, accelerometer tags, PSATs and software. The study started by

catching the blue sharks using a fishing boat to get on the sea, where a longline composed of a mainline, buoys, ganglions, and baited hooks were used. The longline had a horizontal length of 2 miles with 30 to 40 circle hooks and reached a depth of around 10 m (Fig.5).

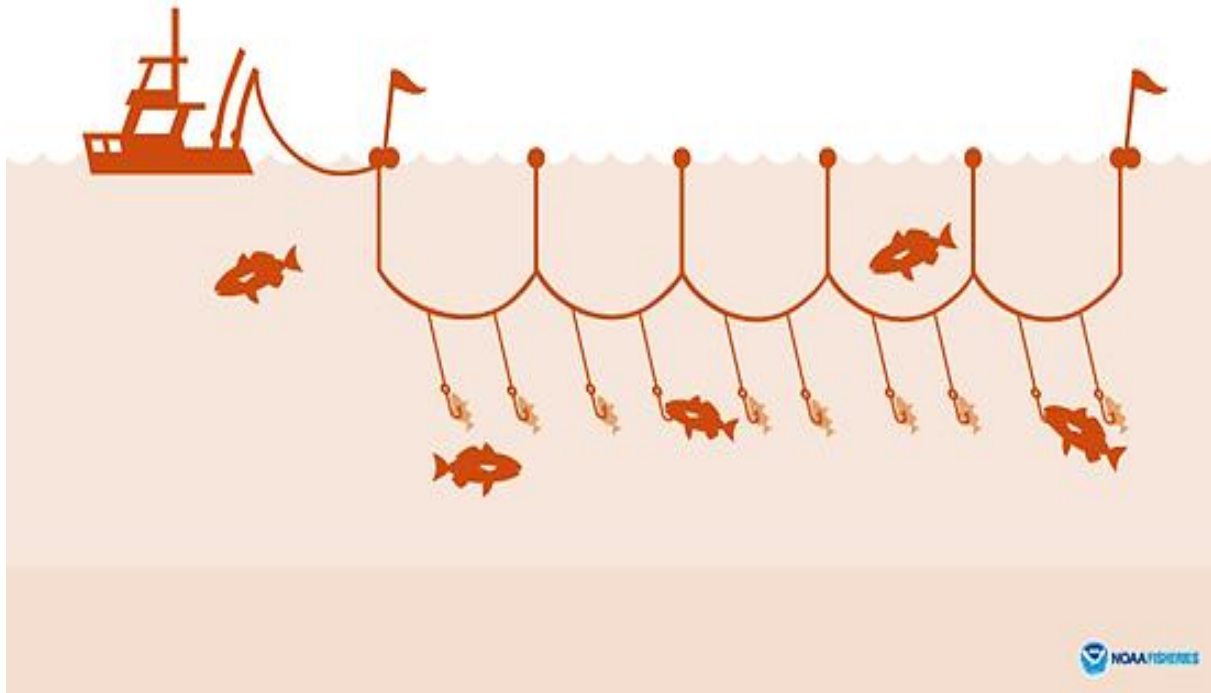


Figure 5: Pelagic longline. Source: (NOAA, 2019).

Two types of tags were used to tag the blue sharks after their catches. The accelerometer tag or the PSAT tag was used depending on the measurement. The accelerometer tag shown in Figure 6 measured the fine-scale blue sharks' activity. It contains a 9-axis motion sensor (accelerometer, gyroscope, magnetometer), enabling the recording of fine-scale three-dimension movements of tagged animals. It also includes several sensors for measuring pressure, temperature, and dissolved Oxygen (DO).

Additionally, the accelerometer tag contains a GPS unit for geolocalisation and recovery procedures, uSD for storing information, and a rechargeable lithium battery. These components are integrated into an electronic board, where a Bluetooth system allows transferring data and setting the tag's deployment parameters. A resin-based package has been designed to accommodate all the electronic components and implement a time-release device that enables the tag to recover, guaranteeing a waterproof system with floating capacity.

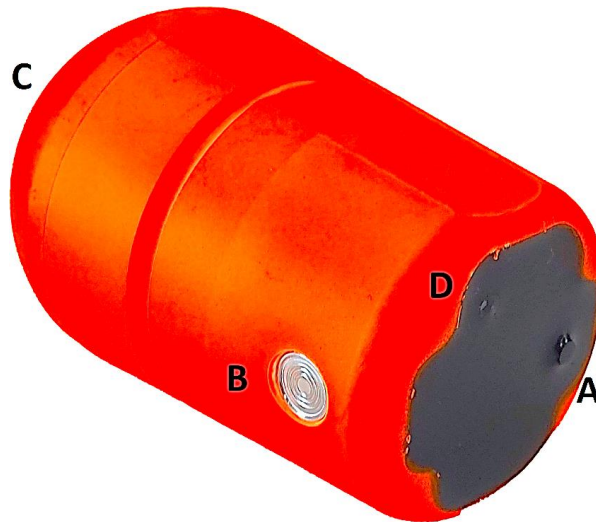


Figure 6: Accelerometer tag. A) Oxygen sensor; B) Depth/temperature sensor; C) GPS unit; D) Led. Source: CIBIO, MOVE group.

The PSAT (Fig.7) was used for the long-term shark movement tracking study. The PSAT is a microcomputer designed to collect data on the environment crossed by a tagged animal. PSATs are satellite tags and archival tags combined in the same package. They measured depth, temperature, time, and light (from geo-locatable information). Their major advantage is that instead of retrieving the tag from the animal to get the data, these devices can send the data to the researcher via satellite.

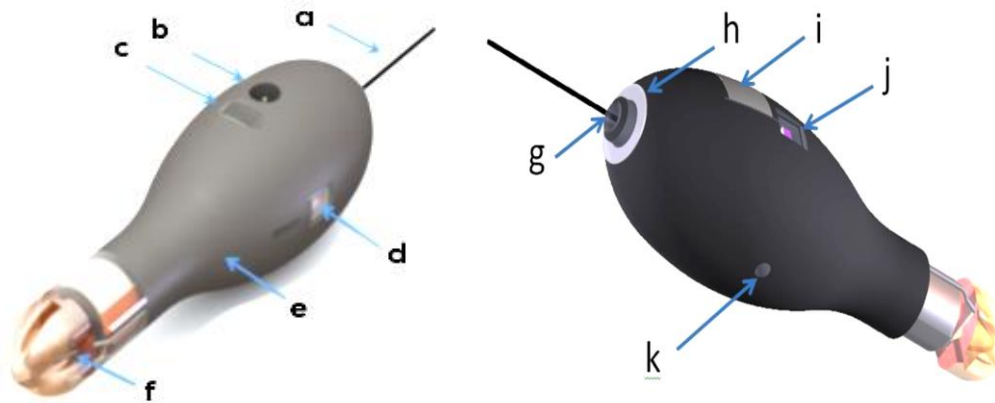


Figure 7: Pop-up satellite archival tag (MiniPAT tag). a) Argos antenna, b) temperature sensor, c) communications port with plug, d) light sensor, e) float, f) release pin, g) LED light, h) wet/dry sensor, i) ground plate, j) light sensor, k) pressure sensor. Source: (Wildlife Computers, 2019).

To process the data obtained, four software packages were used: The Maverick app (to recover the accelerometer tag), R programme version 4.1.1 (2021-08-10), ArcGIS software (licence number: 534299844173) and Igor Pro software (licence number: WAVEMETRICS220221-9039-16120).

3.2 Methods.

3.2.1 Study area

The present study was conducted in the North Atlantic Ocean, where blue sharks' fine-scale and long-term data were collected. The fine-scale data were collected around Faial Island (Azores Archipelago – Portugal), located at 38°34'57" North latitude and 28°42'17" West longitude during three months (July, September 2020 and June 2021), as shown in Figure 8. Meanwhile, the long-term data were collected at various locations in the North Atlantic Ocean during three years (2010, 2011 and 2017), as presented in Figure 9.

