

**Bruno Miguel Monteiro Saraiva**

**The influence of the Sound scattering layers on the  
vertical behaviour of two mesopelagic sharks**



**UNIVERSIDADE DO ALGARVE**

Faculdade de Ciências e Tecnologia

2021

**Bruno Miguel Monteiro Saraiva**

**The influence of the Sound scattering layers on the  
vertical behaviour of two mesopelagic sharks**

**Mestrado em Biologia Marinha**

**Supervisor:** Prof. Nuno Queiroz<sup>a</sup>

**Co-Supervisor:** Prof. David Abecasis<sup>b</sup>

<sup>a</sup> Centro de Investigação em Biodiversidade e Recursos Genéticos/Research Network in Biodiversity and Evolutionary Biology (CIBIO), Campus Agrário de Vairão, Rua Padre Armando Quintas, 4485-668 Vairão, Portugal

<sup>b</sup> Centro de Ciências do Mar/Centre of Marine Sciences (CCMAR), Universidade do Algarve, Campus de Gambelas 8005-139 Faro, Portugal



**UNIVERSIDADE DO ALGARVE**

## **Declaração de autoria de trabalho**

### **The influence of the Sound scattering layers on the vertical behaviour of two mesopelagic sharks.**

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

I hereby declare to be the author of this work, which is original and unpublished. Authors and works consulted are properly cited in the text and included in the list of references.

---

(Bruno Saraiva)

A Universidade do Algarve reserva para si o direito, em conformidade com o disposto no Código do Direito de Autor e dos Direitos Conexos, de arquivar, reproduzir e publicar a obra, independentemente do meio utilizado, bem como de a divulgar através de repositórios científicos e de admitir a sua cópia e distribuição para fins meramente educacionais ou de investigação e não comerciais, conquanto seja dado o devido crédito ao autor e editor respetivos.

The University of Algarve reserves the right, in accordance with the terms of the Copyright and Related Rights Code, to file, reproduce and publish the work, regardless of the methods used, as well as to publish it through scientific repositories and to allow it to be copied and distributed for purely educational or research purposes and never for commercial purposes, provided that due credit is given to the respective author and publisher.

---

(Bruno Saraiva)

## **Acknowledgements**

I would first like to thank my supervisor, Nuno Queiroz, for allowing me to fulfil a childhood dream of working with sharks and for the valuable knowledge he passed me throughout the last two years. I would also like to extend my sincere gratitude to my co-supervisor, Prof. David Abecasis, for introducing me to bio-telemetry during a replacement class of Marine Population Biology and for his willingness to help. A special thanks to the whole MOVE team for their friendship and, particularly, to Marisa Vedor and Ivo Costa, for all the help and patience. Also, to Luana Coelho and Diogo Costa, I must thank for all the companionship and good times during my stay in Porto.

To my family, friends, and my dog, Punk, for all the support that kept me going. To my mom, the strongest person I know, for all the sacrifices she made to allow me to pursue my dreams. To my father, which although his earlier departure always believed in me and showed how proud he was. To my girlfriend for always making me feel better. And, finally, to Cerci Barros, for enduring all my desperate calls for help. Thank you.

At last but not least, I would like to express my deepest appreciation to the Sci-Hub founder, Alexandra Elbakyan, for providing me the tools necessary to finish my thesis during this pandemic.

## Abstract

As apex predators, large sharks sustain the structure and function of marine communities. However, due to the ever-increasing fishing pressure and their slow life-history traits, shark populations have drastically declined in the last decades. Thus, improved knowledge on shark movements is crucial to implement effective management actions to prevent biodiversity loss and the disruption of marine ecosystems. Vertical patterns of apex predators have regularly been associated with foraging behaviours, yet the direct connection with prey's vertical distribution and availability is often missing. In the open ocean, large aggregations of zooplanktonic and micronektonic organisms produce two unique acoustical signatures known as sound scattering layers (SSLs), believed to be an essential food source for oceanic predators. The present study uses pop-up satellite archival transmitters data of 22 blue (*Prionace glauca*) and 17 shortfin mako sharks (*Isurus oxyrinchus*), tracked within the North Atlantic Ocean, to assess the SSLs influence on these species' diel vertical migrations (DVM) and foraging patterns. The sharks' vertical patterns followed the SSLs diel migrations, commonly exhibiting surface-oriented behaviour when daytime micronekton concentrations at the shallow scattering layer (SSL) were higher compared to the upper deep scattering layer (DSL). Also, both species seemed to use the SSLs as foraging grounds, yet, while the mako shark appeared to target non-migrant or semi-migrant prey at the DSL, the blue shark generally favoured higher micronekton concentrations. Nevertheless, temperature and oxygen levels limited the extent of the vertical movements and impact the time spent at depth, sometimes preventing the animals from reaching the DSL. Thus, considering the ongoing expansion of the oxygen minimum zones, some predators might lose access to highly energetic prey and subsequently decrease their fitness. The SSLs showed to affect the sharks' vertical range and time spent at epipelagic waters, revealing a potential use to detect regions with increased fishing risk.

## Resumo

Como predadores de topo, os tubarões mantêm a estrutura e funcionamento das comunidades marinhas, sendo que a sua remoção pode levar a graves consequências ecológicas. No entanto, devido à sobrepesca e às características lentas da história de vida destes animais, as populações de tubarões têm vindo a decrescer drasticamente nas últimas décadas. Assim sendo, a melhoria do conhecimento de como e por que razão estes animais se movem é crucial para a implementação de estratégias de conservação eficazes de maneira a prevenir a perda de biodiversidade e a rutura dos ecossistemas marinhos. A telemetria de satélite e a crescente disponibilidade de dados ambientais de deteção remota, têm vindo a permitir a ligação entre movimento animal e o ambiente físico envolvente em zonas remotas do oceano, possibilitando a compreensão de comportamentos complexos a grandes escalas espaço-temporais.

Os movimentos verticais de predadores de topo têm sido habitualmente associados a comportamentos de procura de alimento, contudo a relação direta com a distribuição vertical e disponibilidade das presas encontra-se geralmente em falta. No oceano aberto, grandes aglomerações de organismos zooplancónicos e micronectónicos dão origem a duas zonas diferenciadas de reflexão acústica denominadas “sound scattering layers” (SSLs), uma zona superior localizada na região epipelágica usualmente referida como “shallow scattering layer” (SSL) e uma zona profunda habitualmente estabelecida no domínio mesopelágico intitulada de “deep scattering layer” (DSL). Uma vez que a DSL está normalmente dividida em camadas, cada uma compreendendo organismos de espécies diferentes e em fases de desenvolvimento distintas, a camada superior da DSL é referida como “upper deep scattering layer” (UDSL) e a inferior como “lower deep scattering layer” (LDSL). Uma parte significativa dos organismos que compõem a DSL alimentam-se entre o pôr e o nascer do sol no domínio epipelágico, formando uma SSL mais densa durante este período. Acredita-se que os organismos ao realizar este comportamento, designado como migração vertical diária (MVD), i.e., residir em águas profundas durante as horas de luz e procurar alimento no domínio epipelágico durante a noite, maximizam as suas probabilidades de sobrevivência ao evitar predadores visuais. No entanto, MVD está presente desde os níveis tróficos mais baixos até aos predadores de topo, sendo considerado o maior deslocamento diário de biomassa no planeta. Uma vez que as SSLs formam uma fonte de alimento essencial no oceano aberto, não seria surpreendente que predadores de topo mudassem o seu comportamento vertical em

resposta das migrações diárias dos organismos residentes nestas camadas. O presente estudo usa dados de 22 tintureiras (*Prionace glauca*) e 17 tubarões anequim (*Isurus oxyrinchus*), seguidos no oceano norte atlântico com “pop-up satellite archival transmitters” (PSAT), e modelos ambientais providenciados pelo “Copernicus Marine Environment Monitoring Service” (CMEMS) com o objetivo de investigar a influencia das SSLs nos padrões de MVD e comportamentos associados à procura de alimento destas duas espécies de tubarões intensivamente exploradas no oceano atlântico.

Os padrões verticais das duas espécies demonstraram acompanhar as migrações diárias dos organismos residentes das SSLs. Comportamentos orientados para a superfície, apenas detetados na zona de convergência entre a corrente norte atlântica e a corrente do labrador (ZCCNA-CL) e na zona de oxigénio mínimo (ZMO) do oceano Atlântico tropical leste, mostraram estar geralmente relacionados com concentrações de micronecton diurnas na SSL superiores às da UDSL. No entanto, um dos tubarões anequim foi observado a realizar um comportamento orientado para a superfície dentro da ZOM durante condições normais da distribuição do micronecton, i.e., concentrações diurnas de micronecton elevadas nas zonas profundas e baixas na SSL. Contrariamente, padrões de DVM regulares ou orientados para a profundidade foram maioritariamente detetados em condições normais, porém a rotatividade entre estes revelou estar possivelmente relacionada com termorregulação comportamental. Tanto a tintureira como o tubarão anequim realizaram mergulhos tipo yo-yo, normalmente associados a comportamentos de procura de alimento, em proximidade com as SSLs, realçando a importância destas grandes aglomerações de organismos para a dieta destes dois predadores. Contudo, houve diferenças significativas no uso das SSLs entre as duas espécies. Enquanto a tintureira favoreceu predominantemente zonas com concentrações de micronecton superiores, o tubarão anequim alcançou frequentemente a DSL durante períodos de baixa concentração de micronecton, provavelmente tendo como alvo presas não migrantes ou semi-migrantes na DSL.

Variações na concentração de oxigénio dissolvido (OD) e na temperatura da água demonstraram limitar a extensão dos movimentos verticais e o tempo gasto em profundidade das duas espécies, por vezes impedindo os animais de alcançarem a DSL. No entanto, o tubarão anequim mostrou ser consideravelmente mais afetado por níveis baixos de OD enquanto a tintureira revelou ser mais sensível a mudanças de temperatura. Sendo ectotérmica, a tintureira está dependente da temperatura externa para se



termorregular. O tubarão anequim, pelo contrário, possui um sistema vascular de troca de calor que lhe permite manter a sua temperatura interna alguns graus acima da exterior. Esta adaptação, juntamente com a posição central do seu músculo locomotor aeróbico, não só lhe confere uma vantagem para explorar águas profundas como também aumenta o seu potencial para natação explosiva. Estas características dão, possivelmente, ao tubarão anequim, uma vantagem para explorar as SSLs mais profundas, mesmo durante períodos com menor abundância de presas. Contudo, estas capacidades são refletidas num consumo acrescido de oxigénio e elevadas necessidades energéticas.

Os resultados deste trabalho destacam a importância das SSLs como fonte de alimento para predadores oceânicos de topo e a sua influência no comportamento vertical destes animais. Posto isto, o modelo oceanográfico “Global Ocean Low and Mid Trophic Levels Biomass Hindcast”, fornecido pela Copernicus, é sugerido como uma potencial ferramenta para identificar regiões de maior suscetibilidade às pescas. Áreas com SSLs mais superficiais e com concentrações de micronecton diurnas na SSL superiores às da UDSL demonstraram aumentar o tempo que os tubarões passam em águas epipelágicas e diminuir a extensão vertical dos seus movimentos, aumentando, conseqüentemente, a sua exposição à pesca pelágica. Além disso, considerando a atual expansão das ZOMs, presas mesopelágicas/batipelágicas tolerantes à hipóxia poderão encontrar refúgio dos seus predadores em águas profundas obrigando estes animais a modificarem a sua dieta. Subseqüentemente, a perda do acesso a estas presas poderá afetar o fitness dos predadores e aumentar a sua suscetibilidade à sobrepesca.

# Index

<b>General Introduction</b> .....	1
<b>Sharks' ecological role and conservation status</b> .....	1
<b>Animal tracking</b> .....	2
Importance of tracking studies .....	2
Historical review.....	3
<b>Sound scattering layers</b> .....	5
<b>Shark movements</b> .....	7
Vertical movements .....	8
<b>Studied species</b> .....	9
Vulnerability to fisheries.....	9
General biology and ecology.....	10
<b>Study objectives</b> .....	12
<b>References</b> .....	12

## **The influence of the sound scattering layers on the vertical behaviour of two mesopelagic sharks**.....21

<b>1 Introduction</b> .....	23
<b>2 Materials and Methods</b> .....	25
2.1 Tagging.....	25
2.2 Location estimates.....	25
2.3 Environmental Data.....	26
2.4 Behavioural analysis.....	27
2.4.1 Percentage of time within epipelagic waters .....	28
2.4.2 Diel vertical behaviour .....	28
2.4.3 Diving behaviour.....	28
2.4.4 Maximum depth model.....	29
<b>3 Results</b> .....	30
3.1 Sound scattering layers.....	30
3.2 Percentage of time within epipelagic waters .....	32
3.3 Diel vertical behaviour .....	32
3.4 Diving behaviour.....	33
3.5 Model results.....	37
<b>4 Discussion</b> .....	38

4.1	Diel behaviour and foraging patterns .....	38
4.2	Shark conservation in a changing ocean.....	44
<b>5</b>	<b>Conclusion and future work .....</b>	<b>47</b>
<b>6</b>	<b>References.....</b>	<b>47</b>
<b>Annexes</b>	<b>.....</b>	<b>57</b>
<b>Supporting Tables</b>	<b>.....</b>	<b>57</b>
<b>Supporting Figures</b>	<b>.....</b>	<b>58</b>

## List of Tables

<b>Table 3.1</b> Summary data for satellite tagged Blue and mako sharks. F, female; M, male. Stars mark individuals with retrieved archival data. Open, open ocean; OMZ, oxygen minimum zone; Front, North Atlantic Current-Labrador Current convergence zone .....	31
<b>Table 3.2</b> Maximum depth model summary. ....	38
<b>Table A1</b> Summary of TAD models. Models' intercepts are not represented.....	57
<b>Table A2</b> Summary of time weighted mean depth models. Models' intercepts are not represented. ....	57
<b>Table A3</b> Summary of layers' distance models. Models' intercepts are not represented. ....	57
<b>Table A4</b> Summary of change point models .....	58

## List of Figures

**Figure 3.1** Daytime and nighttime TAD time series. Dotted lines represent the three sound scattering layers coloured and sized according to the micronekton concentration. Dot size is directly proportional to micronekton concentrations..... 33

**Figure 3.2** Daytime and nighttime maximum depth time series. Lines represent the three sound scattering layers coloured according to the micronekton concentration. Maximum depths are expressed as points colour-coded by species (blue - *Prionace glauca*, red – *Isurus oxyrinchus*). .....34

**Figure 3.3** One-week interval from the archival time series of three individuals. Dashed lines represent the smoothed depth of the three sound scattering layers. Top stripes are coloured according to the micronekton concentration at each layer, stripes' arrangement corresponds to the scattering layers' order. Grey shades indicate nighttime obtained via *suncalc* R package. Dive profiles are colour-coded by species (blue - *Prionace glauca*, red – *Isurus oxyrinchus*).....36

**Figure 3.4** Change point model of *Prionace glauca* (blue shark) and *Isurus oxyrinchus* (mako shark). Blue lines represent the change point posterior density for each chain. Fit lines are represented in grey with the respective quantiles delimited by dashed red lines. Bottom-right plots show the expected values from the posterior predictive distribution. Top-right plots display the different samples from the posterior predictive distribution. ....37

**Figure A1** Boxplot of micronekton concentrations experienced by the tracked individuals. Boxes are colour-coded by species (blue - *Prionace glauca*, red – *Isurus oxyrinchus*). Daytime and nighttime are represented by light and dark colours, respectively.....58

**Figure A2** Shark M12 daytime and nighttime TAD time series. Dotted lines represent the three sound scattering layers coloured and sized according to the micronekton concentration. Dot size is directly proportional to micronekton concentrations. ....59

**Figure A3** Two-weeks interval from shark M6 archival time series. Dashed lines represent the smoothed depth of the three sound scattering layers. Top stripes are coloured according

to the micronekton concentration at each layer, stripes' arrangement corresponds to the scattering layers' order. Grey shades indicate nighttime obtained via suncalc R package. ...60