First, these areas were chosen because of the high probability of the presence of blue sharks in the North Atlantic Ocean (Aquamaps, 2019) and secondly, because they offer a variety of temperatures (Britannica, 2022). In fact, in the North Atlantic Ocean, the region of high surface temperature is wide off the American east coasts but narrow off the African coast, where the Canary Current carry cold water toward the Equator. Therefore, the SST in the North Atlantic Ocean is warmer off the eastern coast than off the western coast at latitudes between 10° and 30 ° N, while this trait is inverted above 30 ° N (Britannica, 2022).

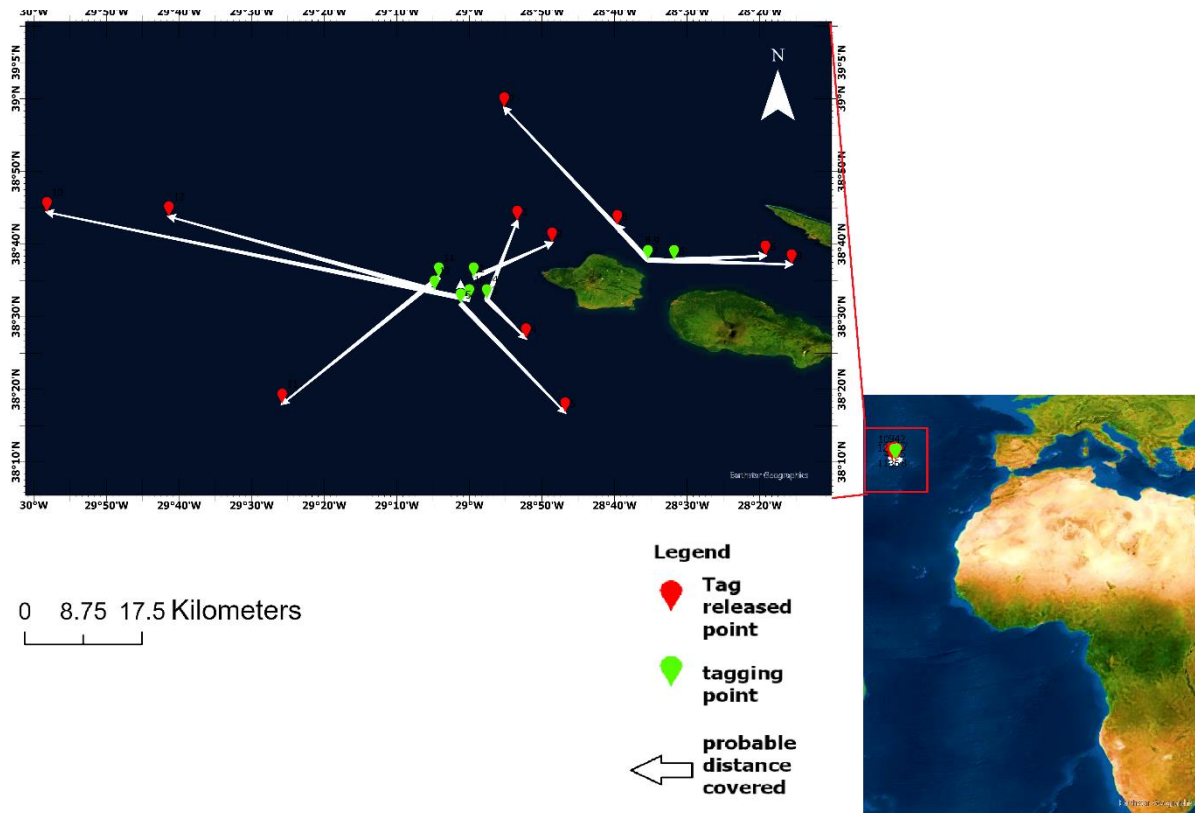


Figure 8: Area of the fine-scale study around Faial Island (Azores Archipelago – Portugal).

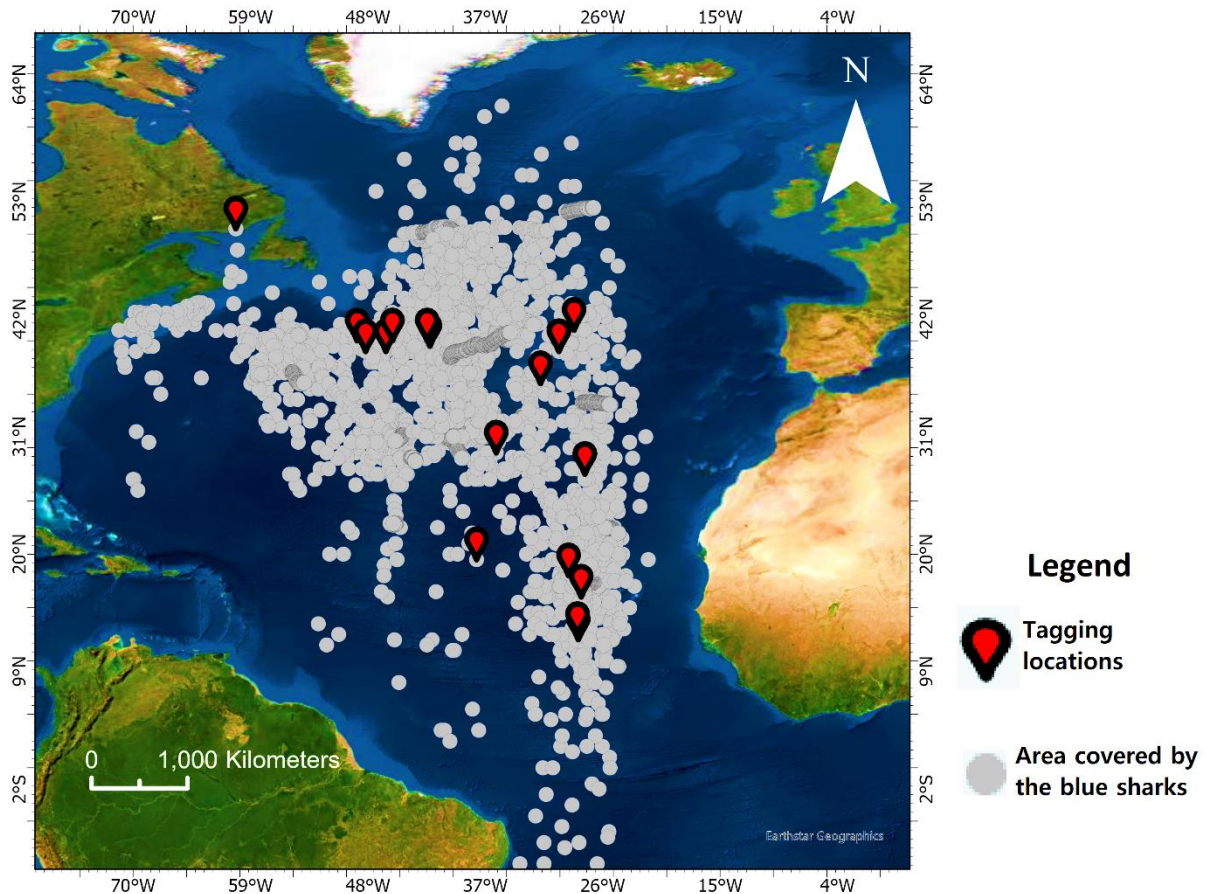


Figure 9: Map of tagging locations and area covered by the blue sharks during long-term monitoring (2010, 2011 and 2017) in the North Atlantic Ocean.

3.2.2 Shark tagging and tag recovery

Collecting fine-scale data from blue sharks involved catching and fixing accelerometer tags on the dorsal fin. First, the tags were programmed, activated, and attached through a hole created on the dorsal fin, using a cable linked to a timer and following a particular orientation. The flat part (black surface) was oriented to the sharks' heads, and the temperature sensor was oriented upward, as shown in Figure 10. Once the shark was released, the accelerometer tags recorded data at different frequencies (20 Hz or 30 Hz) for a maximum of two days.

For the long-term data collection, the PSATs were rigged with a monofilament tether covered with silicone tubing and looped through a small hole in the base of the first dorsal fin of the blue sharks captured. Depth, external temperature, and light-level parameters were archived at 1 s intervals and stored as summary data over set intervals of 6 h (00:00, 06:00, 12:00, and 18:00). For each period, time-at-depth histograms (TAD; aggregated in eight depth

bins, 50, 100, 150, 200, 250, 400, 600, >600 m), minimum and maximum depth and temperature were recorded.