**Figure A4** Spearman's correlation matrix. Circles highlight Coefficients of  $\rho < -0.5$  and  $> 0.5$  .....61

**Figure A5** DHARMA residual diagnostic plots from the maximum depth model. ...61

# List of Abbreviations, Acronyms and Symbols

**AIC** - Akaike's Information Criterion

**ARGOS** - Advanced Research and Global Observation Satellite

**CITES** - Convention on International Trade in Endangered Species

**CMEMS** - Copernicus Marine Environment Monitoring Service

**CTCRW** – Continuous-Time Correlated Random Walk

**day.mnkc.LDSL** - daytime micronekton concentration at the lower deep scattering layer

**day.mnkc.UDSL** - daytime micronekton concentration at the upper deep scattering layer

**day.mnkc.UDSL** - daytime micronekton concentration at the upper deep scattering layer

**DO** - Dissolved Oxygen

**DSL** - Deep Scattering Layer

**DVM** - Diel Vertical Migration

**ETA** - Eastern Tropical Atlantic

**ETP** - Eastern Tropical Pacific

**GLM** - generalized linear models

**GPS** - Global Positioning System

**ICCAT** - International Commission for the Conservation of Atlantic Tunas

**IUCN** - International Union for Conservation of Nature

**LDSL** - Lower Deep Scattering Layer

**mnkc.epi** - concentration of epipelagic micronekton

**mnkc.LDSL** - micronekton concentration at the lower deep scattering layer

**mnkc.lhmmeso** - concentration of lower highly migrant mesopelagic micronekton

**mnkc.lmeso** - concentration of lower mesopelagic micronekton

**mnkc.lmmeso** - concentration of lower migrant mesopelagic micronekton

**mnkc.SSL** – micronekton concentration at the shallow scattering layer

**mnkc.UDSL** - micronekton concentration at the upper deep scattering layer

**mnkc.umeso** - concentration of upper mesopelagic micronekton

**mnkc.ummeso** - concentration of upper migrant mesopelagic micronekton

**MPAs** - Marine Protected Areas

**NAC-LCCZ** - North Atlantic Current-Labrador Current convergence zone

**nDVM** - normal Diel Vertical Migration

**night.mnkc.LDSL** - nighttime micronekton concentration at the lower deep scattering layer

**night.mnkc.SSL** - nighttime micronekton concentration at the shallow scattering layer  
**night.mnkc.UDSL** - nighttime micronekton concentration at the upper deep scattering layer  
**NOAA** - National Oceanic and Atmospheric Administration  
**OMZ** - Oxygen Minimum Zone  
**PDT** - Profile of Depth and Temperature  
**PSAT** - Pop-up Satellite Archival Tags  
**PTT** - Platform Transmitter Terminal  
**rDVM** - reverse Diel Vertical Migration  
**SSL** - Shallow Scattering Layer  
**SSLs** - Sound Scattering Layers  
**SST** - Sea Surface Temperature  
**UDSL** - Upper Deep Scattering Layer  
**zooc** - Concentration of zooplankton



# General Introduction

## Sharks' ecological role and conservation status

Apex predators sustain the structure and function of marine communities not only through direct predation but also by inducing expensive predator avoidance responses (risk effects). Thus, the loss of an apex predator and the subsequent absence of top-down control can lead to unpredictable and extensive cascading effects (Heithaus *et al.*, 2008; Estes *et al.*, 2011).

Sharks are among the most diverse and widespread predators in the contemporary oceans, being dispersed throughout the marine food webs both as apex and mesopredators. Moreover, large declines of great sharks worldwide have been linked to the increase of smaller bodied species and, consequently, to extensive ecological impacts (Ferretti *et al.*, 2010; Heupel *et al.*, 2014). For instance, it is believed that the decline of seven shark populations in North Carolina, USA, has led to the predatory release of the cownose ray. As a result, the expanding ray population's enhanced predation almost depleted the scallop fishery in this region (Myers *et al.*, 2007). On the other hand, large sharks' risk effects have been shown to play an equally significant role in the ecosystems' health. Furthermore, multiple studies have described an indirect relation between tiger shark (*Galeocerdo cuvier*) densities and seagrass meadows' conditions. The degradation of these pristine ecosystems is frequently the result of sea turtles and dugongs' exhaustive grazing activity. However, under the tiger shark presence, these herbivores are forced to change their foraging patterns, distributing their grazing pressure through safer but less productive environments (Heithaus *et al.*, 2007, 2014; Wirsing, Heithaus and Dill, 2007).

Sharks have slow life-history traits and low population growth rates, rendering them substantially less resilient to exploitation than the earlier-maturing and shorter-lived teleost species (Cortés, 2000; Cailliet, Musick and Simpfendorfer, 2005; Dulvy *et al.*, 2008, 2014). Additionally, rebound potentials estimated for billfishes and tunas range from 8 to 34% per year, whereas for sharks, estimations vary between 1 and 14%, with some shark species needing as much as four decades to fully recover from depletion (Au, Smith and Show, 2009). Nevertheless, total global shark mortality, including reported and unreported landings, discards, and shark finning, is estimated to be between 63 and 273 million sharks per year (Worm *et al.*, 2013). Pelagic sharks undergo long movements throughout the ocean-basin and/or exhibit site fidelity to shelf and open ocean habitats

(Queiroz *et al.*, 2019). As a result, they are frequently caught in open ocean fisheries, particularly in longline vessels targeting more lucrative species such as tunas and billfish. Although historically pelagic sharks were mostly caught as by-catch, shark retention rates have been increasing due to missing management regulations, growing international markets, and their highly prized fins (Camhi *et al.*, 2008; Dulvy *et al.*, 2014; Campana, 2016). Consequently, the global abundance of oceanic elasmobranchs has declined by 71% since 1970 due to an 18-fold increase in relative fishing pressure, raising the global extinction risk to the point that three-quarters of these species are threatened with extinction (Pacoureaux *et al.*, 2021).

Until recently, besides the shark finning prohibition, there were no international management plans for any shark species. Yet, over the last few years, this has been changing. Some species have now internationally catch limits in force, while others are entirely protected (Worm *et al.*, 2013; Campana, 2016; ICCAT, 2019). Nonetheless, sharks' management and conservation are far from great, mainly due to the lack of accurate information on sharks' populational parameters and spatial ecology (Sims, 2010; Worm *et al.*, 2013; Campana, 2016; Byrne *et al.*, 2017).

## **Animal tracking**

### **Importance of tracking studies**

Detailed knowledge of movements, behaviour, distribution patterns, and their respective drivers is essential for the sustainable management and conservation of commercially valuable species. However, monitoring highly mobile and wide-ranging species such as sharks might often be challenging (Hammerschlag, Gallagher and Lazarre, 2011; Hussey *et al.*, 2015; Dwyer *et al.*, 2019; Nandintsetseg *et al.*, 2019; Williamson *et al.*, 2019). Before animal tracking, only very coarse and basic fisheries-dependent data was available to identify potential migrations and putative fish stocks (Sims, 2010). Advances in tracking technologies have allowed an improved understanding of complex spatial and temporal behavioural dynamics, including daily and seasonal migrations (Sims *et al.*, 2005; Hueter, Tyminski and de la Parra, 2013; Lea *et al.*, 2015), size and sexual segregation (Klimley, 1987; Nakano and Stevens, 2008), and habitat preferences (Schaefer and Fuller, 2002; Queiroz *et al.*, 2012). Such information is not only crucial to implement effective management actions but also to predict future habitat displacements or losses. For example, Queiroz *et al.* (2019), combining satellite-tracked movements of

pelagic sharks and global fishing fleets, detected a considerable space-use overlap between two commercially valuable species (blue and shortfin mako sharks) and longline vessels associated with a considerable increase in fishing effort. Such findings were essential for the listing of the shortfin mako shark (*Isurus oxyrinchus*) on the appendix II of the Convention on International Trade in Endangered Species (CITES). Additionally, [Vedor et al. \(2021\)](#), using satellite tracking data, showed that the combining effects of decreasing dissolved oxygen at depth, high sea surface temperatures, and increased surface-layer net primary production substantially reduced the blue shark (*Prionace glauca*) maximum dive depths, which consequently increased its exposure to longline fisheries. Moreover, considering the ongoing ocean warming and the resulting expansion of the world's oxygen minimum zones (OMZ), [Vedor et al. \(2021\)](#) highlight the need for stronger fisheries controls to counteract the deoxygenation effects on shark catches.

## **Historical review**

Fish tagging goes back to at least the 1600s ([McFarlane, Wydoski and Prince, 1990](#)), yet only around the 1800s, tagging studies began to expand and comprising a broader range of species. First tagging techniques were relatively simple, consisting of capture-mark-recapture methods, which continued to be extensively used since then. Capture-recapture studies can give important insights into the animals' spatiotemporal movements and distribution, individual growth, or even exploitation levels. However, data collection is entirely dependent on the tags' retrieval during fishing operations, and the acquired information can only provide a rudimentary understanding of the animals' spatial ecology (i.e., what happened between release and capture locations remains unknown). Still, despite the limited information, these methods are low-cost and easy to employ ([Kohler and Turner, 2001](#); [Sims, 2010](#)).

During the mid-1950s, acoustic tracking was born, offering useful horizontal and vertical information on animal movements without the need for recapture. Typically, acoustic transmitters are small and can either be surgically implanted or externally attached to the animals. These devices emit high-frequency sound pulses that allow portable (active tracking) or stationary (passive tracking) acoustic receivers to detect and locate the acoustic tags ([Arnold and Dewar, 2001](#); [Sims, 2010](#); [Hussey et al., 2015](#); [Harcourt et al., 2019](#)). The detection range (radius) of the receivers is relatively small (<1000 m), which enables the recovery of fine-scale movement data but creates an obstacle for the study of highly mobile species in the open ocean. Hence, nowadays, acoustic research has been

primarily focused on coastal, estuarine, and freshwater ecosystems (Hussey *et al.*, 2015; Harcourt *et al.*, 2019).

A few years later, in the late 1970s, satellite tracking emerged, allowing data collection at exact times, over large spatiotemporal scales, without being dependent on fisheries returns. This technology was only possible thanks to the ARGOS (Advanced Research and Global Observation Satellite) system of satellites, which can locate an Argos platform transmitter terminal (PTT) attached to an animal anywhere on the planet whenever the PTT has surfaced for enough time (Sims, 2010). PTT's geographical position is determined through Doppler-shift calculations produced by Argos Data Collection and Location Service every time a satellite receives two or more signals. Nevertheless, since electromagnetic waves cannot propagate in saltwater and the accuracy of the position is dependent on the number of transmissions received by the satellite, for some shark species that rarely come and stay at the surface, PTTs might be less suitable (Sims, 2010; Hammerschlag, Gallagher and Lazarre, 2011). Archival tags (biologgers) were introduced in the 1990s, allowing to collect and store data on multiple physical parameters (e.g., depth, temperature, and light intensity) simultaneously at selected time intervals. However, as Capture-recapture tagging, this method was entirely dependent on fisheries returns (Arnold and Dewar, 2001). The solution to this problem came in the form of a hybrid electronic tag merging data-logging with satellite transmission. This externally attached tag, named pop-up satellite archival transmitter (PSAT), after a preprogrammed time, is automatically released from the animal, floats to the surface, and starts transmitting to the ARGOS receivers both its location and the summary data. High-resolution archival data can be obtained if the tag is physically recovered (Block *et al.*, 1998; Arnold and Dewar, 2001). Furthermore, based on light intensity data, the PSAT-tagged animal's daily positions can be determined employing the algorithms supplied by the tag's manufacturer (Arnold and Dewar, 2001; Sims, 2010; Hammerschlag, Gallagher and Lazarre, 2011). However, light-based position estimates can only provide accuracies of roughly 60 to 180 km (Bradshaw, Sims and Hays, 2007). Hence, to evaluate smaller-scale or higher-resolution horizontal movements, several studies still rely on PTTs (Hammerschlag, Gallagher and Lazarre, 2011).

Additionally, new electronic tags have been emerging due to the need for improved spatial accuracy of horizontal movements and reduce temporal gaps. For instance, although the positions determined via PTTs have a considerably higher resolution than

PSATs' light-based estimates, at best, PTTs' accuracy remains within 150m of the tag's actual position. In this sense, a new generation of Argos-linked tags containing a fastloc Global Positioning System (GPS) receiver was recently developed. The fastloc GPS technology enables faster acquisition of the satellite constellation for location fixing (in less than 80ms), yet the satellite ephemeris data still needs to be transmitted via Argos for its remote recovery. The fastloc GPS accuracy is substantially higher than the PTTs, with 95% of the positions determined via fastloc GPS occurring within 18m of the tag's actual location if up to 10 satellites are acquired for the calculations (Costa *et al.*, 2010; Sims, 2010; Hammerschlag, Gallagher and Lazarre, 2011).

Moreover, recent data logging-tags that combine multiple sensors have been used to derive animal trajectories through dead reckoning (Wilson, Shepard and Liebsch, 2008). By recording up to 14 different parameters in infra-second intervals, including a tri-axial accelerometer, these biologgers, often called "daily diary" tags, can provide accurate information on the animals' fine-scale movements, behaviour (i.e., identify/verify foraging attempts/success), energy expenditure, and physical environment over large spatiotemporal scales. Nevertheless, a disadvantage of "daily diary" tags is that most large fish do not return regularly to the same site, making it difficult to retrieve the tags. Thus, this promising technology may not yet be suitable for studying highly mobile species over large periods of time (Sims, 2010).

## **Sound scattering layers**

Similarly to light, sound waves are not homogeneously transmitted through space. Instead, during propagation, they are often scattered, reflected, or absorbed. In water, sound can spread for much greater distances than light, yet the ocean is far from a perfect acoustic medium. Sound waves are regularly scattered by suspended solids, biota, and entrained gas or simply converted to heat and absorbed. These effects generate singular acoustic signals that can be recorded by sonars or similar instruments (Simmonds and MacLennan, 2005).

The sound scattering layers (SSLs) were firstly described around the middle of the last century. Ever since, these unique acoustical signatures, created by the distinctive densities of marine organisms' body structures like swim bladders and lipid inclusions, have been reported at various depths and locations worldwide (Benoit-Bird and Au, 2004; Benoit-Bird, Dahood and Würsig, 2009; Hazen and Johnston, 2010; Ariza *et al.*, 2016).

Mesopelagic fish are believed to be the major components of the SSLs, yet several other zooplanktonic and micronektonic taxa inhabit these layers, including cephalopods, decapods, and euphausiids (Irigoién *et al.*, 2014; Ariza *et al.*, 2016; Bianchi and Mislan, 2016). These large aggregations of mesopelagic organisms are believed to be a vital food source for numerous oceanic macropredators inhabiting the open ocean (Norheim, Klevjer and Aksnes, 2016).

Two sound-reflecting regions are often observed in the ocean. One shallow scattering layer (SSL) present within the epipelagic region (0 – 200 m depth), and a wider deep scattering layer (DSL) established at the mesopelagic domain (200 – 1000 m depth). However, the latter is generally allocated into multiple strata, each comprising distinct species and developmental stages (Dietz, 1962; Hays, 2003; Ariza *et al.*, 2016). Moreover, a significant share of the organisms composing the DSL feeds between dusk and dawn at the epipelagic domain, forming a denser SSL during this period. This behaviour, named diel vertical migration (DVM), has been reported as the major biomass displacement on earth, occurring on a daily basis in every ocean (Klevjer, Torres and Kaartvedt, 2012; Ariza *et al.*, 2016). It is believed that organisms performing normal DVM (nDVM), i.e., residing in deeper waters during daylight hours and foraging in shallower waters at night (dusk ascent – dawn descent), maximize their survival rates by avoiding visual predators (Klevjer *et al.*, 2016). Nevertheless, less common DVM patterns, such as the reverse DVM (rDVM) (dusk descent – dawn ascent), have been described (Tarling *et al.*, 2001; Sims *et al.*, 2005). The percentage of migrant micronekton varies between regions, ranging from ~20%, in the Indian Ocean, up to ~90%, in the Eastern Pacific. Still, considering that, on average, roughly 50% of these animals exhibit DVM patterns, as much as 500 million tonnes of mesopelagic fish are believed to move across the water column every day (Klevjer *et al.*, 2016). Moreover, the DSL commonly displays faster descends than ascends, and the migration speed might vary according to the organisms performing DVM (Klevjer, Torres and Kaartvedt, 2012; Bianchi and Mislan, 2016).

Most organisms inhabiting the DSL are largely dependent on oxygen concentrations. Thus, when oxygen levels drop, both the size of the migrant portion and the DSL depth are expected to decrease. However, a substantial fraction of the DSL often remains in hypoxic conditions during the daytime. This permanence within poorly oxygenated waters might provide a refuge from large predators with superior oxygen requirements.

Under low oxygen concentrations, there is no other factor influencing the DSL vertical position. In oxygen-rich conditions, however, as turbidity, temperature, and chlorophyll concentration increase, the DSL depth decreases (Bianchi and Mislán, 2016; Klevjer *et al.*, 2016). Furthermore, the organisms inhabiting the DSL appear to move within a light range, avoiding high and low light thresholds. Hence, the DVM of the DSL is believed to follow a light comfort zone (Norheim, Klevjer and Aksnes, 2016).

## **Shark movements**

Animal movement results from the outcome of different biotic and abiotic factors, working over various temporal and spatial scales (Nathan, 2008; Nathan *et al.*, 2008; Sims, 2010). Movement usually implies extra energy expenditures and often increases the animal mortality risk. Therefore, each movement consists of a trade-off between benefits and costs (Fahrig, 2007). Highly mobile animals, such as pelagic sharks, are able to explore a wide range of habitats and typically exhibit extensive ocean-basin movements. For example, white sharks (*Carcharodon carcharias*) were observed performing trans-oceanic migrations linking South African and Australian populations (Bonfil *et al.*, 2005). Sharks' movements and habitat selection have been frequently associated to environmental conditions and foraging behaviour (Sims and Quayle, 1998; Nasby-Lucas *et al.*, 2009; Queiroz *et al.*, 2012; Williamson *et al.*, 2019). Still, many shark species have brain mass: body mass ratios overlapping the range for mammals and birds, thus exhibiting complex behaviours such as sexual and size segregation (Northcutt, 1977; Klimley, 1987).

Predators' movement patterns are strongly connected to prey distribution and availability (Sims, 2003). Hence, when food resources are unevenly distributed across the environment, these animals tend to aggregate over prey rich areas. Sharks, for instance, are known to create large aggregations over highly productive regions like frontal systems or prominent topographic features (Sims *et al.*, 2000; Worm, Lotze and Myers, 2003; Venegas *et al.*, 2011; Queiroz *et al.*, 2012; Miller *et al.*, 2015). The influence of prey availability and type on sharks' habitat selection can be explored using the optimal foraging theory, which assumes that animals choose their habitat based on the net energy gain regardless of the temperature regime (Sims, 2003). Nevertheless, several studies have shown that habitat selection is often more complicated. Animal movement is usually connected to ecological and physiological constraints. Thus, abiotic factors, such as temperature and oxygen concentrations, continuously affect sharks' behaviour (Wallman

and Bennett, 2006; Schlaff, Heupel and Simpfendorfer, 2014; Byrne *et al.*, 2019). For example, blue and shortfin mako sharks tracked throughout the North Atlantic Ocean displayed a confined thermal niche, yet the two species favoured the more productive regions within the niche boundaries (Queiroz *et al.*, 2016). Furthermore, the behavioural energetics hypothesis attempts to fill the optimum foraging theory gaps, suggesting that food and temperature play a shared role in the animals' movement patterns. In this sense, sharks might not only select the habitat with the highest net energetic value compared to others, but also perform energy-saving measures such as moving to optimal temperatures during non-feeding periods (Wildhaber and Crowder, 1990; Sims *et al.*, 2006).

## **Vertical movements**

Pelagic predators perform wide-ranging movements throughout the water column, which might change accordingly to environmental conditions and prey availability (Dagorn *et al.*, 2006; Campana *et al.*, 2011; Thorrold *et al.*, 2014). Moreover, like other marine organisms, predators regularly exhibit DVM. However, the processes underlying such behaviour often remain unclear (Pade *et al.*, 2009; Queiroz *et al.*, 2012; Bond *et al.*, 2015; Coffey *et al.*, 2017). As mentioned before, diel patterns are usually connected to predator avoidance responses, yet due to the relatively large body size of oceanic predators, such as tunas and sharks, predation avoidance is unlikely to be triggering DVM in these animals. Hence, DVM patterns of apex predatory species have regularly been associated with foraging or searching behaviours (Carey, Scharold and Kalmijn, 1990; Hays, 2003; Sims *et al.*, 2005; Andrews *et al.*, 2009; Queiroz *et al.*, 2012). Navigation and thermoregulation have also been suggested to explain the diel vertical movements observed in large predators. For instance, scanning the water column in search of chemical information or following the earth's magnetic gradients might provide valuable navigational cues (Carey, Scharold and Kalmijn, 1990; Klimley *et al.*, 2002). Predators can also dive into deep colder waters to reduce metabolic costs and swim near the surface to re-warm, maintaining an optimal temperature (Campana *et al.*, 2011).

Furthermore, focusing on the Lesser-spotted dogfish (*Scyliorhinus canicula*) diel behaviour, Sims *et al.* (2006) proposed that under the absence of significant predation levels, ectotherms increase their fitness by selecting an appropriate combination of thermal and foraging resources (bioenergetics hypothesis). On the contrary, Andrews *et al.* (2009) suggested that the ectothermic sixgill shark's (*Hexanchus griseus*) diel vertical patterns were strictly associated with the preys' vertical distribution (optimal foraging



theory). Additionally, several studies have described changes in sharks' DVM patterns among different habitats. For example, the porbeagle (*Lamna nasus*) and the basking shark (*Cetorhinus maximus*) exhibited rDVM in well-mixed waters, while in well-stratified waters, both sharks displayed nDVM (Sims *et al.*, 2005; Pade *et al.*, 2009). Regarding the basking shark, Sims *et al.* (2005) suggested that the variations in the observed DVM patterns might be connected to zooplankton predator-prey interactions resulting in the rDVM (i.e., reside in deeper waters at night and approach the surface during the day) of this specie's favoured prey. Interestingly, blue sharks tracked over a frontal system in the North Atlantic Ocean exhibited no apparent differences between day and night vertical distributions, remaining in epipelagic waters during both periods (Queiroz *et al.*, 2012).

Moreover, vertical movements of oceanic predators have commonly been associated with foraging events at the DSL. Dagorn, Bach and Josse, (2000) reported a clear relation between the bigeye tuna (*Thunnus obesus*) vertical movements and the SSLs, where tracked tunas generally swam within the first 100m (SSL depth) of the water column at night and dove roughly until 500m depth (DSL depth) during daylight hours. These animals also followed the dawn and dusk migrations of the organisms inhabiting the DSL. Yet, in a more recent study, the DSL depth revealed to be an irrelevant predictor of the bigeye tuna daytime swimming depths (Lam, Galuardi and Lutcavage, 2014). The characterization of the SSLs was formerly dependent on labour-intensive acoustic and net sampling methods restricted to relatively small areas (Dagorn, Bach and Josse, 2000; Sims *et al.*, 2005). Thus, the influence of these large aggregations of pelagic organisms on predators' vertical behaviour is still poorly understood. Nevertheless, besides the clear relationship observed in the bigeye tuna, associations with the SSLs have been proposed for other predatory species such as the white shark (Nasby-Lucas *et al.*, 2009), the shortfin mako shark (Sepulveda *et al.*, 2004), the scalloped hammerhead shark (*Sphyrna lewini*) (Spaet *et al.*, 2017) and the bigeye thresher shark (*Alopias superciliosus*) (Nakano *et al.*, 2003; Preti *et al.*, 2008).

## **Studied species**

### **Vulnerability to fisheries**

Blue and shortfin mako sharks, hereafter just mako shark, are the most caught pelagic shark species in the Atlantic Ocean, representing about 73% and 17% of total pelagic

shark catch between 1980 and 2005, respectively (Camhi *et al.*, 2008). Moreover, a recent study revealed that both species are aggregated within the highest potential fishing-risk zone in the North Atlantic Ocean, estimating a space use overlap with longline fisheries of 62% for the mako shark and 76% for the blue shark (Queiroz *et al.*, 2019).

Comparatively to other elasmobranchs, the blue shark has a relatively high fecundity, with a gestation period ranging from 9 to 12 months and average litter sizes of roughly 30 pups (up to 135) (Nakano and Stevens, 2008). Hence, this species has been considered to be reasonably resilient to the impacts of fishing pressure. Still, studies suggest a large population decline in the Northwest Atlantic Ocean since the mid-80s (Baum *et al.*, 2003; Hueter and Simpfendorfer, 2008). On the contrary, the mako shark has considerably slower life-history traits. Female mako sharks reach maturity at a late age, from 6 to 18 years (Campana, Marks and Joyce, 2005; Stevens, 2008). Moreover, this species gives birth to an average of 12 pups (from 4 to 25) after a gestation period of 15–18 months. After birth, females might rest another 18 months until the next reproductive event (Mollet *et al.*, 2000). Thus, making the mako shark remarkably vulnerable to overfishing.

Despite the high exploitation rates, the blue shark is currently recognized as near threatened by the International Union for the Conservation of Nature (IUCN) Red List (Rigby *et al.*, 2019b). Whereas the mako shark is recognized as globally endangered in the IUCN Red List (Rigby *et al.*, 2019a) and listed on CITES appendix II. Furthermore, the International Commission for the Conservation of Atlantic Tunas (ICCAT) has recently proposed annual blue shark catch limits of 39,102 t and 28,923 t, concerning the North and South Atlantic, respectively (ICCAT, 2019). Nevertheless, no agreement has yet been achieved regarding the mako shark (ICCAT, 2019), with current catches largely exceeding the quota recommended by ICCAT's scientific committee (ICCAT SCRS, 2020).

## **General biology and ecology**

Blue and mako sharks are two oceanic mesopelagic species, dispersed over tropical and temperate oceans, roughly from 60° N to 50° S, favouring higher latitudes (Compagno, Dando and Fowler, 2005; Nakano and Stevens, 2008; Stevens, 2010) and inhabiting from surface waters to at least 1000 m depth (Queiroz *et al.*, 2012; Queiroz unpublished). These species are highly migratory, performing extensive movements throughout the open ocean in response to environmental conditions and, possibly, to prey distribution and availability (Kohler and Turner, 2008; Stevens, 2010; Queiroz *et al.*, 2012, 2016, 2019;

Rogers *et al.*, 2015). Also, both these species are known to actively select regions with steep thermal gradients and/or high productivity (Lohmann, Lohmann and Endres, 2008; Rogers *et al.*, 2015; Queiroz *et al.*, 2016, 2019).

The blue shark is the most abundant and best-studied of all oceanic sharks (Nakano and Stevens, 2008). In the North Atlantic Ocean, the blue shark's population is considered panmictic (Kohler and Turner, 2008), yet there is a clear sexual and size segregation (Vandeperre *et al.*, 2014). Juvenile blue sharks are believed to remain in the nursery areas until they reach around 130cm of length, not engaging in the extensive migrations observed in adults until then (Nakano and Stevens, 2008; Stevens, 2010). Likewise, size and sexual segregation also occur with mako sharks but not as pronounced (Stevens, 2010).

As a member of the Carcharhinidae family, the blue shark is ectothermic, i.e., it cannot control its body temperature, being dependent on external temperatures to thermoregulate (Nakano and Stevens, 2008; Bernal *et al.*, 2012). Yet, this species supports wide-ranging temperatures from at least 7.2 to 27.2 °C (Queiroz *et al.*, 2012). On the contrary, the mako shark belongs to the Lamnidae family, possessing a vascular heat exchange system (*rete mirabile*), enabling it to keep its internal temperature about 7 to 10 degrees Celsius higher than the ambient conditions (endothermy) (Carey and Teal, 1969). Mako shark's thermal tolerance is not very different from the blue shark, supporting temperatures from at least 4.6 to 24.1 °C (Abascal *et al.*, 2011). However, differences become evident in both the frequency and duration of these species' vertical oscillations, with mako sharks being able to perform more frequent and prolonged excursions into deep cooler-waters (Bernal *et al.*, 2012).

Furthermore, similarly to tunas, lamnid sharks' red, aerobic locomotion muscle is positioned tight to the vertebral column and concentrated around the mid-body region, maintaining it at an optimum working temperature. This adaptation theoretically enables the mako shark to sustain a higher aerobic swimming metabolism and have an increased potential for burst swimming. These capabilities, combined with the fusiform body, and the thunniform propulsion method, set the mako shark among the fastest swimmers in the ocean (Bernal *et al.*, 2005; Campana, Marks and Joyce, 2005; Sepulveda, Graham and Bernal, 2007). Nevertheless, the mako shark's high-speed swimming and the increased metabolic costs associated with endothermy are reflected in its extreme oxygen consumption rates. Moreover, the power-performance curve (swimming speed vs. oxygen

consumption) slope estimated for a juvenile mako shark is around 0.92 (Sepulveda, Graham and Bernal, 2007), being considerably higher than the slopes observed in ectothermic shark species, which commonly range between 0.27 and 0.36 (Bernal *et al.*, 2012). Owing to this increased oxygen demand, mako sharks exhibit a general tendency to remain in waters with oxygen concentrations above 3 ml L<sup>-1</sup> (Abascal *et al.*, 2011).

Additionally, to cope with its elevated energetic requirements, the mako shark needs to consume from 4.42% to 4.66 % of its body mass per day, depending on its age (Wood *et al.*, 2009). Whereas the blue shark only requires a daily ration of about 1% of its body mass (Schindler *et al.*, 2002). These two pelagic predators have similar diets primarily composed of mesopelagic fish and cephalopods (Nakano and Stevens, 2008; Stevens, 2008), commonly found in the deep scattering layers (Irigoién *et al.*, 2014; Ariza *et al.*, 2016). However, while cephalopods make up the bulk of the blue shark's diet (Clarke *et al.*, 1996; Sosa-Nishizaki, 2010; Preti *et al.*, 2012), the mako shark has a preference for teleost species, including large animals like the swordfish (*Xiphias gladius*) (Maia *et al.*, 2006; Preti *et al.*, 2012; Rogers *et al.*, 2012).

## Study objectives

The present work aims to contribute to the development of informed management and conservation plans for the two most exploited pelagic shark species in the Atlantic Ocean by improving the current understanding of their vertical behaviour. In this sense, since foraging is considered one of the major factors influencing large predators' movements, this study first identifies whether blue and mako sharks modify their diel behaviour in function of the micronekton distribution within the SSLs. Secondly, it examines the consequences of changing sea temperatures and dissolved oxygen concentrations on the association between the studied species and the SSLs. Lastly, the effect of blue and mako sharks' metabolic and dietetic differences on their usage of the DSL are discussed.

## References

- Abascal, F. J. et al. (2011) 'Movements and environmental preferences of the shortfin mako, *Isurus oxyrinchus*, in the southeastern Pacific Ocean', *Marine Biology*, 158(5), pp. 1175–1184. doi: 10.1007/s00227-011-1639-1.
- Andrews, K. S. et al. (2009) 'Diel activity patterns of sixgill sharks, *Hexanchus griseus*: the ups and downs of an apex predator', *Animal Behaviour*. Elsevier Ltd, 78(2), pp. 525–536. doi: 10.1016/j.anbehav.2009.05.027.

- Ariza, A. et al. (2016) ‘Vertical distribution, composition and migratory patterns of acoustic scattering layers in the Canary Islands’, *Journal of Marine Systems*. Elsevier B.V., 157, pp. 82–91. doi: 10.1016/j.jmarsys.2016.01.004.
- Arnold, G. and Dewar, H. (2001) ‘Electronic Tags in Marine Fisheries Research: A 30-Year Perspective’, pp. 7–64. doi: 10.1007/978-94-017-1402-0\_2.
- Au, D. W., Smith, S. E. and Show, C. (2008) ‘Shark Productivity and Reproductive Protection, and a Comparison with Teleosts’, in Camhi, M. D., Pikitch, E. K., and Babcock, E. A. (eds) *Sharks of the Open Ocean: Biology, Fisheries and Conservation*. Blackwell Publishing Ltd., pp. 298–308. doi: 10.1002/9781444302516.ch26.
- Baum, J. K. et al. (2003) ‘Collapse and conservation of shark populations in the Northwest Atlantic’, *Science*, 299(5605), pp. 389–392. doi: 10.1126/science.1079777.
- Benoit-Bird, K. J. and Au, W. W. L. (2004) ‘Diel migration dynamics of an island-associated sound-scattering layer’, *Deep-Sea Research Part I: Oceanographic Research Papers*, 51(5), pp. 707–719. doi: 10.1016/j.dsr.2004.01.004.
- Benoit-Bird, K. J., Dahood, A. D. and Würsig, B. (2009) ‘Using active acoustics to compare lunar effects on predator-prey behavior in two marine mammal species’, *Marine Ecology Progress Series*, 395, pp. 119–135. doi: 10.3354/meps07793.
- Bernal, D. et al. (2005) ‘Mammal-like muscles power swimming in a cold-water shark’, *Nature*, 437(7063), pp. 1349–1352. doi: 10.1038/nature04007.
- Bernal, D. et al. (2012) ‘Energetics, Metabolism, and Endothermy in Sharks and Rays’, in Carrier, J. C., Musick, J. A. J., and Heithaus, M. R. (eds) *Biology of Sharks and Their Relatives*. Second Edition. CRC Press, pp. 211–237. doi: 10.5860/choice.50-2067.
- Bianchi, D. and Mislán, K. A. S. (2016) ‘Global patterns of diel vertical migration times and velocities from acoustic data’, *Limnology and Oceanography*, 61(1), pp. 353–364. doi: 10.1002/lno.10219.
- Block, B. A. et al. (1998) ‘A new satellite technology for tracking the movements of Atlantic bluefin tuna’, *Proceedings of the National Academy of Sciences of the United States of America*, 95(16), pp. 9384–9389. doi: 10.1073/pnas.95.16.9384.
- Bond, M. E. et al. (2015) ‘Vertical and horizontal movements of a silvertip shark (*Carcharhinus albimarginatus*) in the Fijian archipelago’, *Animal Biotelemetry*. BioMed Central, 3(1), pp. 1–7. doi: 10.1186/s40317-015-0055-6.
- Bonfil, R. et al. (2005) ‘Transoceanic migration, spatial dynamics, and population linkages of white sharks’, *Science*, 310(5745), pp. 100–103. doi: 10.1126/science.1114898.
- Bradshaw, C. J. A., Sims, D. W. and Hays, G. C. (2007) ‘Measurement error causes scale-dependent threshold erosion of biological signals in animal movement data’, *Ecological Applications*, 17(2), pp. 628–638. doi: 10.1890/06-0964.
- Byrne, M. E. et al. (2017) ‘Satellite telemetry reveals higher fishing mortality rates than previously estimated, suggesting overfishing of an apex marine predator’, *Proceedings of the Royal Society B: Biological Sciences*, 284(1860). doi: 10.1098/rspb.2017.0658.
- Byrne, M. E. et al. (2019) ‘Behavioral response of a mobile marine predator to environmental variables differs across ecoregions’, *Ecography*, 42(9), pp. 1569–1578. doi: 10.1111/ecog.04463.