After 24 or 48 hours, the accelerometer tag automatically detaches from the shark and floats on the Ocean's surface via its buoyancy capability. After 45 minutes, it turns to satellite mode and starts sending the position via satellite (positions were received via email or SMS). The maverick application was used during the recovery trip, which indicates the tag position. However, in the case of the PSAT, it's not built to be recovered but made to send information to satellites.



Figure 10: Accelerometer tag orientation on the dorsal fin of a blue shark. Source: Photo credit, Ivo da Costa.

3.2.3 Data description

Eleven blue sharks were tagged with accelerometer tags as part of the fine-scale study, allowing to obtain data composed of environmental data (depth, temperature and oxygen) and acceleration data on the X, Y and Z axis, as shown in Table 1. The long-term study allowed the acquisition of depth data, time spent at temperature bins (TAT) (Table 2) and time spent at depths (TAD) data (Table 3) from eighteen blue sharks.

Table 1: Example of acceleration (accX, accY and accZ) and environmental (depth, temperature and oxygen) data from blue sharks tagged around Faial Island (Azores Archipelago – Portugal) during the fine-scale study. Shark_Id: shark Identification, accX: acceleration on X axis, accY: acceleration on Y axis, accZ: acceleration on Z axis.

| Shark_Id | accX | accY | accZ | depth | temperature | oxygen |
|----------|----------|----------|---------|-------|-------------|--------|
| Blue2 | -0.23107 | -0.31134 | 0.58487 | 0.4 | 21.9 | 233.32 |
| Blue2 | -0.37454 | -0.12468 | 0.77714 | 0.6 | 21.8 | 233.46 |
| Blue2 | -0.63977 | -0.12566 | 0.5329 | 0.7 | 21.8 | 233.96 |
| Blue2 | -0.74274 | -0.06466 | 0.45116 | 1.5 | 21.8 | 234.24 |
| Blue2 | -0.47482 | 0.55242 | 0.54388 | 2.6 | 21.8 | 234.47 |
| Blue2 | 0.40675 | 0.75494 | 0.79959 | 4.7 | 21.8 | 233.97 |

Table 2: Example of time-at-temperature (TAT) data from the long-term study in the North Atlantic. DeployID: deployment identification. HistType: histogram type.

| DeployID | HistType | Date | Latitude | Longitude | Bin1 | Bin2 | Bin3 |
|-----------|----------|------------------|----------|-----------|------|------|------|
| TATLIMITS | | | | | -2 | 2 | 5 |
| 86396 | TAT | 27/06/2010 12:00 | 42.667 | -45.7 | 0 | 0 | 0 |
| 86396 | TAT | 27/06/2010 18:00 | 42.667 | -45.7 | 0 | 0 | 0 |
| 86396 | TAT | 28/06/2010 00:00 | 42.272 | -46.168 | 0 | 0 | 0 |
| 86396 | TAT | 28/06/2010 06:00 | 42.272 | -46.168 | 0 | 0 | 0 |
| 86396 | TAT | 28/06/2010 12:00 | 42.272 | -46.168 | 0 | 0 | 0 |
| 86396 | TAT | 28/06/2010 18:00 | 42.272 | -46.168 | 0 | 0 | 0 |

Table 3: Example of time-at-depth (TAD) data from the long-term study in the North Atlantic. DeployID: deployment identification. HistType: histogram type.

| DeployID | HistType | Date | Latitude | Longitude | Bin1 | Bin2 | Bin3 |
|-----------|----------|------------------|----------|-----------|------|------|------|
| TADLIMITS | | | | | 0 | 5 | 10 |
| 86396 | TAD | 27/06/2010 12:00 | 42.667 | -45.7 | 53.8 | 2.3 | 0 |
| 86396 | TAD | 27/06/2010 18:00 | 42.667 | -45.7 | 0 | 0 | 0 |
| 86396 | TAD | 28/06/2010 00:00 | 42.272 | -46.168 | 0 | 0 | 1.7 |
| 86396 | TAD | 28/06/2010 06:00 | 42.272 | -46.168 | 2.2 | 6.3 | 0.1 |
| 86396 | TAD | 28/06/2010 12:00 | 42.272 | -46.168 | 0 | 0 | 0 |
| 86396 | TAD | 28/06/2010 18:00 | 42.272 | -46.168 | 0 | 0.7 | 2.2 |

3.2.4 Data processing

ODBA calculation

The calculation of ODBA was based on the data collected from eleven blue sharks (Table 4) around Faial Island. Both depth and temperature were sampled at 1 Hz. Since after release, the shark usually makes a deep stress dive until it becomes active again. This recovery data was removed based on when the shark was tagged until its first deep dive. Once the tag came up to the surface after 24 hours or 48 hours, it continued to record "post-recorded data" that was no longer linked to the shark activity. The post-recorded data were identified and removed based on the timer (24h or 48h).

After removing the stress, the pop-up periods and all recorded data at the depth from 0 to 1 meter were removed using masks. The static part from the raw acceleration data on each axis was removed using established methods (Sato *et al.*, 2003) based on the lower peak's power spectral density analysis (PSD) value and the dynamic on each X, Y and Z-axis was calculated. Finally, ODBA was calculated for each shark by the sum of the absolute dynamic value of the X, Y and Z-axis (Payne *et al.*, 2018). The full ODBA was resampled to retain values coinciding with the temperature measurements recorded at 1 Hz, and data recorded between 0 to 1 meter was removed.

Table 4: Summary of the eleven blue sharks tracked. shark_Id: shark identification number, FL: folk length, TL: total length, Rtimer: Release timer.

| Id | Sex | FL | TL | BodyMass_kg | Frequency | Rtimer |
|-----------|------------|-----------|-----------|--------------------|------------------|---------------|
| blue2 | M | 173 | 210 | 32.6 | 30 | 24h |
| blue3 | M | 194 | 235 | 46.5 | 30 | 24h |
| blue4 | M | 182 | 220 | 37.8 | 30 | 24h |
| blue5 | M | 207 | 250 | 56.6 | 30 | 24h |
| blue6 | M | 180 | 215 | 36.7 | 20 | 24h |
| blue7 | M | 187 | 225 | 41.4 | 20 | 48h |
| blue8 | M | 230 | 275 | 79.1 | 20 | 24h |
| blue9 | M | 205 | 240 | 55.2 | 20 | 24h |
| blue10 | F | 224 | 272 | 72.8 | 30 | 48h |
| blue11 | M | 217 | 262 | 65.6 | 20 | 48h |
| blue12 | M | 232 | 270 | 81.3 | 30 | 48h |

The thermal performance curve (TPC) and identification of the thermal niche

Since intrinsic physiology and behaviour are central parameters for improving mechanistic understanding of species' niches (Kearney, 2006), measuring temperature's influence on ODBA of wild sharks is a useful approach to understanding the thermal limits of their performance (Payne *et al.*, 2018). When measured in the wild, ODBA does not directly represent the variation in physiological performance but represents the combination of intrinsic physiological constraints and behavioural decisions made in a dynamic environment (Payne *et al.*, 2016). Before building the thermal performance curve:

- the mean temperature per 1 °C bin (Lear *et al.*, 2019) was calculated;
- ODBA was aggregated by temp bins for each blue shark and rescaled to 1;
- all sharks' files were merged;
- the ODBA grand mean (aggregate all ODBA by temperature bins) was calculated.

Finally, to create the thermal performance curve, the points obtained after plotting the ODBA values against temperature values were fitted using the R package `nls.multstart` proposed by (Padfield *et al.*, 2021).

The TAT and TAD data were used to identify the thermal niche. For that, temperature bins of 1 °C were created, the time was expressed in hour, and the time was aggregated based on the temperature bins. Finally, the meantime obtained was converted into a percentage. The preferred temperature range and the optimal temperature value from the TPC were coupled to identify the thermal niche finally.