- Cailliet, G. M., Musick, J. A. and Simpfendorfer, C. A. (2005) 'Ecology and Life History Characteristics of Chondrichthyan Fish', in *Sharks, Rays and Chimaeras: The Status of the Chondrichthyan Fishes*, Status Survey., pp. 12–18.
- Camhi, M. D. et al. (2008) 'A Global Overview of Commercial Fisheries for Open Ocean Sharks', in Camhi, M. D., Pikitch, E. K., and Babcock, E. A. (eds) *Sharks of the Open Ocean: Biology, Fisheries and Conservation*. Blackwell Publishing Ltd., pp. 166–192. doi: 10.1002/9781444302516.ch14.
- Campana, S. E. et al. (2011) 'Migration pathways, behavioural thermoregulation and overwintering grounds of blue sharks in the Northwest Atlantic', *PLoS ONE*, 6(2). doi: 10.1371/journal.pone.0016854.
- Campana, S. E. (2016) 'Transboundary movements, unmonitored fishing mortality, and ineffective international fisheries management pose risks for pelagic sharks in the Northwest Atlantic', *Canadian Journal of Fisheries and Aquatic Sciences*, 73(10), pp. 1599–1607. doi: 10.1139/cjfas-2015-0502.
- Campana, S. E., Marks, L. and Joyce, W. (2005) 'The biology and fishery of shortfin mako sharks (*Isurus oxyrinchus*) in Atlantic Canadian waters', *Fisheries Research*, 73(3), pp. 341–352. doi: 10.1016/j.fishres.2005.01.009.
- Carey, F. G., Scharold, J. V. and Kalmijn, A. J. (1990) 'Movements of blue sharks (*Prionace glauca*) in depth and course', *Marine Biology*, 106(3), pp. 329–342. doi: 10.1007/BF01344309.
- Carey, F. G. and Teal, J. M. (1969) 'Mako and porbeagle: warm-bodied sharks', 28(2138), pp. 199–204.
- Clarke, M. et al. (1996) 'The diet of the blue shark (*Prionace glauca*) in Azorean waters', *Life and Marine Sciences*, 14A, pp. 41–56.
- Coffey, D. M. et al. (2017) 'Oceanographic drivers of the vertical distribution of a highly migratory, endothermic shark', *Scientific Reports*. Springer US, 7(1), pp. 1–14. doi: 10.1038/s41598-017-11059-6.
- Compagno, L., Dando, M. and Fowler, S. (2005) 'A field guide to the sharks of the world'. London (United Kingdom) Collins.
- Cortés, E. (2000) 'Life History Patterns and Correlations in Sharks', *Reviews in Fisheries Science*, 8(4), pp. 299–344. doi: 10.1080/10408340308951115.
- Costa, D. P. et al. (2010) 'Accuracy of ARGOS locations of pinnipeds at-sea estimated using fastloc GPS', *PLoS ONE*, 5(1). doi: 10.1371/journal.pone.0008677.
- Dagorn, L. et al. (2006) 'Deep diving behaviour in yellowfin tuna (*Thunnus albacares*)', *Aquatic Living resources*, 19, pp. 85–88.
- Dagorn, L., Bach, P. and Josse, E. (2000) 'Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry', *Marine Biology*, 136(2), pp. 361–371. doi: 10.1007/s002270050694.
- Dietz, R. S. (1962) 'The Sea's Deep Scattering Layers', *Scientific American*, 207(2), pp. 44–50. doi: 10.1038/scientificamerican0862-44.
- Dulvy, N. et al. (2014) 'Extinction risk and conservation of the world's sharks and rays', *eLife*, 3, pp. 1–34. doi: 10.7554/eLife.00590.

- Dulvy, N. K. et al. (2008) 'You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays', *Aquatic conservation: Marine and Freshwater Ecosystems*, 18, pp. 459–482.
- Dwyer, R. G. et al. (2019) 'Using individual-based movement information to identify spatial conservation priorities for mobile species', *Conservation Biology*, 33(6), pp. 1426–1437. doi: 10.1111/cobi.13328.
- Estes, J. A. et al. (2011) 'Trophic downgrading of planet earth', *Science*, 333(6040), pp. 301–306. doi: 10.1126/science.1205106.
- Fahrig, L. (2007) 'Non-optimal animal movement in human-altered landscapes', *Functional Ecology*, 21(6), pp. 1003–1015. doi: 10.1111/j.1365-2435.2007.01326.x.
- Ferretti, F. et al. (2010) 'Patterns and ecosystem consequences of shark declines in the ocean', *Ecology Letters*, 13(8), pp. 1055–1071. doi: 10.1111/j.1461-0248.2010.01489.x.
- Hammerschlag, N., Gallagher, A. J. and Lazarre, D. M. (2011) 'A review of shark satellite tagging studies', *Journal of Experimental Marine Biology and Ecology*. Elsevier B.V., 398(1–2), pp. 1–8. doi: 10.1016/j.jembe.2010.12.012.
- Harcourt, R. et al. (2019) 'Animal-borne telemetry: An integral component of the ocean observing toolkit', *Frontiers in Marine Science*, 6(JUN). doi: 10.3389/fmars.2019.00326.
- Hays, G. C. (2003) 'A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations', *Hydrobiologia*, 503, pp. 163–170. doi: 10.1023/B:HYDR.0000008476.23617.b0.
- Hazen, E. L. and Johnston, D. W. (2010) 'Meridional patterns in the deep scattering layers and top predator distribution in the central equatorial Pacific', *Fisheries Oceanography*, 19(6), pp. 427–433. doi: 10.1111/j.1365-2419.2010.00561.x.
- Heithaus, M. R. et al. (2007) 'State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem', *Journal of Animal Ecology*, 76(5), pp. 837–844. doi: 10.1111/j.1365-2656.2007.01260.x.
- Heithaus, M. R. et al. (2008) 'Predicting ecological consequences of marine top predator declines', *Trends in Ecology and Evolution*, 23(4), pp. 202–210. doi: 10.1016/j.tree.2008.01.003.
- Heithaus, M. R. et al. (2014) 'Seagrasses in the age of sea turtle conservation and shark overfishing', *Frontiers in Marine Science*, 1, pp. 1–6. doi: 10.3389/fmars.2014.00028.
- Heupel, M. R. et al. (2014) 'Sizing up the ecological role of sharks as predators', *Marine Ecology Progress Series*, 495, pp. 291–298. doi: 10.3354/meps10597.
- Hueter, R. E. and Simpfendorfer, C. A. (2008) 'Case Study: Trends in Blue Shark Abundance in the Western North Atlantic As Determined by a Fishery-Independent Survey', in Camhi, M. D., Pikitch, E. K., and Babcock, E. A. (eds) *Sharks of the Open Ocean: Biology, Fisheries and Conservation*. Blackwell Publishing Ltd., pp. 236–241. doi: 10.1002/9781444302516.ch19.
- Hueter, R. E., Tyminski, J. P. and de la Parra, R. (2013) 'Horizontal Movements, Migration Patterns, and Population Structure of Whale Sharks in the Gulf of Mexico and Northwestern Caribbean Sea', *PLoS ONE*, 8(8). doi: 10.1371/journal.pone.0071883.
- Hussey, N. E. et al. (2015) 'Aquatic animal telemetry: A panoramic window into the underwater world', *Science*, 348(6240), p. 1255642. doi: 10.1126/science.1255642.

International Commission for the Conservation of Atlantic Tunas (2019) '26th Regular Meeting of the International Commission for the Conservation of Atlantic Tunas (Palma de Mallorca, Spain)', pp. 1–3. Available at: <https://www.iccat.int/en/Meetings.asp>.

International Commission for the Conservation of Atlantic Tunas (2020), "2020 Standing Committee on Research and Statistics (SCRS) advice to the commission" (Madrid, Spain).

Irigoiien, X. et al. (2014) 'Large mesopelagic fishes biomass and trophic efficiency in the open ocean', *Nature communications*, 5(1), p. 3271. doi: 10.1038/ncomms4271.

Klevjer, T. A. et al. (2016) 'Large scale patterns in vertical distribution and behaviour of mesopelagic scattering layers', *Scientific Reports*. Nature Publishing Group, 6(1), pp. 1–11. doi: 10.1038/srep19873.

Klevjer, T. A., Torres, D. J. and Kaartvedt, S. (2012) 'Distribution and diel vertical movements of mesopelagic scattering layers in the Red Sea', *Marine Biology*, 159(8), pp. 1833–1841. doi: 10.1007/s00227-012-1973-y.

Klimley, A. P. (1987) 'The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*', *Environmental Biology of Fishes*, 18(1), pp. 27–40. doi: 10.1007/BF00002325.

Klimley, A. P. et al. (2002) 'Movements and swimming behavior of three species of sharks in La Jolla Canyon, California', *Environmental Biology of Fishes*, 63(2), pp. 117–135. doi: 10.1023/A:1014200301213.

Kohler, N. E. and Turner, P. A. (2001) 'Shark tagging: A review of conventional methods and studies', *Environmental Biology of Fishes*, 60(1–3), pp. 191–223. doi: 10.1023/A:1007679303082.

Kohler, N. E. and Turner, P. A. (2008) 'Stock Structure of the Blue Shark (*Prionace Glauca*) in the North Atlantic Ocean Based on Tagging Data' in Camhi, M. D., Pikitch, E. K., and Babcock, E. A. (eds) *Sharks of the Open Ocean: Biology, Fisheries and Conservation*. Blackwell Publishing Ltd., pp. 339–350. doi: 10.1002/9781444302516.ch30.

Lam, C. H., Galuardi, B. and Lutcavage, M. E. (2014) 'Movements and oceanographic associations of bigeye tuna (*Thunnus obesus*) in the Northwest Atlantic', *Canadian Journal of Fisheries and Aquatic Sciences*, 71(10), pp. 1529–1543. doi: 10.1139/cjfas-2013-0511.

Lea, J. S. E. et al. (2015) 'Repeated, long-distance migrations by a philopatric predator targeting highly contrasting ecosystems', *Scientific Reports*. Nature Publishing Group, 5(March), pp. 1–11. doi: 10.1038/srep11202.

Lohmann, K. J., Lohmann, C. M. F. and Endres, C. S. (2008) 'The sensory ecology of ocean navigation', *Journal of Experimental Biology*, 211(11), pp. 1719–1728. doi: 10.1242/jeb.015792.

Maia, A. et al. (2006) 'Food habits of the shortfin mako, *Isurus oxyrinchus*, off the southwest coast of Portugal', *Environmental Biology of Fishes*, 77(2), pp. 157–167. doi: 10.1007/s10641-006-9067-7.

McFarlane, G., Wydoski, R. and Prince, E. (1990) 'Historical Review of the Development of External Tags and Marks', *American Fisheries Society Symposium*, 7.



- Miller, P. I. et al. (2015) 'Basking sharks and oceanographic fronts: Quantifying associations in the north-east Atlantic', *Functional Ecology*, 29(8), pp. 1099–1109. doi: 10.1111/1365-2435.12423.
- Mollet, H. F. et al. (2000) 'Reproductive biology of the female shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, with comments on the embryonic development of lamnoids', *Fishery Bulletin*, 98(2), pp. 299–318.
- Myers, R. A. et al. (2007) 'Cascading effects of the loss of apex predatory sharks from a coastal ocean', *Science*, 315(5820), pp. 1846–1850. doi: 10.1126/science.1138657.
- Nakano, H. et al. (2003) 'Acoustic tracking of bigeye thresher shark, *Alopias superciliosus*, in the eastern Pacific Ocean', *Marine Ecology Progress Series*, 265, pp. 255–261. doi: 10.3354/meps265255.
- Nakano, H. and Stevens, J. D. (2008) 'The Biology and Ecology of the Blue Shark, *Prionace Glauca*', in Camhi, M. D., Pikitch, E. K., and Babcock, E. A. (eds) *Sharks of the Open Ocean: Biology, Fisheries and Conservation*. Blackwell Publishing Ltd., pp. 140–151. doi: 10.1002/9781444302516.ch12.
- Nandintsetseg, D. et al. (2019) 'Challenges in the conservation of wide-ranging nomadic species', *Journal of Applied Ecology*, 56(8), pp. 1916–1926. doi: 10.1111/1365-2664.13380.
- Nasby-Lucas, N. et al. (2009) 'White shark offshore habitat: A behavioral and environmental characterization of the eastern pacific shared offshore foraging area', *PLoS ONE*, 4(12). doi: 10.1371/journal.pone.0008163.
- Nathan, R. et al. (2008) 'A movement ecology paradigm for unifying organismal movement research', *PNAS*, 105(49), pp. 19052–19059.
- Nathan, R. (2008) 'An emerging movement ecology paradigm', *PNAS*, 105(49), pp. 19050–19051. doi: 10.1073/pnas.0808918105.
- Norheim, E., Klevjer, T. A. and Aksnes, D. L. (2016) 'Evidence for light-controlled migration amplitude of a sound scattering layer in the Norwegian Sea', *Marine Ecology Progress Series*, 551, pp. 45–52. doi: 10.3354/meps11731.
- Northcutt, R. G. (1977) 'Elasmobranch central nervous system organization and its possible evolutionary significance', *Integrative and Comparative Biology*, 17(2), pp. 411–429. doi: 10.1093/icb/17.2.411.
- Pacoureau, N. et al. (2021) 'Half a century of global decline in oceanic sharks and rays', *Nature*. Springer US, 589(7843), pp. 567–571. doi: 10.1038/s41586-020-03173-9.
- Pade, N. G. et al. (2009) 'First results from satellite-linked archival tagging of porbeagle shark, *Lamna nasus*: Area fidelity, wider-scale movements and plasticity in diel depth changes', *Journal of Experimental Marine Biology and Ecology*, 370(1–2), pp. 64–74. doi: 10.1016/j.jembe.2008.12.002.
- Preti, A. et al. (2008) 'Feeding habits of the bigeye thresher shark (*Alopias superciliosus*) sampled from the California-based drift gillnet fishery', *California Cooperative Oceanic Fisheries Investigations Reports*, 49, pp. 202–211.

- Preti, A. et al. (2012) ‘Comparative feeding ecology of shortfin mako, blue and thresher sharks in the California Current’, *Environmental Biology of Fishes*, 95(1), pp. 127–146. doi: 10.1007/s10641-012-9980-x.
- Queiroz, N. et al. (2012) ‘Spatial Dynamics and Expanded Vertical Niche of Blue Sharks in Oceanographic Fronts Reveal Habitat Targets for Conservation’, *PLoS ONE*, 7(2). doi: 10.1371/journal.pone.0032374.
- Queiroz, N. et al. (2016) ‘Ocean-wide tracking of pelagic sharks reveals extent of overlap with longline fishing hotspots’, *PNAS*, 113(6). doi: 10.1073/pnas.1510090113.
- Queiroz, N. et al. (2019) ‘Global spatial risk assessment of sharks under the footprint of fisheries’, *Nature*, 572(7770), pp. 461–466. doi: 10.1038/s41586-019-1444-4.
- Rigby, C. L. et al. (2019a) ‘*Isurus oxyrinchus*, shortfin mako’, *The IUCN Red List of Threatened Species*<sup>TM</sup>. Available at: <http://dx.doi.org/10.2305/IUCN.UK.2019-1.RLTS.T39341A2903170.en>
- Rigby, C. L. et al. (2019b) ‘*Prionace glauca*, Blue shark’, *The IUCN Red List of Threatened Species*<sup>TM</sup>. Available at: <https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T39381A2915850.en>.
- Rogers, P. J. et al. (2012) ‘A quantitative comparison of the diets of sympatric pelagic sharks in gulf and shelf ecosystems off southern Australia’, *ICES Journal of Marine Science*, 69(8), pp. 1382–1393. doi: 10.1093/icesjms/fss100.
- Rogers, P. J. et al. (2015) ‘Living on the continental shelf edge: Habitat use of juvenile shortfin makos *Isurus oxyrinchus* in the Great Australian Bight, southern Australia’, *Fisheries Oceanography*, 24(3), pp. 205–218. doi: 10.1111/fog.12103.
- Schaefer, K. M. and Fuller, D. W. (2002) ‘Movements, behavior, and habitat selection of bigeye tuna (*Thunnus obesus*) in the eastern equatorial Pacific, ascertained through archival tags’, *Fishery Bulletin*, 100(4), pp. 765–788.
- Schindler, D. E. et al. (2002) ‘Sharks and tunas: Fisheries impacts on predators with contrasting life histories’, *Ecological Applications*, 12(3), pp. 735–748. doi: 10.1890/1051-0761(2002)012[0735:SATFIO]2.0.CO;2.
- Schlaff, A. M., Heupel, M. R. and Simpfendorfer, C. A. (2014) ‘Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review’, *Reviews in Fish Biology and Fisheries*, 24(4), pp. 1089–1103. doi: 10.1007/s11160-014-9364-8.
- Sepulveda, C. A. et al. (2004) ‘Movement patterns, depth preferences, and stomach temperatures of free-swimming juvenile mako sharks, *Isurus oxyrinchus*, in the Southern California Bight’, *Marine Biology*, 145(1), pp. 191–199. doi: 10.1007/s00227-004-1356-0.
- Sepulveda, C. A., Graham, J. B. and Bernal, D. (2007) ‘Aerobic metabolic rates of swimming juvenile mako sharks, *Isurus oxyrinchus*’, *Marine Biology*, 152(5), pp. 1087–1094. doi: 10.1007/s00227-007-0757-2.
- Simmonds, J. and MacLennan, D. (2005) *Fisheries Acoustics: Theory and Practice. Second, Ocean Pulse*. Second Edition. Edited by T. J. Pitcher. Blackwell Science. doi: 10.1007/978-1-4899-0136-1\_14.

- Sims, D. W. et al. (2000) 'Annual social behaviour of basking sharks associated with coastal front areas', *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 267(1455), pp. 1897–1904. doi: 10.1098/rspb.2000.1227.
- Sims, D. W. (2003) 'Tractable models for testing theories about natural strategies: foraging behaviour and habitat selection of free-ranging sharks', *Journal of Fish Biology*, 63, pp. 53–73. doi: 10.1046/j.1095-8649.2003.00207.x.
- Sims, D. W. et al. (2005) 'Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark', *Journal of Animal Ecology*, 74(4), pp. 755–761. doi: 10.1111/j.1365-2656.2005.00971.x.
- Sims, D. W. et al. (2006) 'Hunt warm, rest cool: Bioenergetic strategy underlying diel vertical migration of a benthic shark', *Journal of Animal Ecology*, 75(1), pp. 176–190. doi: 10.1111/j.1365-2656.2005.01033.x.
- Sims, D. W. (2010) 'Tracking and analysis techniques for understanding free-ranging shark movements and behavior', in Carrier, J. C., Musick, J. A., and Heithaus, M. R. (eds) *Sharks and Their Relatives II: Biodiversity, Adaptive Physiology, and Conservation*. CRC Press. pp. 351–392. doi: 10.1201/9781420080483.
- Sims, D. W. and Quayle, V. A. (1998) 'Selective foraging behaviour of basking sharks on zooplankton in a small-scale front', *Nature*, 393(6684), pp. 460–464. doi: 10.1038/30959.
- Sosa-Nishizaki, O. (2010) 'Food and feeding habits of the blue shark *Prionace glauca* caught off Ensenada, Baja California, Mexico, with a review on its feeding', *Journal of the Marine Biological Association of the United Kingdom*, 90, pp. 977–994. doi: 10.1017/S0025315409991597.
- Spaet, J. L. Y. et al. (2017) 'Extensive use of mesopelagic waters by a Scalloped hammerhead shark (*Sphyrna lewini*) in the Red Sea', *Animal Biotelemetry*. BioMed Central, 5(1), pp. 1–12. doi: 10.1186/s40317-017-0135-x.
- Stevens, J. D. (2008) 'The Biology and Ecology of the Shortfin Mako Shark, *Isurus Oxyrinchus*', in Camhi, M. D., Pikitch, E. K., and Babcock, E. A. (eds) *Sharks of the Open Ocean: Biology, Fisheries and Conservation*. Blackwell Publishing Ltd., pp. 87–94. doi: 10.1002/9781444302516.ch7.
- Stevens, J. D. (2010) 'Epipelagic oceanic elasmobranchs', in Carrier, J. C., Musick, J. A., and Heithaus, M. R. (eds) *Sharks and Their Relatives II: Biodiversity, Adaptive Physiology, and Conservation*. CRC Press. pp. 3–36. Available at: <http://hdl.handle.net/102.100.100/108788?index=1>.
- Tarling, G. A. et al. (2001) 'The swarm dynamics of northern krill (*Meganyctiphanes norvegica*) and pteropods (*Cavolinia inflexa*) during vertical migration in the Ligurian Sea observed by an acoustic Doppler current profiler', *Deep-Sea Research Part I: Oceanographic Research Papers*, 48(7), pp. 1671–1686. doi: 10.1016/S0967-0637(00)00105-9.
- Thorrold, S. R. et al. (2014) 'Extreme diving behaviour in devil rays links surface waters and the deep ocean', *Nature Communications*. Nature Publishing Group, 5, pp. 1–7. doi: 10.1038/ncomms5274.
- Vandeperre, F. et al. (2014) 'Movements of blue sharks (*Prionace glauca*) across their life history', *PLoS ONE*, 9(8). doi: 10.1371/journal.pone.0103538.

- Vedor, M. et al. (2021) ‘Climate-driven deoxygenation elevates fishing vulnerability for the ocean’s widest ranging shark’, *eLife*, 10, pp. 1–29. doi: 10.7554/elife.62508.
- Venegas, R. de la P. et al. (2011) ‘An unprecedented aggregation of whale sharks, *Rhincodon typus*, in Mexican coastal waters of the Caribbean sea’, *PLoS ONE*, 6(4). doi: 10.1371/journal.pone.0018994.
- Wallman, H. L. and Bennett, W. A. (2006) ‘Effects of parturition and feeding on thermal preference of Atlantic stingray, *Dasyatis sabina* (Lesueur)’, *Environmental Biology of Fishes*, 75(3), pp. 259–267. doi: 10.1007/s10641-006-0025-1.
- Wildhaber, M. L. and Crowder, L. (1990) ‘Testing a Bioenergetics-Based Habitat Choice Model: Bluegill (*Lepomis macmchirus*) Responses to Food Availability and Temperature’.
- Williamson, M. J. et al. (2019) ‘Satellite remote sensing in shark and ray ecology, conservation and management’, *Frontiers in Marine Science*, 6(MAR), pp. 1–23. doi: 10.3389/fmars.2019.00135.
- Wilson, R. P., Shepard, E. L. C. and Liebsch, N. (2008) ‘Prying into the intimate details of animal lives: Use of a daily diary on animals’, *Endangered Species Research*, 4(1–2), pp. 123–137. doi: 10.3354/esr00064.
- Wirsing, A. J., Heithaus, M. R. and Dill, L. M. (2007) ‘Fear factor: Do dugongs (*Dugong dugon*) trade food for safety from tiger sharks (*Galeocerdo cuvier*)?’’, *Oecologia*, 153(4), pp. 1031–1040. doi: 10.1007/s00442-007-0802-3.
- Wood, A. D. et al. (2009) ‘Recalculated diet and daily ration of the shortfin mako (*Isurus oxyrinchus*), with a focus on quantifying predation on bluefish (*Pomatomus saltatrix*) in the northwest Atlantic Ocean’, *Fishery Bulletin*, 107(1), pp. 76–88.
- Worm, B. et al. (2013) ‘Global catches, exploitation rates, and rebuilding options for sharks’, *Marine Policy*. Elsevier, 40(1), pp. 194–204. doi: 10.1016/j.marpol.2012.12.034.
- Worm, B., Lotze, H. K. and Myers, R. A. (2003) ‘Predator diversity hotspots in the blue ocean’, *PNAS*, 100(17), pp. 9884–9888. doi: 10.1073/pnas.1333941100.

# **The influence of the sound scattering layers on the vertical behaviour of two mesopelagic sharks**

Bruno Saraiva, David Abecasis<sup>b</sup> & Nuno Queiroz<sup>a</sup>

<sup>a</sup> Centro de Investigação em Biodiversidade e Recursos Genéticos/Research Network in Biodiversity and Evolutionary Biology (CIBIO), Campus Agrário de Vairão, Rua Padre Armando Quintas, 4485-668 Vairão, Portugal

<sup>b</sup> Centro de Ciências do Mar/Centre of Marine Sciences (CCMAR), Universidade do Algarve, Campus de Gambelas 8005-139 Faro, Portugal

**Keywords:** sound scattering layers; diel vertical migration; blue shark; shortfin mako shark; top predators; foraging.

## **Abstract**

As apex predators, large sharks sustain the structure and function of marine communities. However, due to the ever-increasing fishing pressure and their slow life-history traits, shark populations have drastically declined in the last decades. Thus, improved knowledge on shark movements is crucial to implement effective management actions to prevent biodiversity loss and the disruption of marine ecosystems. Vertical patterns of apex predators have regularly been associated with foraging behaviours, yet the direct connection with prey's vertical distribution and availability is often missing. In the open ocean, large aggregations of zooplanktonic and micronektonic organisms produce two unique acoustical signatures known as sound scattering layers (SSLs), believed to be an essential food source for oceanic predators. The present study uses pop-up satellite archival transmitters data of 22 blue (*Prionace glauca*) and 17 shortfin mako sharks (*Isurus oxyrinchus*), tracked within the North Atlantic Ocean, to assess the SSLs influence on these species' diel vertical migrations (DVM) and foraging patterns. The sharks' vertical patterns followed the SSLs diel migrations, commonly exhibiting surface-oriented behaviour when daytime micronekton concentrations at the shallow scattering layer (SSL) were higher compared to the upper deep scattering layer (DSL). Also, both species seemed to use the SSLs as foraging grounds, yet, while the mako shark appeared to target non-migrant or semi-migrant prey at the DSL, the blue shark generally favoured higher micronekton concentrations. Nevertheless, temperature and oxygen levels limited the extent of the vertical movements and impact the time spent at depth, sometimes preventing the animals from reaching the DSL. Thus, considering the ongoing expansion of the oxygen minimum zones, some predators might lose access to highly energetic prey and subsequently decrease their fitness. The SSLs showed to affect the sharks' vertical range and time spent at epipelagic waters, revealing a potential use to detect regions with increased fishing risk.

# 1 Introduction

As apex predators, large sharks sustain the structure and function of marine communities either through direct predation or risk effects (Heithaus *et al.*, 2008; Estes *et al.*, 2011). However, the ever-increasing fishing pressure combined with sharks' K-selected life histories, i.e., slow growth rate, long gestation periods, low fecundity, and late sexual maturity, has led to extensive shark declines worldwide, raising concerns about potential impacts on the ecosystems' health (Cortés, 2000; Cailliet, Musick and Simpfendorfer, 2005; Dulvy *et al.*, 2008, 2014; Ferretti *et al.*, 2010; Heupel *et al.*, 2014). Pelagic sharks perform wide-ranging movements throughout the open ocean and/or display site fidelity to shelf and open ocean regions (Queiroz *et al.*, 2019). Such behaviours often expose these animals to large numbers of fishing vessels in the high seas, being frequently captured in open ocean fisheries, mainly by longline vessels focusing on more lucrative teleost species. Even if pelagic sharks are regularly classified as by-catch, missing management regulations, growing international markets, and their highly profitable fins, have led to the increase of shark retention rates (Camhi *et al.*, 2008; Dulvy *et al.*, 2014; Campana, 2016). The blue shark (*Prionace glauca*) is the most caught pelagic shark species in the Atlantic Ocean, representing 73% of the total pelagic shark catch from 1980 to 2005, followed by the shortfin mako shark (*Isurus oxyrinchus*), hereafter just mako shark, which accounted for 17% (Camhi *et al.*, 2008). Furthermore, Queiroz *et al.* (2019) showed that blue and mako sharks are aggregated within the highest potential fishing-risk zone in the North Atlantic Ocean, with a space use overlap with longline fisheries of 76% and 62%, respectively.

Pelagic shark catches remain largely unregulated, frequently misidentified, and unrecorded (Barker and Schluessel, 2005; Dulvy *et al.*, 2008, 2014), leading to highly uncertain stock assessments and subsequently inadequate management decisions (Worm *et al.*, 2013). Moreover, effective management and conservation actions rely on the complete understanding of how and why species move, migrate, and aggregate (Nandintsetseg *et al.*, 2019). Recent advances in tracking technology and the increasing availability of remotely sensed environmental data have permitted the link between animal movement and their physical environment over large spatiotemporal scales, providing an improved understanding of complex spatial and temporal behavioural dynamics (Sims, 2010; Hussey *et al.*, 2015; Harcourt *et al.*, 2019).

In the open ocean, large aggregations of micronektonic and zooplanktonic organisms generate two distinctive reflecting regions, the so-called sound scattering layers (SSLs). A shallow scattering layer (SSL) present in the epipelagic region, and a larger deep scattering layer (DSL) established at the mesopelagic domain. The latter is generally divided into multiple levels comprising different species and development stages (Dietz, 1962; Hays, 2003; Ariza *et al.*, 2016). A considerable share of the organisms inhabiting these layers feeds between dawn and dusk in shallow waters, creating a denser SSL at night, and reside in deeper waters during the day. This behaviour, named diel vertical migration (DVM), is thought to maximize these animals' survival rates by avoiding visual predators (Klevjer, Torres and Kaartvedt, 2012; Ariza *et al.*, 2016; Klevjer *et al.*, 2016). Still, DVM is not restricted to low trophic levels, being frequently observed in large predators, such as sharks (Hays, 2003).

Due to the low predation risk conferred by their relatively large body size, vertical patterns of large predators have commonly been associated with foraging or searching behaviours (Carey, Scharold and Kalmijn, 1990; Hays, 2003; Sims *et al.*, 2005; Andrews *et al.*, 2009; Queiroz *et al.*, 2012). Likewise, navigation and thermoregulation have also been suggested to explain the vertical movements observed in these animals. For example, predators can scan the water column in search of navigational cues in the form of chemical information or magnetic gradients (Carey, Scharold and Kalmijn, 1990; Klimley *et al.*, 2002). Moreover, diving into deeper cold waters might reduce metabolic costs, while swimming in shallow waters can help maintain an optimal temperature (Campana *et al.*, 2011). On the other hand, Sims *et al.* (2006) proposed that the vertical behaviour observed in ectothermic sharks is an appropriate combination of thermal and foraging resources.

Furthermore, the SSLs are believed to be a vital food source for many oceanic macropredators inhabiting the open ocean (Norheim, Klevjer and Aksnes, 2016). Thus, several authors have debated the role of these large aggregations of mesopelagic organisms on the vertical behaviour and foraging patterns observed in oceanic top predators (Dagorn, Bach and Josse, 2000; Nakano *et al.*, 2003; Sepulveda *et al.*, 2004; Preti *et al.*, 2008; Nasby-Lucas *et al.*, 2009; Spaet *et al.*, 2017). However, due to the characterization of the SSLs being formerly dependent on labour-intensive acoustic and net sampling methods restricted to relatively small areas (Dagorn, Bach and Josse, 2000;



*Sims et al., 2005*), the importance of the SSLs on predators' vertical behaviour remains poorly understood.