Present and future swimming activity maps

Visualising the present blue sharks' horizontal swimming activities involved temperature and ODBA data obtained from the eleven blue sharks tagged with accelerometer tags. The mean sea surface temperature (SST) raster data for 2010, 2011 and 2017 were downloaded from the NASA OceanColor website (NASA, 2022). The yearly mean SST was calculated per grid cell using ArcGIS Pro. Both ODBA and SST data were coupled based on the temperature similarities. Finally, the mean potential horizontal swimming activities maps were generated using R. The prediction of the future swimming activity of blue sharks involved using SST prediction data from the sixth phase of the Coupled Model Intercomparison Project (CMIP6) based on the climate scenario of 4 times the current amount of CO₂ in the atmosphere. The predicted mean ODBA obtained was coupled with the predicted SST based on temperature similarities, and the resulting data were plotted in R.

4. Results

4.1 Blue sharks' overall dynamic body acceleration and thermal performance curve

The processing of environmental and acceleration data from the eleven blue sharks tagged around Faial Island showed that the blue sharks' activities took place in water temperatures varying from 10 °C to 22 °C, with an overall body dynamic acceleration ranging from 0.03 g to 0.66 g (g-force) listed in Table 5. As shown in Figure 11, the thermal performance curve (in blue colour) suggests that the blue sharks studied on the fine-scale tolerated temperatures from 10 °C to 22 °C.

The spike on the curve represents the optimal temperature at which the blue sharks were the most active (20.86 °C). Furthermore, this thermal performance curve pattern indicated that the blue sharks' activity increased from 10 °C to 20.86 °C and decreased with temperatures above 20.86 °C. However, the present results did not show the minimum and maximum critical temperature values experienced by the sharks tagged.

Table 5: Statistic table of temperatures encountered and ODBA performed by the blue sharks during the fine-scale study. Island. Max_temp: maximum temperature, Min_temp: minimum temperature, Mean_temp: mean temperature, Max_odba: Maximum ODBA, Min_odba: minimum ODBA, Mean_odba: mean ODBA.

| Max_temp | Min_temp | Mean_tep | Max_odba | Min_odba | Mean_odba |
|----------|----------|----------|------------|------------|------------|
| 22 | 10 | 16 | 0.66044292 | 0.03138498 | 0.30979981 |

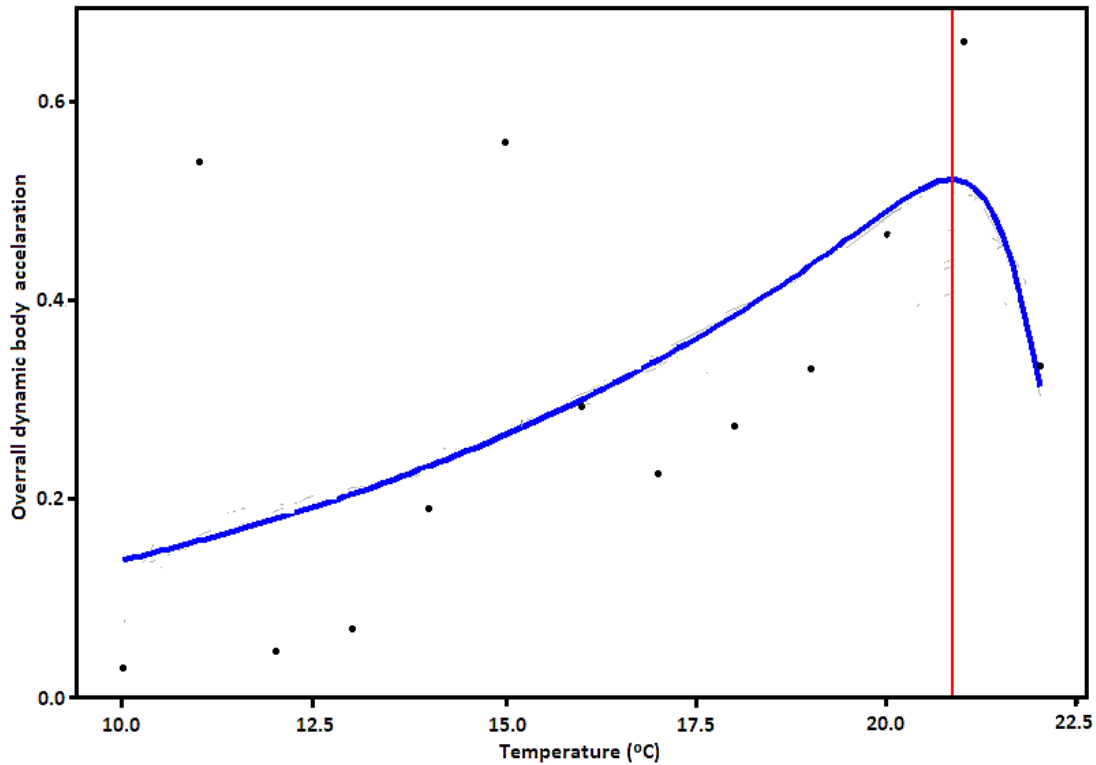


Figure 11: Thermal performance curve of blue sharks tagged fine-scale study around Faial Island (Azores Archipelago–Portugal).

4.2 Identification of the thermal preferences

For the identification of the thermal preference, the results showed that the eighteen blue sharks tagged with PSAT spent different times at a given temperature range according to the seasons, as shown in Figure 12. The results suggested that in spring, blue sharks mainly swam in the 15-22 °C temperature range, with the highest time (38%) spent between 16-18 °C. Over the whole summer season, they predominately swam in the temperature range of 14-22 °C and above 25 °C, with the longest time (23%) spent between 18-20 °C. Additionally, in the autumn season, they spent much of their highest time (25%) in temperatures above 25 °C, whereas in the winter season, they swam in the 12-25 °C temperature range, spending most of their highest time (43%) in the temperature range of 22-24 °C. In general, during the long-term study (2010, 2011 and 2017), blue sharks swam in water temperatures ranging from 15 °C to temperatures above 25 °C (Fig.13). These temperatures encountered by blue sharks were at different depths, with a prevalence at the upper 50 m depths (Fig.14).

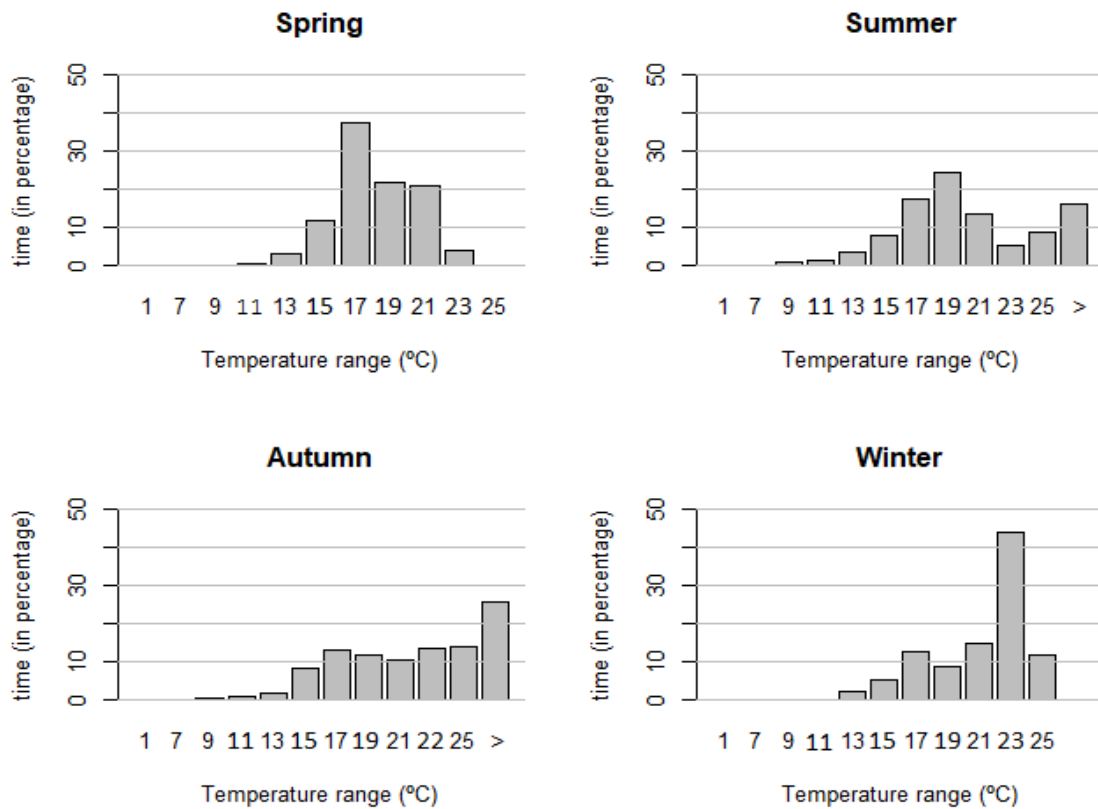


Figure 12: Percentage of time spent by blue sharks in the temperature range during the spring, summer, autumn and winter seasons.