The present study uses pop-up satellite archival transmitters (PSAT) data recovered from 22 blue sharks and 17 mako sharks tracked over the North Atlantic Ocean and remote sensed environmental data to investigate the influence of the SSLs on these species' foraging patterns and diel vertical behaviour. It aims to improve the general understanding of blue and mako sharks' vertical use, thus providing valuable information for developing effective management and conservation plans for these highly exploited sharks. Furthermore, owing to the different metabolic strategies of the studied species, the results presented here might be considered for a broader range of oceanic predators.

## **2 Materials and Methods**

### **2.1 Tagging**

Between April 2009 and April 2018, 22 blue sharks and 17 mako sharks were tagged in the North Atlantic Ocean. Tagging procedures took place on board of longline-fishing vessels during commercial fishing operations. The sharks were captured using baited longlines and placed in the vertical position alongside the vessel during the gear-hauling phase. While the sharks were suspended, Pop-up satellite archival transmitters (PSAT; models: Mk10 and MiniPAT, Wildlife Computers, WA, USA; PSATFLEX, Lotek Wireless Inc.) were fixed with a monofilament tether (250 lb test) coated with silicone tubing and looped through a small hole made in the base of the first dorsal fin. The entire procedure, including body-length measurements and sex identification, took less than 5 minutes (*Queiroz et al., 2016*). Tagging procedures were approved by institutional ethical review committees and performed by licensed, trained, and experienced personnel. Once active, the tags recorded depth, external temperature, and light-level parameters at varying intervals (from 1 to 10 s) and stored the data in summary bins of 6 (2009 – 2016 tags) and 12 hours (2017-2018 tags).

### **2.2 Location estimates**

The animals' tracks were estimated using either satellite-relayed summary data or high-resolution archival data from physically recovered tags. Daily locations were determined using software provided by the tags' manufacturer (WC-GPE, global position estimator program suite), where longitude estimates were based on the local time of midnight or midday, estimated through the daily maximal rate of change in light intensity. Latitude

was determined via day-length estimates (Wilson, 1992). Anomalous longitude estimates, provoked by dive-induced modifications in the determined timings of dawn and dusk from light curves, and their respective latitudes, were automatically removed by the WC-GPE software.

An integrated state-space model (unscented Kalman filter, UKFSST (Lam, Nielsen and Sibert, 2008); using spatially complete NOAA Optimum Interpolation Quarter Degree Daily SST Analysis data) was applied to rectify the raw geolocations estimates and obtain the most probable track. Additionally, the Kalman position estimates were further revised using bathymetric data using the R package *analyzepsat* (Galuardi, 2019). Finally, a daily time-series of locations was estimated using a continuous-time correlated random walk (CTCRW) Kalman filter (Jonsen, Flemming and Myers, 2005), performed in R (*crawl* R package (Johnson, London and Wilson, 2015)). The CTCRW state-space model was employed for each track, generating a single position estimate per day.

### 2.3 Environmental Data

The SSLs were defined using the recently available oceanographic product, Global Ocean Low and Mid Trophic Levels Biomass Hindcast (GLOBAL\_REANALYSIS\_BIO\_001\_033, From 1998-01-07 to 2019-06-26) at 0.25 x 0.25° cell resolution with one depth level (2D), provided by the Copernicus Marine Environment Monitoring Service (CMEMS). This product comprises the weekly mean depth [m] of the epipelagic, upper, and lower mesopelagic layers, also known as SSL, Upper and Lower deep scattering layers (UDSL, LDSL), as well as the concentration [g m<sup>-2</sup>] of zooplanktonic (zooc) and micronektonic organisms. The last is divided into the following functional groups: epipelagic (*mnkc.epi*), upper mesopelagic (*mnkc.umeso*), migrant upper mesopelagic (*mnkc.ummeso*), lower mesopelagic (*mnkc.lmeso*), migrant lower mesopelagic (*mnkc.lmmeso*), and highly migrant lower mesopelagic (*mnkc.lhmmeso*). Thus, the micronekton concentration at each layer during day and night was determined as follows:

$$\text{day.mnkc.SSL} = \text{mnkc.epi}$$

$$\text{night.mnkc.SSL} = \text{mnkc.epi} + \text{mnkc.ummeso} + \text{mnkc.lhmmeso}$$

$$\text{day.mnkc.UDSL} = \text{mnkc.umeso} + \text{mnkc.ummeso}$$

$$\text{night.mnkc.UDSL} = \text{mnkc.umeso} + \text{mnkc.lmmeso}$$

$$\text{day.mnkc.LDSL} = \text{mnkc.lmeso} + \text{mnkc.lmmeso} + \text{mnkc.lhmmeso}$$

$$\text{night.mnkc.LDSL} = \text{mnkc.lmeso}$$

Two additional environmental products were downloaded from CMEMS. The Global Ocean Physics Reanalysis monthly product ([GLOBAL\\_REANALYSIS\\_PHY\\_001\\_031](#); from 1993-01-01 to 2018-12-31) for temperature [°C], with 0.083° x 0.083° cell resolution and 50 depth levels between 0 and 5500 m, and the Global Ocean Biogeochemistry Hindcast monthly product ([GLOBAL\\_REANALYSIS\\_BIO\\_001\\_029](#); from 1993-01-01 to 2019-12-23) for dissolved oxygen concentration (DO [mmol m<sup>-3</sup>]), with 0.25° x 0.25° cell resolution and 75 depth levels between 0 and 5500 m. The environmental data was interpolated to each meter between 0 and 2000m depth, and cell resolutions averaged to 0.25° x 0.25°. The dissolved oxygen concentration was converted to ml L<sup>-1</sup> dividing mmol m<sup>-3</sup> by 44.66 mol. Geolocation errors were considered while extracting the data by averaging the environmental values within 0.53 degrees longitude and 1.08 degrees latitude of each daily position estimate.

## 2.4 Behavioural analysis

Daytime was considered to be between 12:00 and 18:00, and nighttime between 00:00 and 06:00. Time bins coincident with crepuscular periods (06:00-12:00 and 18:00-00:00) were excluded from the analyses.

Daytime and nighttime micronekton concentrations experienced by blue and mako sharks were compared within each layer (day vs. night) and between layers (SSL vs. UDSL, SSL vs. LDSL, UDSL vs. LDSL) using the pairwise Wilcoxon rank-sum test. Sound scattering layers depths outside and inside the Eastern Tropical Atlantic (ETA) oxygen minimum zone (OMZ) were also compared employing the same method.

Time-at-depth (TAD) data of sharks tagged between 2009 and 2016 was gathered in 14 depth bins (0, 5, 10, 20, 30, 50, 70, 100, 150, 200, 250, 400, 600, >600 m). Moreover, due to 2017 and 2018 tags storing data in 12-hour summary bins, the TAD for each 6-hour interval was calculated using medium-resolution archival data (5 to 7.5 min) provided by these tags. Depth bins were specified to match the older tags, and time intervals with missing data were removed from the calculations.

Profile of depth and temperature (PDT) and TAD data were used to estimate the maximum depth for each 6-hour summary data of all sharks tagged between 2009 and

2016. Still, like TAD estimates, maximum depths from 2017 and 2018 were determined via medium-resolution archival data.

#### **2.4.1 Percentage of time within epipelagic waters**

Since the SSL was frequently found above 150m (95.51 % of all data), the epipelagic domain was defined as the first 150m of the water column. Observations where the SSL was deeper than 150m and the UDSL was shallower than 200m were removed, conserving 91.77% of the data. The percentage of time each species expended above 150m was then compared between day and night employing a pairwise Wilcoxon rank-sum test. Moreover, the relationship between the percentage of time that blue and mako sharks spent within epipelagic waters and the micronekton concentration at the SSL (mnkc.SSL) was examined using two separate univariate generalized linear models (GLM) family binomial linked to logit.

#### **2.4.2 Diel vertical behaviour**

Daytime and nighttime TAD data were clustered in 8 depth bins (0–50, 50–100, 100–150, 150–200, 200–250, 250–400, 400–600, >600 m). Subsequently, a continuous TAD matrix was computed for day and night utilizing the `interp.loess` function with a Kernel span of 0.0125 (`tgpr` R package (Gramacy and Taddy, 2010)). Day and night matrixes were then visually assessed to classify the sharks' DVM patterns and explore their relation to the micronekton distribution. Three classes of normal DVM (nDVM) were distinguished based on the TAD for at least five consecutive days (Queiroz *et al.*, 2012): depth-oriented nDVM was considered if the sharks spent over 50% of daytime deeper than the SSL and most nighttime above it; regular nDVM when more than 50% of the day and most of the night was spent above the SSL; surface-oriented behaviour was defined by both day and night times being mostly spent over the SSL, usually with no apparent differences.

#### **2.4.3 Diving behaviour**

The time-weighted average depth was determined for each shark employing the `weighted.mean` function available in R software using the central point of the TAD bins and the maximum depth for each time bin. Then, to examine the influence of the scattering layers' depth variations on the sharks' averaged depth, the SSL, UDSL, and LDSL depths were separately regressed on blue and mako sharks' average daytime and nighttime depths using univariate GLM family Gamma, linked to log.

Furthermore, the distance of each scattering layer to the maximum depths reached by the tagged animals was determined as follows:

$$\text{Layer's Distance} = \sqrt{(\text{Layer Depth} - \text{Maximum Depth})^2}$$

SSL, UDSL, and LDSL distances from blue and mako sharks were subsequently compared between day and night using a pairwise Wilcoxon rank-sum test. The relation between the layers' distance and their respective micronekton concentration was explored using a univariate GLM family Gamma linked to log for the SSL and UDSL, and a GLM family gaussian linked to log for the LDSL. Mako sharks tagged inside the ETA OMZ were excluded since the depth compression caused by the low DO levels could mask the micronekton's influence (Vedor *et al.*, 2021). Moreover, the GLOBAL\_REA\_NALYSIS\_BIO\_001\_033 model is based on primary production estimates derived from chlorophyll\_a concentrations, which are likely overestimated in coastal waters due to the biases induced by bottom reflectance, sediments, and active substances in the water (Lehodey and Titaud, 2019). Hence, abnormally high micronekton concentrations at the UDSL (mnkc.UDSL >200 m g<sup>-2</sup>) seen in blue shark observations near Boston's coast were dropped before the analysis. Regression models were built separately for each species.

Furthermore, a potential SSL micronekton concentration threshold, where the sharks' mean distance to the SSL sharply increases, was explored for each species using a change-point model (mcp R package (Lindeløv, 2020)) family gaussian linked to log with 50 chains. As previously, mako sharks inside the ETA OMZ were removed from the analysis.

#### **2.4.4 Maximum depth model**

A multivariate GLM family Gamma linked to the log was developed to evaluate the importance of SSLs compared to other environmental parameters and to compare the two species' behavioural responses. After removing dives exceeding the LDSL depth by more than 150m, blue and mako sharks' maximum daytime and nighttime depths were used as the response variable while the SSL depth, mnkc.SSL, micronekton concentration at the LDSL (mnkc.LDSL), sea surface temperature (SST), and DO at 100m depth were set as the initial predictors. Temperature and DO data were inferred from the previously mentioned CMEMS environmental products instead of the tags' in situ measurements. Moreover, an interaction between each predictor and a binary variable representing the species was included in the model to test behavioural variations among blue and mako sharks.

All data was previously rescaled within a [0,1] range using the Min-Max Normalization method to prevent possible bias created by heterogeneous scales (Li and Liu, 2011; Härdle and Simar, 2015). A Spearman's rank correlation matrix was employed to assess potential multicollinearity (Žydelis *et al.*, 2011; Schmiing *et al.*, 2013). Variables with correlation coefficients of  $p < -0.5$  and  $> 0.5$  were not included in the same group of initial predictors. Furthermore, the optimum model was assembled via stepwise backward elimination using Akaike's Information Criterion (AIC) (Burnham, Anderson and Huyvaert, 2011). Finally, the residuals and fit were examined using the DHARMA R package. In short, DHARMA uses a simulation-based approach to generate scaled residuals for generalized linear (mixed) models that can be interpreted as instinctively as the residuals from a linear regression (Hartig, 2020).

### 3 Results

Twenty-two blue sharks and 17 mako sharks were tracked within the North Atlantic Ocean between 2009 and 2018 (Table 3.1). Retrieved data comprised a total of 2184 tracking days (average track time:  $99.27 \pm 42.18 \text{ d}^{-1}$ ) for blue sharks and 1265 days (average track time:  $74.41 \pm 35.89 \text{ d}^{-1}$ ) for mako sharks. However, due to low-quality location estimates, only 1566 and 1240 tracking days (not including archival data) from blue and mako sharks, respectively, were used in this study. Moreover, complete archival data was recovered from three blue sharks and one mako shark (Table 3.1).

#### 3.1 Sound scattering layers

Throughout the tracking period, blue sharks came across a mean SSL depth of  $115 \pm 24\text{m}$ , a mean UDSL depth of  $344 \pm 71\text{m}$ , and a mean LDSL depth of  $818 \pm 132\text{m}$ . In comparison, mako sharks experienced a mean SSL depth of  $103 \pm 21\text{m}$ , a mean UDSL depth of  $309 \pm 63\text{m}$ , and a mean LDSL depth of  $718 \pm 140\text{m}$ . The SSLs inside the ETA OMZ were significantly shallower (Wilcoxon rank-sum test  $p\text{-value} < 0.0001$ ). Furthermore, the micronekton concentration at each layer was significantly different between day and night (Wilcoxon rank-sum test  $p\text{-value} < 0.0001$ ) (Figure A1). SSL micronekton concentrations were greater at night, while the UDSL and LDSL micronekton concentrations increased during the day. Generally, the LDSL micronekton concentration was the highest by daylight, followed by the UDSL (Wilcoxon rank-sum test

**Table 3.1** Summary data for satellite tagged Blue and mako sharks. F, female; M, male. Stars mark individuals with retrieved archival data. Open, open ocean; OMZ, oxygen minimum zone; Front, North Atlantic Current-Labrador Current convergence zone

Shark	Species	Fork length (cm)	Sex	Tagging date	Days at liberty	Location
B1	Blue	260	M	21/08/2011	127	Open
B2	Blue	250	M	22/08/2011	116	Open
B3*	Blue	240	M	26/08/2011	120	Open
B4	Blue	200	M	26/08/2011	119	Open
B5	Blue	185	M	26/06/2010	88	Front
B6	Blue	192	F	27/06/2010	87	Front/Open
B7	Blue	240	F	21/08/2011	81	Open/OMZ
B8	Blue	240	F	26/08/2011	120	Open
B9	Blue	260	F	29/06/2010	119	Front/Open
B10	Blue	240	F	30/06/2010	179	Fron
B11*	Blue	200	M	25/06/2010	120	Front
B12	Blue	210	M	25/06/2010	112	Front
B13	Blue	235	M	25/06/2010	179	Front
B14	Blue	220	F	27/08/2011	110	Open
B15*	Blue	220	F	28/08/2011	93	Open/OMZ
B16	Blue	240	F	21/01/2017	37	OMZ/Open
B17	Blue	265	M	17/02/2017	35	OMZ
B18	Blue	255	F	24/01/2017	34	OMZ/Open
B19	Blue	200	F	24/01/2017	47	Open/OMZ
B20	Blue	230	M	26/01/2017	19	OMZ
B21	Blue	230	F	25/01/2017	121	Open/OMZ
B22	Blue	230	M	28/01/2017	121	OMZ/Open
M1	Shortfin mako	140	M	25/06/2010	59	Front
M2	Shortfin mako	125	M	23/04/2009	29	Front
M3	Shortfin mako	220	M	30/06/2010	87	Front
M4	Shortfin mako	170	F	24/04/2009	59	Open
M5	Shortfin mako	130	M	03/07/2010	89	Front
M6*	Shortfin mako	180	M	27/06/2010	114	Front
M7	Shortfin mako	130	F	04/07/2010	117	Front/Open
M8	Shortfin mako	165	F	05/07/2010	119	Front
M9	Shortfin mako	220	F	21/08/2011	117	Open
M10	Shortfin mako	255	F	22/08/2011	117	Open
M11	Shortfin mako	170	M	03/09/2011	113	Front
M12	Shortfin mako	170	M	27/01/2017	17	OMZ
M13	Shortfin mako	160	F	24/01/2017	37	OMZ
M14	Shortfin mako	170	M	23/04/2018	63	OMZ
M15	Shortfin mako	180	M	23/04/2018	44	OMZ
M16	Shortfin mako	170	M	24/04/2018	60	OMZ
M17	Shortfin mako	180	M	24/04/2018	24	OMZ

p-value < 0.0001). This pattern was reversed at night, with the maximum micronekton concentration changing to the SSL (Wilcoxon rank-sum test p-value < 0.0001). Nevertheless, in a few observations near the North Atlantic Current-Labrador Current convergence zone (NAC-LCCZ) and inside the ETA OMZ, the SSL displayed higher daytime micronekton concentrations than the UDSL. Moreover, during nighttime significant micronekton concentration differences between the UDSL and LDSL were only found for blue sharks' tracks (Wilcoxon rank-sum test; blue shark p-value < 0.0001, mako shark p-value = 0.1048).