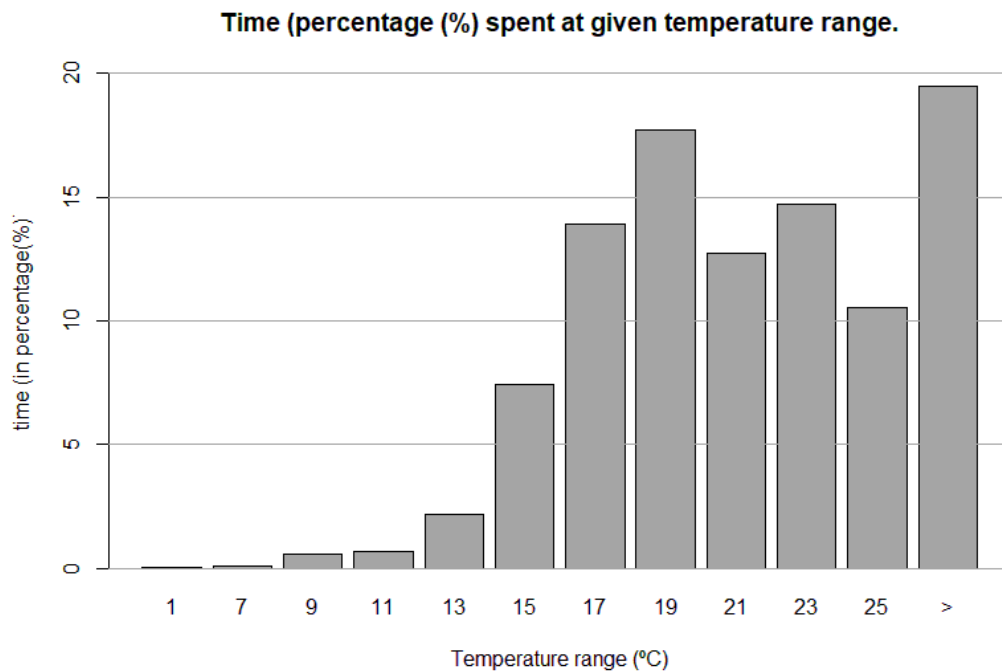


Figure 13: Percentage of average time spent by blue sharks in the temperature range in 2010, 2011 and 2017.

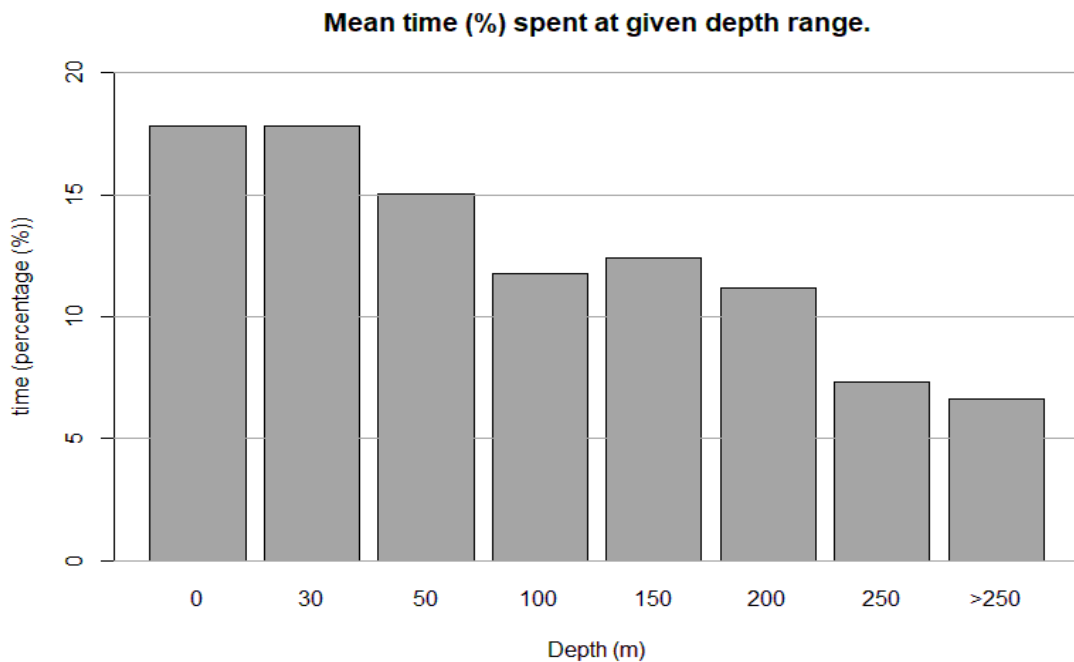


Figure 14: Average time spent by blue sharks at different depths in 2010, 2011 and 2017.

4.3 Current swimming performance maps

Based on the fine-scale swimming performances (ODBA) of blue sharks, it appeared that areas suitable for their activities on the water surface varied with the seasons. On average, during the three years (2010, 2011 and 2017), the Ocean surface (at 3 m) in the North Atlantic varied from 0 °C to 30 °C (Fig.15a). With the seasonal SST variation, it was noticed that during spring and winter seasons, the area with temperatures suitable for higher swimming activity was located from 30 °N to 60 °N, as shown in Figure 15b.

.Furthermore, during the summer and autumn, where SSTs were much higher than in the spring and winter, the areas favourable for blue shark swimming activity decreased by twice their extent compared to their extent in the spring and winter, concentrating on the Northern Atlantic. In other words, the area suitable for higher swimming activity shifts to high latitudes.

However, at depths of 100 m, where the Ocean temperature is lower than the temperature of surface waters, the results showed that almost the entire area was favourable for shark activity, except areas around the Gulf Stream and the western part of the North Equatorial Current (Fig.16a & 16b). Therefore, the area suitable for higher swimming activity appeared to vary with the seasons and ocean temperature.

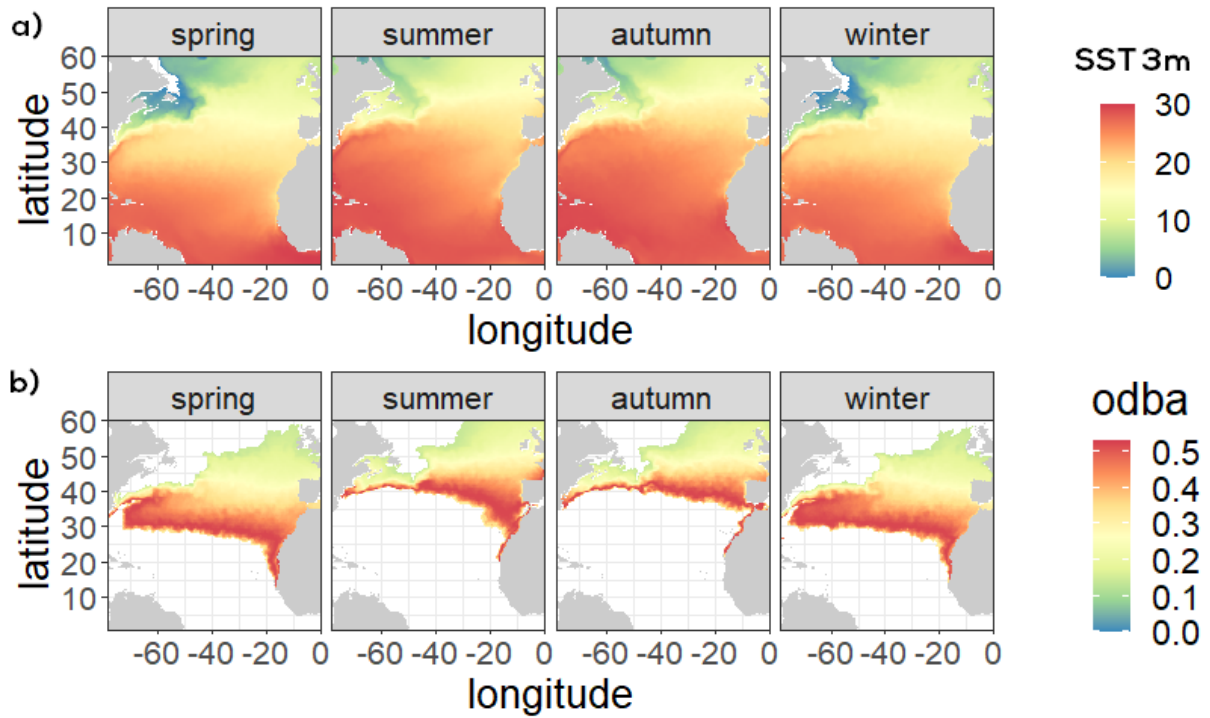


Figure 15: Present SST and swimming performance map. a) Mean SST (3 m) of 2010, 2011 and 2017; b) Area where blue sharks could be active at 3 m.

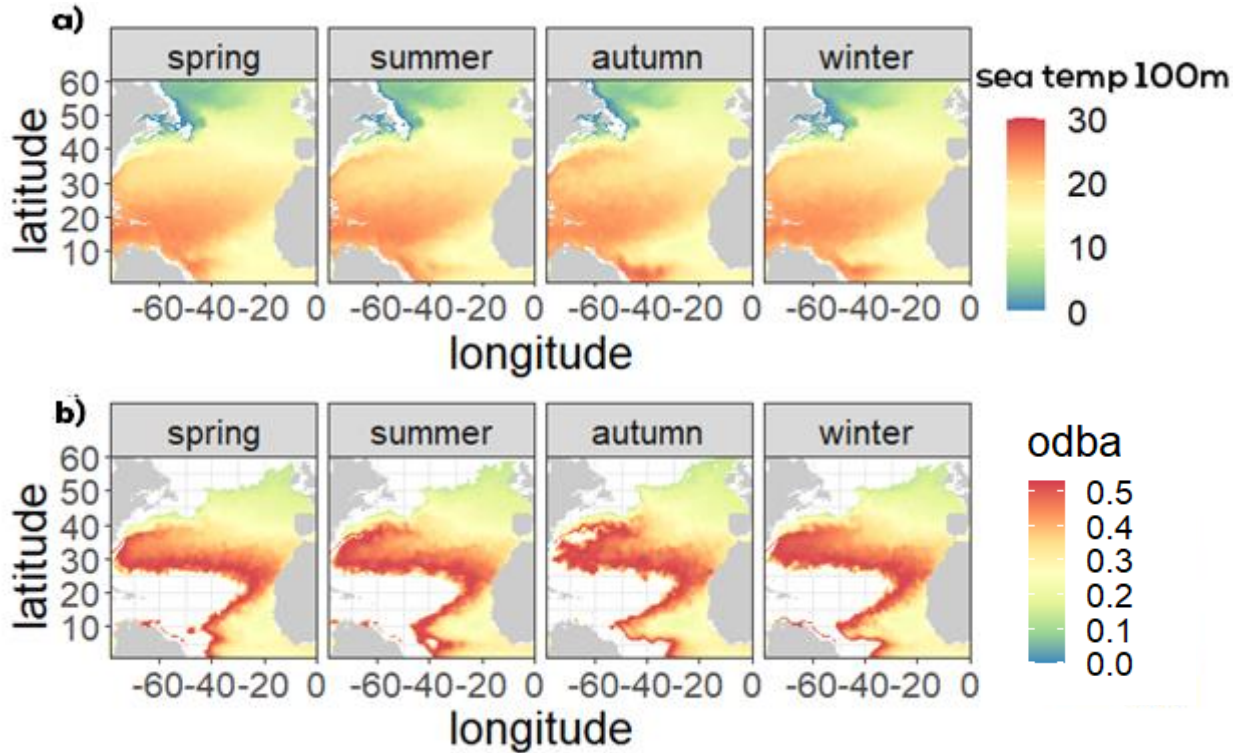


Figure 16: Present SST and swimming performance map c) Mean SST (100 m) of 2010, 2011 and 2017; d) Area where blue sharks could be active at 100 m.

4.4 Future swimming performance map

The comparison of the mean SST for the three years (2010, 2011 and 2017) (Fig.17a) and the one of 2050 (Fig.17b) showed a maximum value of 35 °C and a minimum of 10 °C; meanwhile, the mean SST of the three years had a maximum temperature of 30 °C with a minimum of 0 °C. After coupling the ODBA temperature values with the temperature values from the PSAT, it turned out that the favourable areas for higher swimming activity in 2010, 2011 and 2017 were located between 35 °N and 60 °N (Fig.17c). For future swimming performance map, the prediction map (2050) as shown in the Figure 17d, displayed a further shift of activity northward from 42 °N to 60 °N. These results indicated that if climate-induced ocean warming continues, blue shark activity will be affected by a northward shift.

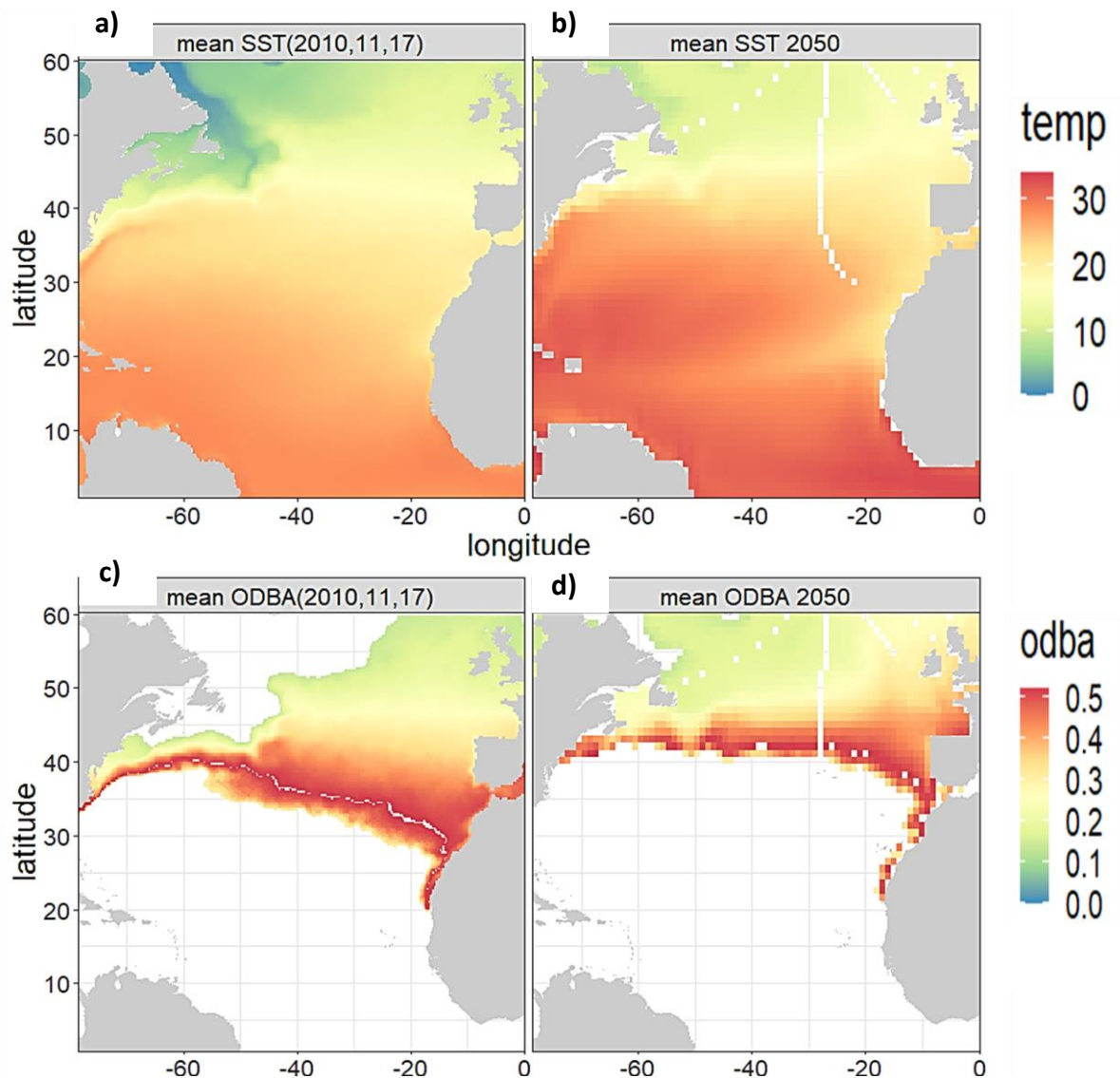


Figure 17: Future SST and swimming performance map. a) Present mean SST; b) Future mean SST; c) Present mean swimming activities d) future swimming activities.