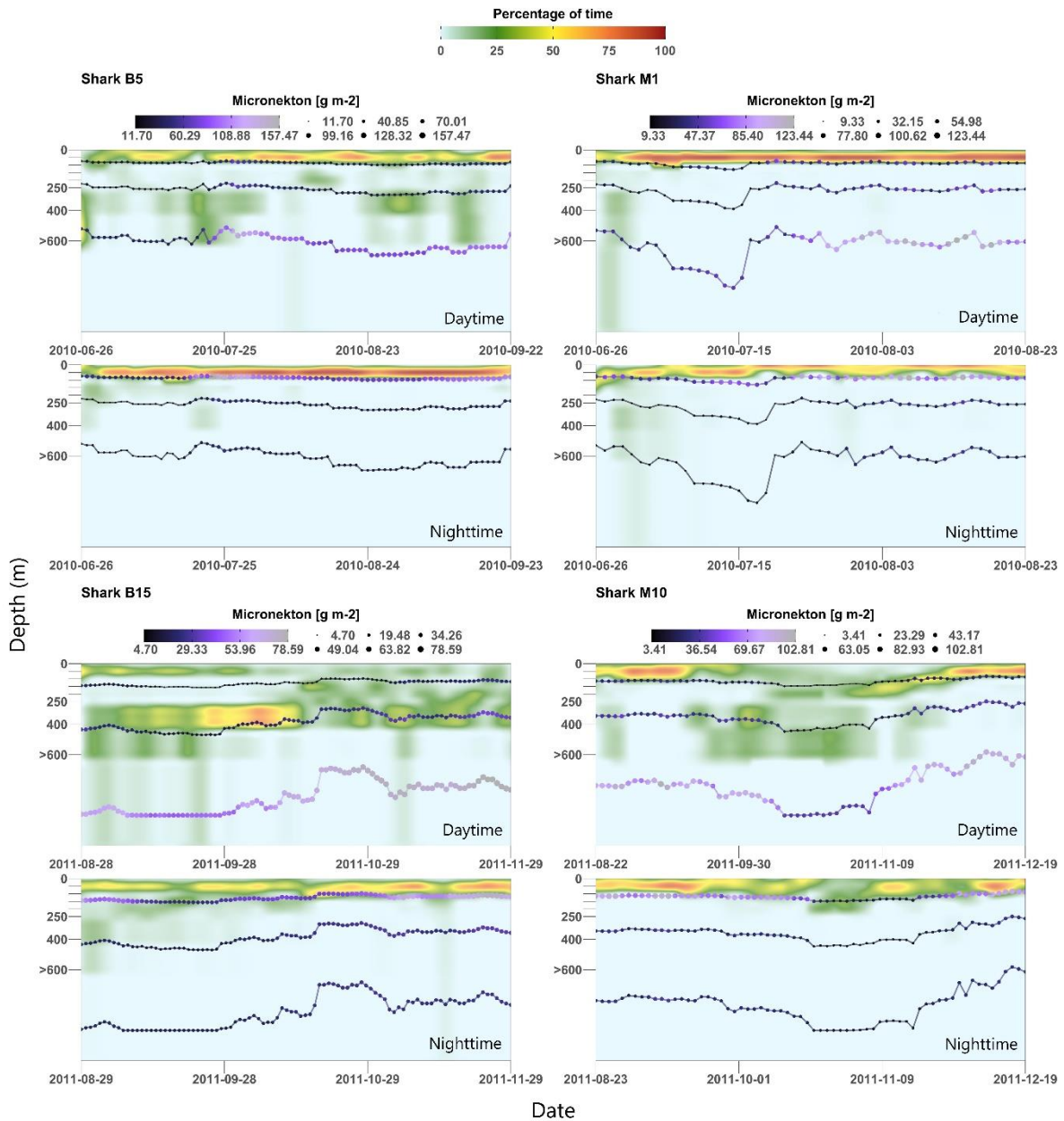
### **3.2 Percentage of time within epipelagic waters**

The two species showed a significant increase of the time spent in epipelagic waters at night (Wilcoxon rank-sum test p-value < 0.0001). Moreover, during daytime, the median percentage of time above 150m for blue and mako sharks was 56.25% (range: 0 – 100%) and 94.20% (range: 0 – 100%), respectively, whereas, at night, the median reached 100% (blue range: 22.70 – 100%, mako range: 0 – 100%) in both species. Regression analysis showed a positive relationship between the SSL micronekton concentration and the percentage of time above 150m (regression analysis, p-value < 0.0001). However, the variation explained by the models was only 19% (Efron's R<sup>2</sup>) for blue sharks and 7% (Efron's R<sup>2</sup>) for mako sharks (Table A1).

### **3.3 Diel vertical behaviour**

Two blue sharks (B12 and B17) and one mako shark (M14) were not included in DVM analysis due to poor-quality TAD matrixes. Throughout the tracking period, sharks commonly displayed regular and depth-oriented nDVM (Figure 3.1, shark B15, shark M10). At night, the tagged animals stayed mostly above the SSL, where the micronekton concentration was highest, while during the day, with the inversion of the micronekton distribution, the time spent above the SSL was substantially reduced. Still, there was no apparent relation between the micronekton distribution and the distinction of these two diel behaviours. Notwithstanding, surface-oriented behaviour was detected in some sharks in proximity to the NAC-LCCZ and inside the ETA OMZ. In most cases, this sort of response appeared to be triggered by an increased daytime micronekton concentration at the SSL compared to the UDSL (Figure 3.1, shark B5 beginning of the track, shark M1). However, a surface-oriented behaviour against the micronekton distribution was identified in one mako shark (M12) inside the OMZ (Figure A2).



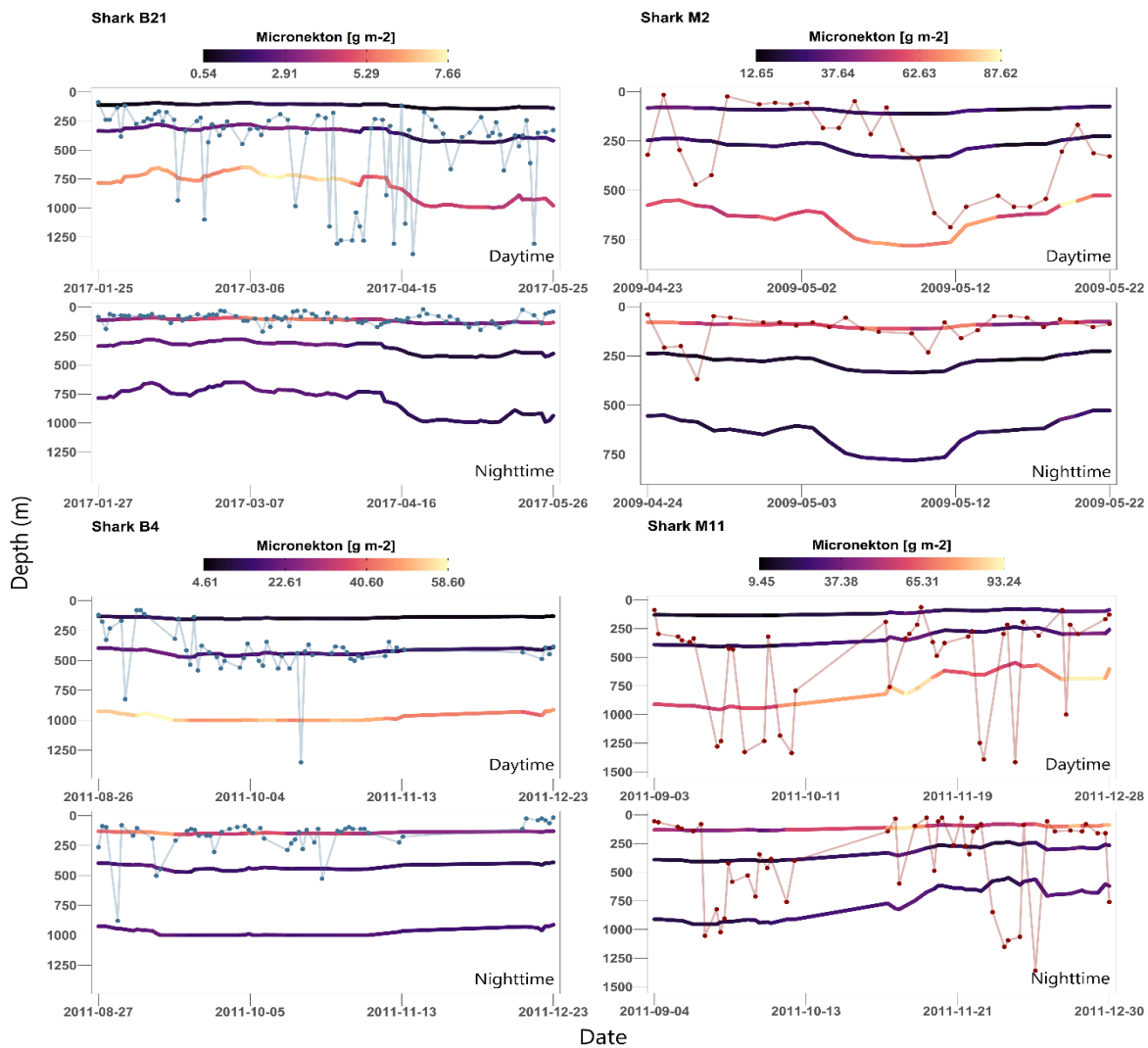


**Figure 3.1** Daytime and nighttime TAD time series. Dotted lines represent the three sound scattering layers coloured and sized according to the micronekton concentration. Dot size is directly proportional to micronekton concentrations.

### 3.4 Diving behaviour

The time-weighted average depth of blue and mako sharks was positively related with the SSLs depth ( $p$ -value  $< 0.0001$ ). However, the models' explained variation differed between day and night, with greater Efron's  $R^2$  values during the night for the blue shark and during the day for the mako shark (Table A2). Moreover, most maximum dives of both species stopped at the SSLs surroundings and seemed to be following their depth variations along time (Figure 3.2). During daylight hours, just 8.52% of blue sharks' maximum depths and 20.88% of mako sharks' maximum depths remained above the SSL with a median SSL distance of 236m and

117m, respectively. In contrast, at night, the percentage of blue and mako shark's maximum depths that did not pass the SSL was 48.54% and 55.11%, respectively. Nighttime distances to the SSL were significantly smaller (Wilcoxon rank-sum test p-value < 0.0001), with blue and mako sharks median SSL distances reaching 44m and 51m each. Furthermore, 46.07% and 47.84% of the blue shark's maximum daytime and nighttime depths fell between the SSL and the UDSL. However, UDSL distances were considerably reduced during the day (Wilcoxon rank-sum test p-value < 0.0001), with a median daytime distance of 91m compared to 225m at night. Regarding the mako shark, 46.18% and 26.26% of maximum daytime and nighttime depths stayed within the SSL and the UDSL. Mako shark's UDSL distances were significantly smaller during the day (Wilcoxon rank-sum test p-value < 0.0001), with a median daytime distance of 136m

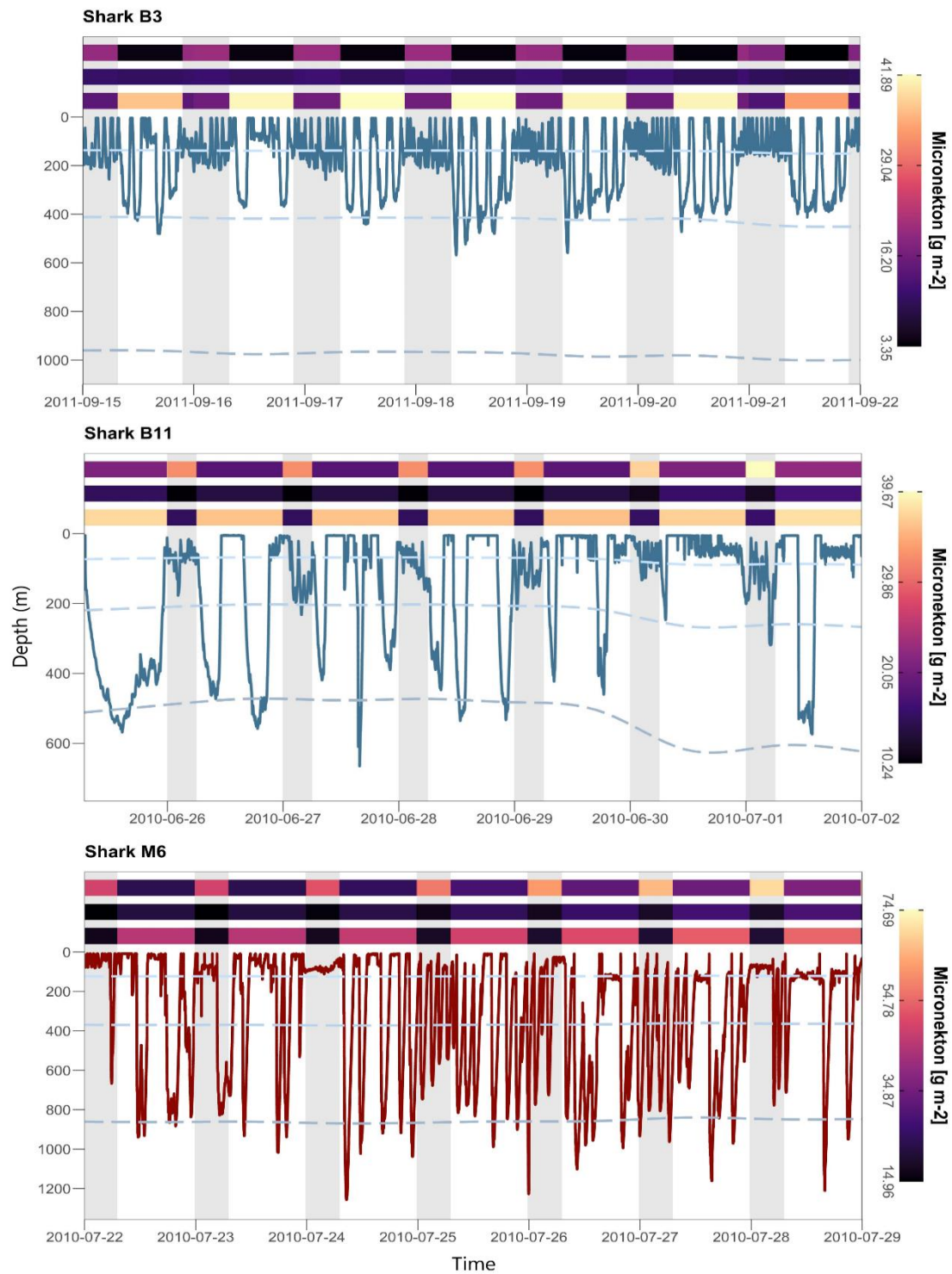


**Figure 3.2** Daytime and nighttime maximum depth time series. Lines represent the three sound scattering layers coloured according to the micronekton concentration. Maximum depths are expressed as points colour-coded by species (blue - *Prionace glauca*, red – *Isurus oxyrinchus*).

contrasting with a median distance of 228m at night. Moreover, the percentage of maximum daytime depths occurring between the upper and lower DSLs was 37.82% and 25.88% for blue and mako sharks, respectively. Whereas, at night, only 3.20% of the blue shark's maximum depths and 13.89% of the mako shark's maximum depths fell within the two-deep scattering layers. Daytime LDSL distances were significantly smaller in both species (Wilcoxon rank-sum test  $p$ -value  $< 0.0001$ ). Blue and mako sharks median LDSL distances were correspondingly 496m and 487m during the day and 696m and 596m at night. Moreover, by daylight, 51 of the blue shark's maximum depths ( $\pm 2.43$  per individual) and 38 of the mako shark's maximum depths ( $\pm 2.24$  per individual) transcended the LDSL depth for more than 100m, whereas during nighttime, this number decreased to 3 in blue sharks ( $\pm 0.14$  per individual) and 21 in mako sharks ( $\pm 1.24$  per individual).