5. Discussion

5.1 Swimming activity performance

The results of the TPC have revealed that the blue sharks studied had a swimming activity ranging from 10 to 22 °C, representing the thermal tolerance range. The optimal swimming performance was observed at 20.86 °C, defining the optimal swimming performance temperature. This result could suggest that blue sharks will be most abundant in water temperatures of 20.86 °C because they have higher performance at that temperature. If longline fishing boats target those higher-performance areas, blue sharks can be more susceptible to fishing (Campana et al., 2004). However, the TPC's critical maximum and minimum temperature were absent because the animals did not reach them. This absence could mean that the blue sharks studied avoided temperatures inconsistent with their physiological process. By looking at the thermal strategy of the shallow reef-dwelling epaulette shark (*Hemiscyllium ocellatum*), Nay et al., 2021 have similarly observed that highly variable thermal environments challenge marine ectotherms and assume behavioural strategies to avoid temperature extremes and seek thermal environments close to their preferred temperatures.

5.2 Temperature preference

Based on the fact that blue sharks have a wide range of temperature tolerance, it allows them to spend their free-ranging time at different temperature ranges. The temperature preferences study findings showed that blue sharks generally spend much of their time in temperatures ranging from 13 °C to over 25 °C. In their investigations on short-term movements and diving behaviour of blue sharks tracked by satellite in the North-East Atlantic Ocean, Queiroz et al. (2010) found similar results. They reported that blue sharks occupied a broad vertical habitat, ranging from the surface to depths of several hundred metres, with the water temperature ranging from 10.6 to 24.6°C. Also, many other researchers, such as Musyl et al. (2011), Rochman et al. (2021) and Howey et al. (2022), respectively found temperatures ranging from 9.4 to 26.9 °C, 9°C to 26 °C and from 7.7 °C to 22.5 °C. Likewise, Dulvy et al. (2014), in their studies of blue sharks, found similar results where the preferred temperature of blue sharks ranged from 12 to 20°C.

One possible explanation for the temperature variations experienced by the blue sharks is that, as their muscles follow water temperature, they come to warm waters to recover the heat lost at depth before the muscle cools down due to the deep water temperature (Carey & Gibson,

1987). Andrzejczek et al. (2018) also explained that these temperature variations in large marine ectotherms were due to the movement through the water column to maintain a thermal range required for survival. These types of blue sharks' activities at different temperatures have been described as thermoregulatory strategies by Carey et al. (1990). Indeed, each fish has a "preferred" temperature, i.e. a range of temperatures favourable to its life, above and below which it cannot survive, called minimum and maximum critical temperature. Outside these temperatures, the metabolism of the fish changes, causing them to limit their movements so as not to expend energy and to suffer significant stress (Savoiepeche, 2017).

However, the authors Meekan et al. (2015) used another approach to explain this behaviour of blue sharks. According to them, this variety of temperatures experienced by blue sharks might be because these marine predators of tropical waters with high metabolic rates have to cope with an oligotrophic ecosystem, where prey is poorly distributed. To survive in these environments, they must be cost-effective foragers and maintain their body temperature within an optimal range. This suggests that the migratory movements of blue sharks are not only driven by water temperature but also by prey availability (Nakano & Seki, 2003). By studying the range of depths where blue sharks spend most of their time, it was found that they dive from the surface to depths greater than 250 m in the Ocean, with most of the time spent at depths ranging from the ocean surface to 50 m depths. Many researchers have revealed similar results from studying the vertical diving behaviour of blue sharks. For instance, Stevens et al. (2010), in their study about satellite tagging of blue sharks and other pelagic sharks of Eastern Australia, got similar results. They showed that blue sharks have a regular diving behaviour from surface waters to depths of about 1,000 m, with 35–58% of their time spent above 50 m.

Other research conducted by other researchers, such as Queiroz et al. (2010), showed that the blue sharks used much of the available water column but more often occupied the surface layers, spending at least 50% of their time between the surface and 20 m depth. Carey et al. (1990) and Watanabe et al. (2021) explained that this behaviour was a hunting tactic in response to prey distribution and behavioural thermoregulation. Nonetheless, these limited movements of blue sharks in a very narrow range of the water column in the upper mixed layer could also be associated with mating (Howey et al., 2022). By coupling the thermal performance curve and the temperature preferences results, it was deduced that the optimal thermal niche for the blue shark was around 18 °C to 21 °C. Both preferred depth (upper 50 m) and optimal thermal niche found indicated that blue sharks usually stay near the water surface, where they may be subjected to a high accidental catch rate (Campana et al., 2004).

5.3 Current and future swimming activity map

The swimming activity map expressing horizontal temperature distribution suitable for blue sharks' higher swimming activity showed a seasonal variation. The analysis showed that, as the seasonal SST varies, the area with temperatures ideal for higher swimming activity was located between 30 °N to 60 °N during the spring and winter seasons. And for the summer and autumn, where the SST was much higher, the surface waters likely to be favourable for blue shark activity halved in spring and winter, concentrating in the Northern Atlantic Ocean. This variation of the surface area favourable to shark activity from the Equator to the more northerly regions of the Atlantic Ocean and vice versa could be explained at various levels. One possible explanation for this observation is that blue sharks spend most of their time at the surface of the Ocean, which offers a favourable temperature for their activities than the deep waters. This forces them to migrate to surface waters, allowing them to swim better and regulate their body temperature. That observation was made by Hillyer & Silman (2010), explaining that Climate change induces a modification of distribution ranges since species adapt their distribution according to their physiological tolerance to changing environmental conditions.

Overall, in this study, the current swimming activity map (2010, 2011 and 2017) and the future swimming activity map (2050) showed that the location of blue shark activity varied with ocean temperature. After comparing both maps, a Northward shift in blue shark activity has been noticed. This remark was also made by Chapman (2019), explaining that; when water temperatures rise, it is likely that animals move their range polewards to stay comfortable. In the same way, many other researchers, such as Hillyer & Silman (2010), stated that marine fishes and invertebrates would tend to shift their distributions to higher latitudes and/or deeper depths where the temperature is favourable for their activities. That observation made by Hillyer & Silman (2010) validates our results (Fig.18), suggesting that, on average, deeper waters (100 m) provide more surface area for shark activity than surface waters which often experience temperatures beyond the thermal range tolerated by blue sharks.

Indeed, the warmer waters affect directly (A. Clarke & Fraser, 2004) and indirectly ectothermic shark behaviour (Climate, 2015). The direct effect of ocean warming on ectothermic sharks is that it interferes in their biochemical reactions and energy metabolism (A. Clarke & Fraser, 2004), allowing them to assume some function such as behavioural thermoregulation (Carey *et al.*, 1990) or pushing them to use of microhabitats to avoid high temperatures (Dell *et al.*, 2014). The indirect effect of warmer waters is disturbing the sharks' prey's location (Climate, 2015). As the water warms, many sharks' prey are easily affected by

the water temperature; these prey move towards the poles, causing the sharks to follow them (Kanski, 2015). However, given the long generation time of elasmobranchs, a genetic adaptation of thermal performance may not keep pace with climate change in many species (Lear *et al.*, 2019).

6. Conclusions and recommendations

The present study attempted to identify the thermal preference of free-ranging blue sharks and how ocean temperature may affect their swimming performance and spatial distribution. The use of accelerometer tags has allowed determining that the ODBA ranged from 0.03g to 0.66g, with temperatures varying from 10 °C to 22 °C, where the optimal temperature was 20.86 °C. The data from the PSAT revealed that the temperature crossed by the blue sharks was from 1 °C to 25 °C and above, with a variation of time spent at various temperature ranges and little time spent at temperatures below 13 °C and most time above that temperature. On average, their preferred temperature (where they spent the highest time) was from 19 °C to 20 °C and above 25 °C. Both preferred temperature and optimal swimming performance temperature coupled gave a thermal niche between 18 °C and 21 °C.

On the other hand, it appears that the areas favourable for proper swimming activity varied with the season and the blue sharks spent much time at the surface of the water (upper 50m), experiencing different temperatures with a variation in swimming performance. These results indicated that the preferred depth and thermal niche of blue sharks do not protect them from the risk of being fished. Moreover, with climate change, the present study showed that the areas favourable to higher swimming activity will become more concentrated in the high latitudes by 2050. This study gave an insight into how the blue shark might behave in the face of climate-induced ocean warming.

However, to better understand and explain how the blue shark responds to temperature changes, the physiological process involved in regulating body temperature should be considered and studied in more detail to assess the reactions underlying this regulation and to evaluate the effect of temperature on temperature these reactions. Furthermore, as the temperature is not the only Ocean physical parameter affecting blue sharks, fully understanding the impact of the changes in environmental conditions will require considering other parameters such as oxygen, chlorophyll and salinity. In future research, it would also be interesting to create the future climate conditions in the laboratory to make simulations and determine the real impact climate change could have on sharks' behaviour, similarly to the 'mega-flume' seagoing swim-tunnel respirometer used by Payne *et al.* (2015). From the above, one can say that knowing how sharks will behave in the face of climate change will not directly save them but rather raise the alarm to continue to learn about the consequences of climate change and adopt resilient behaviour to mitigate global warming.

7. References

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Appendix

The following tables show partials or complete data used to perform the above analysis.

Appendix 1: Table of time spent at different depths (TAD) by the blue sharks tagged with PSAT.

| Depth (meter) | TAD |
|------------------|----------|
| 0 | 0.628602 |
| 30 | 0.628154 |
| 50 | 0.530095 |
| 100 | 0.415007 |
| 150 | 0.437364 |
| 200 | 0.394501 |
| 250 | 0.258606 |
| > 250 | 0.234103 |

Appendix 2: Table of time spent at different temperature ranges (TAT) by the blue sharks tagged with PSAT.

| Temperature (°C) | TAT |
|---------------------|----------|
| 1 | 0.000294 |
| 7 | 0.006485 |
| 9 | 0.035348 |
| 11 | 0.045243 |
| 13 | 0.140779 |
| 15 | 0.478442 |
| 17 | 0.899014 |
| 19 | 1.142055 |
| 21 | 0.821175 |
| 23 | 0.950771 |
| 25 | 0.679759 |
| 26 | 1.258394 |

Appendix 3: Table of the overall dynamic body acceleration (rescaled to 1) performed at different temperature ranges by the blue sharks tagged the accelerometer tags.

| temp | odba_resc |
|-------------|------------------|
| 10 | 0.031939 |
| 11 | 0.539953 |
| 12 | 0.045558 |
| 13 | 0.070829 |
| 14 | 0.196094 |
| 15 | 0.557749 |
| 16 | 0.312945 |
| 17 | 0.313523 |
| 18 | 0.224622 |
| 19 | 0.297904 |
| 20 | 0.427323 |
| 21 | 0.649488 |
| 22 | 0.322601 |

Appendix 4: Table (partial table) of the mean sea surface temperature data (at 3 m) for 2010, 2011 and 2017, downloaded from the NASA OceanColor website (NASA, 2022).

| long | lat | mean_sst |
|-------------|------------|-----------------|
| -79.875 | 59.875 | 1.513693 |
| -79.625 | 59.875 | 1.569636 |
| -79.375 | 59.875 | 1.6438 |
| -79.125 | 59.875 | 1.696473 |
| -78.875 | 59.875 | 1.803858 |
| -78.625 | 59.875 | 2.009394 |
| -78.375 | 59.875 | 2.264694 |
| -78.125 | 59.875 | 2.452582 |
| -77.875 | 59.875 | 2.534807 |
| -77.625 | 59.875 | 2.556898 |
| -77.375 | 59.875 | 2.530487 |
| -77.125 | 59.875 | 0 |
| -69.875 | 59.875 | 0 |
| -69.625 | 59.875 | 0.973195 |
| -69.375 | 59.875 | 0.951566 |
| -69.125 | 59.875 | 0.89026 |
| -68.875 | 59.875 | 0.79235 |
| -68.625 | 59.875 | 0.573037 |
| -68.375 | 59.875 | 0.39024 |

Appendix 5:Table (partial table) of the mean sea surface temperature data (at 100 m) for 2010, 2011 and 2017, downloaded from the NASA OceanColor website (NASA, 2022).

| long | lat | mean_sst |
|-------------|------------|-----------------|
| -69.375 | 59.875 | 0 |
| -69.125 | 59.875 | 0 |
| -68.875 | 59.875 | -0.3924 |
| -68.625 | 59.875 | -0.41522 |
| -68.375 | 59.875 | -0.416 |
| -68.125 | 59.875 | -0.38576 |
| -67.875 | 59.875 | -0.35485 |
| -67.625 | 59.875 | -0.34833 |
| -67.375 | 59.875 | 0 |
| -67.125 | 59.875 | 0 |
| -66.875 | 59.875 | -0.21494 |
| -66.625 | 59.875 | -0.24068 |
| -66.375 | 59.875 | -0.27763 |
| -66.125 | 59.875 | -0.31396 |
| -65.875 | 59.875 | -0.34012 |
| -65.625 | 59.875 | -0.34574 |
| -65.375 | 59.875 | -0.32675 |
| -65.125 | 59.875 | 0 |
| -64.875 | 59.875 | 0 |
| -64.625 | 59.875 | 0 |
| -61.125 | 59.875 | 0.057229 |
| -60.875 | 59.875 | 0.477315 |
| -60.625 | 59.875 | 1.177163 |
| -60.375 | 59.875 | 2.197176 |
| -60.125 | 59.875 | 3.146717 |
| -59.875 | 59.875 | 3.653645 |
| -59.625 | 59.875 | 3.82929 |
| -59.375 | 59.875 | 3.898487 |
| -59.125 | 59.875 | 3.958614 |

Appendix 6: Table (partial table) of mean sea surface temperature forecast data (at 0 m) for 2050, downloaded from the sixth phase of the Coupled Model Intercomparison Project (CMIP6), based on the 4 xC02 climate emission scenario.

| long | lat | Pred_SST_2050 |
|-------------|------------|----------------------|
| -68.875 | 59.875 | -0.3924 |
| -68.625 | 59.875 | -0.41522 |
| -68.375 | 59.875 | -0.416 |
| -68.125 | 59.875 | -0.38576 |
| -67.875 | 59.875 | -0.35485 |
| -67.625 | 59.875 | -0.34833 |
| -67.375 | 59.875 | 0 |
| -67.125 | 59.875 | 0 |
| -66.875 | 59.875 | -0.21494 |
| -66.625 | 59.875 | -0.24068 |
| -66.375 | 59.875 | -0.27763 |
| -66.125 | 59.875 | -0.31396 |
| -65.875 | 59.875 | -0.34012 |
| -65.625 | 59.875 | -0.34574 |
| -65.375 | 59.875 | -0.32675 |
| -65.125 | 59.875 | 0 |
| -64.875 | 59.875 | 0 |
| -64.625 | 59.875 | 0 |
| -64.375 | 59.875 | 0 |
| -64.125 | 59.875 | 0 |
| -63.875 | 59.875 | 0 |
| -63.625 | 59.875 | -0.5338 |
| -63.375 | 59.875 | -0.48054 |
| -63.125 | 59.875 | -0.38627 |
| -62.875 | 59.875 | -0.32844 |