Archival time-series profiles (Figure 3.3) from physically recovered tags revealed frequent vertical oscillatory movements varying between day and night. At night, the sharks' yo-yo-like diving behaviour was generally constricted to the SSL depths, while during daylight hours, these movements became longer fluctuating between surface waters and the two DSLs. Still, small-range oscillations were seen when the sharks reached the DSLs' surroundings. It is essential to notice that under a reversed daytime micronekton distribution ( $mnkc.SSL > mnkc.UDSL < mnkc.LDSL$ ), the blue shark B11 (Figure 3.3) rarely target the UDSL, showing a preference for the LDSL during the day. On the other hand, the mako shark M6, with the same micronekton conditions throughout the majority of its track, displayed two distinct dive patterns. During the time interval represented in Figure 3.3 this shark was targeting the upper and lower DSL during day and night, ignoring micronekton concentrations. Yet, this behaviour was intercalated with periods of increased permanence in shallower waters where the shark did intermittent deep dives far below the LDSL (Figure A3).

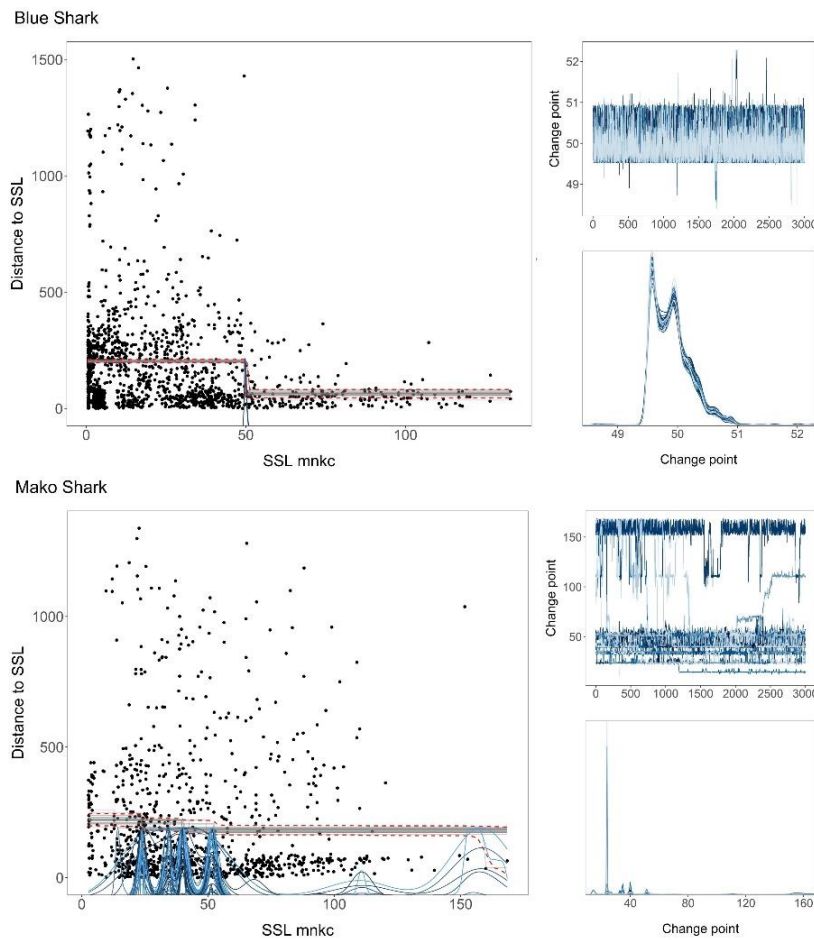
A negative relationship between the layer's distance and its respective micronekton concentration (i.e., the sharks' distance to the layer decreased with the increase of the layer's micronekton concentration) was found for the SSL and LDSL in both species. However, the effect of the micronekton concentration on the mako shark's SSL distance was very close to the threshold of statistical significance ( $p$ -value  $\pm 0.0454$ ) with an explained variation of 0.42% ( $R^2$  Efron). Moreover, the explained variation from LDSL distance models was substantially superior to the SSL models. No significant relation was



**Figure 3.3** One-week interval from the archival time series of three individuals. Dashed lines represent the smoothed depth of the three sound scattering layers. Top stripes are coloured according to the micronekton concentration at each layer, stripes' arrangement corresponds to the scattering layers' order. Grey shades indicate nighttime obtained via suncalc R package. Dive profiles are colour-coded by species (blue - *Prionace glauca*, red – *Isurus oxyrinchus*)

detected for the UDSL (Table A3). Dive profiles suggest that the blue shark's use of the sound scattering layers is more dependent on higher micronekton concentrations than the mako shark, which often appears to target specific layers disregarding micronekton concentrations (Figure 3.2, shark M11 and 3.3, shark M6).

Furthermore, point change analysis revealed a significant increase in the mean distance of blue shark's maximum depths to the SSL below  $\pm 49.90$  g m<sup>-2</sup> (lower  $\pm 49.52$ ; upper  $\pm 50.49$ ) while the mako shark's model was not able to converge (Figure 3.4), thus supporting the previous hypothesis. See table A4 for model summary.



**Figure 3.4** Change point model of *Prionace glauca* (blue shark) and *Isurus oxyrinchus* (mako shark). Blue lines represent the change point posterior density for each chain. Fit lines are represented in grey with the respective quantiles delimited by dashed red lines. Bottom-right plots show the expected values from the posterior predictive distribution. Top-right plots display the different samples from the posterior predictive distribution.

### 3.5 Model results

The best model, explaining 22% (Efron's R<sup>2</sup>) of the maximum depth variability, was given by:

$$\begin{aligned} \text{Maximum Depth} \sim & \text{mnkc.SSL} + \text{mnkc.LDSL} + \text{SST} + \text{DO} + \text{mnkc.SSL} * \text{Species} \\ & + \text{mnkc.LDSL} * \text{Species} + \text{SST} * \text{Species} + \text{DO} * \text{Species} \end{aligned}$$

The mnkc.SSL and mnkc.LDSL showed a significant effect on the maximum depths reached by the two species. However, as expected, the two covariates had different weights and opposite effects. The mnkc.SSL exerted a strong negative influence on the sharks' maximum depths, whereas the mnkc.LDSL had a weaker but positive impact. Also, the species interaction was significant for both the mnkc.SSL and mnkc.LDSL, revealing a more powerful influence of micronekton concentrations on blue sharks' maximum depths.

SST and DO had a positive effect on the two species' maximum depths. Nevertheless, SST exhibited a stronger influence on the blue shark, while the DO was particularly relevant for the mako shark. In short, the blue sharks' maximum depths proved to be better explained by mnkc.SSL while mako sharks' maximum depths were mostly affected by DO levels. See Table 3.2 for the model summary. Spearman's correlation matrix and diagnostic plots are presented in Figures A4 and A5, respectively.

**Table 3.2** Maximum depth model summary.

	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
<b>(Intercept)</b>	-2.5779	0.0761	-33.865	< 2e-16
<b>mnkc.SSL</b>	-0.9165	0.1689	-5.425	6.31e-08
<b>mnkc.LDSL</b>	0.3971	0.1444	2.750	0.005997
<b>O2.100m</b>	1.1683	0.1277	9.148	< 2e-16
<b>SST</b>	0.3552	0.1034	3.435	0.000601
<b>mnkc.SSL:species(blue)</b>	-1.1990	0.2230	-5.377	8.22e-08
<b>mnkc.LDSL:species(blue)</b>	1.2288	0.1833	6.705	2.45e-11
<b>O2.100m:species(blue)</b>	-0.4572	0.1494	-3.061	0.002232
<b>SST:species(blue)</b>	0.3892	0.1055	3.689	0.000230

## 4 Discussion

### 4.1 Diel behaviour and foraging patterns

A significant share of the organisms inhabiting the SSLs performs nDVM, residing at deeper waters during daytime and swimming towards the surface to feed at night. Such behaviour is believed to maximize the animals' survival rates by avoiding visual predators. However, DVM is not restricted to low trophic levels, occurring throughout the trophic web (Hays, 2003). It would not be surprising that large animals with a low

predation risk, such as sharks, modify their diving behaviour in search of their prey. Hence, DVM of apex predatory species has regularly been associated with foraging or searching behaviours (Carey, Scharold and Kalmijn, 1990; Hays, 2003; Sims *et al.*, 2005; Andrews *et al.*, 2009; Queiroz *et al.*, 2012).

In the present study, the tracked individuals spent significantly less time within epipelagic waters during the day, commonly exhibiting diel movements in accordance with the micronekton's vertical distribution. However, mako sharks showed a higher daytime permanence within the epipelagic domain with a median time of 94.20% compared to 56.25% from blue sharks. Previous studies tracking mako sharks over the Southern California Bight, an area known for its extremely low DO levels (McClatchie *et al.*, 2010; Booth *et al.*, 2014), described a similar preference for surface waters (Klimley *et al.*, 2002; Sepulveda *et al.*, 2004; Abascal *et al.*, 2011). Thus, the present results might be associated with the permanent residence inside the ETA OMZ observed in six mako sharks. Furthermore, the positive relationship between the micronekton concentration at the SSL and the time spent at epipelagic waters seen in both blue and mako sharks highlights the importance of prey availability in these predators' depth use. Nevertheless, the smaller percentage of explained variation in mako sharks' model may be the result of other factors influencing the sharks' vertical behaviour.

The tracked animals mainly displayed regular and depth-oriented nDVM, spending more time below the SSL during the day and approaching the surface at night. Although both DVM patterns followed the micronekton's vertical migration, there was no apparent relation between the micronekton vertical distribution and the distinction of these two diel behaviours. Hence, fluctuations between regular and depth-oriented nDVM are probably connected with metabolic optimization. In the present analysis, both species' maximum depth showed to be positively influenced by SST, yet the ectothermic blue shark was significantly more affected. Still, variations between regular and depth-oriented nDVM were detected in both species. Increased permanence in warmer surface waters may give the sharks an advantage while chasing their prey by keeping their muscles working at the optimum temperature (Bennett, 1985, 1990; Johnston and Temple, 2002). This behaviour might be particularly important for the blue shark, which cannot maintain a stable internal temperature (Carey and Teal, 1969). On the other hand, animals performing depth-oriented nDVM might reduce metabolic losses and improve foraging efficiency by resting in colder waters (Sims *et al.*, 2006; Campana *et al.*, 2011; Papastamatiou, Iosilevskii, *et*

*al.*, 2018). Reverse thermoregulatory behaviour (i.e., diving to cool off) has been described in ectothermic species, like the lesser spotted dogfish (*Scyliorhinus canicula*) and the Atlantic stingray (*Dasyatis sabina*) (Sims *et al.*, 2006; Wallman and Bennett, 2006), as well as in endothermic species, such as the bluefin tuna (*Thunnus orientalis* and *Thunnus thynnus*), porbeagle (*Lamna nasus*) and salmon sharks (*Lamna ditropis*) (Kitagawa *et al.*, 2006; Teo *et al.*, 2007; Campana, Joyce and Fowler, 2010; Coffey *et al.*, 2017).

Surface-oriented nDVM was observed in some of the sharks tracked over the NAC-LCCZ and the ETA OMZ, being generally associated with similar or superior daytime micronekton concentrations at the SSL in relation to the UDSL. Nonetheless, under the same conditions, shark B11 chose to target higher micronekton concentrations at the LDSL, thus displaying a more depth-oriented behaviour. Similarly, although shark M2 exhibited a surface-oriented behaviour at the NAC-LCCZ, its maximum depth profile showed daytime maximum dives consistently reaching the LDSL. These patterns might be associated with a selective foraging behaviour further discussed in this work.

Oceanic fronts such as the NAC-LCCZ are characterized by a strong lateral flow and an increased vertical advection induced by the Coriolis effect (Olson *et al.*, 1994; Olson, 2002). Such forces commonly lead to enhanced productivity, mostly due to intense upwelling events, and to the passive accumulation of planktonic and micronektonic organisms caused by horizontal convergence (Lutjeharms, Walters and Allanson, 1985; Le Fèvre, 1987). Moreover, depending on the degree of swimming capacity, the organisms inhabiting these areas might not overcome vertical advection, thus becoming trapped at shallower layers or vice versa (Franks, 1992; Graham, Pagès and Hamner, 2001; Olson, 2002). Therefore, large predators targeting these regions may enhance their fitness by foraging in prey-dense patches and simultaneously reduce energy costs associated with deep diving.

On the other hand, the elevated daytime micronekton concentration at the SSL observed in some of the tracks passing over the ETA OMZ was likely induced by low DO levels. The SSLs are inhabited by various species and different development stages (Dietz, 1962; Hays, 2003; Ariza *et al.*, 2016) with different oxygen tolerances (Seibel, 2011). Thus, under low DO concentrations, some of the organisms typically performing nDVM may not be able to do their usual downward migration at dawn. For instance, Klevjer *et al.* (2016) described a strong relationship between DO levels and the proportion of animals



inhabiting the SSLs that performed nDVM. Likewise, [Bianchi and Mislan \(2016\)](#) suggested that organisms with low tolerance to hypoxic conditions may optimize their time spent at deep hypoxic waters during intense light periods by arriving at the SSL earlier and leaving it later. Nevertheless, although the increased prey density at shallower waters might be advantageous for the sharks foraging inside the OMZ, the low oxygen levels may equally limit their diving behaviour ([Stramma \*et al.\*, 2011](#); [Vedor \*et al.\*, 2021](#)).

For example, a mako shark (M12) tracked within the OMZ displayed a surface-oriented behaviour while experiencing low daytime micronekton concentrations at the SSL. The exceptionally high metabolic rate and fast swimming of the mako shark is reflected on its extremely high oxygen consumption rates compared to ectothermic shark species ([Sepulveda, Graham and Bernal, 2007](#); [Bernal \*et al.\*, 2012](#)). In previous studies, mako sharks tracked around the Eastern Tropical Pacific OMZ showed a general permanence in waters with DO concentrations above 3 ml L<sup>-1</sup> and rarely entered areas below 2 ml L<sup>-1</sup> ([Vetter \*et al.\*, 2008](#); [Abascal \*et al.\*, 2011](#)). Similarly, other large endothermic species such as tunas and billfishes have shown an increased permanence in surface waters inside OMZs ([Prince \*et al.\*, 2010](#); [Stramma \*et al.\*, 2011](#)). Model results revealed a positive effect of DO concentrations in the maximum depth of the two studied species. However, the influence of DO levels on the mako shark was considerably superior, being the stronger of all predictors, whereas the blue shark was mostly affected by micronekton concentrations. Nonetheless, [Vedor \*et al.\* \(2021\)](#) described a vertical habitat compression in blue sharks passing through the core of the OMZ. Hence, even though the mako shark is more affected by DO concentrations, both species are likely to change their foraging behaviour under low DO levels.

The time-weighted average depths of blue and mako sharks were positively influenced by the scattering layers depth during day and night, supporting an interaction between the sharks and the SSLs. Moreover, the tracked individuals' maximum depths were generally consistent with the layers' vertical position, being typically around the SSL at night and shifting between the upper and lower DSL during daylight hours. Further supporting this interaction, the archival time series from physically recovered tags regularly showed sharks performing vertical oscillations in proximity to the SSLs. Several pelagic fishes are known to perform yo-yo diving ([Holland, Brill and Chang, 1990](#); [Heithaus \*et al.\*, 2002](#); [Klimley \*et al.\*, 2002](#)). However, different hypotheses have been attributed to this behaviour, including behavioural thermoregulation, energetically efficient swimming,

navigation, and foraging (Carey, Scharold and Kalmijn, 1990; Heithaus *et al.*, 2002; Nasby-Lucas *et al.*, 2009; Nakamura *et al.*, 2011). During the night, the yo-yo patterns observed in the tracked individuals were generally constricted to the SSL depth, while during the day, besides smaller ranged oscillations at the upper and lower DSLs' surroundings, the sharks did regular excursions to surface waters. Thus, similarly to the bigeye tuna (*Thunnus obesus*) behaviour described by Dagorn, Bach and Josse (2000), the short-range yo-yo movements observed in the tracked individuals were likely associated with searching or feeding events at the SSLs, while the brief excursions to surface waters were perhaps to thermoregulate or balance oxygen concentrations.

Nevertheless, some of the sharks' maximum dives did not stop at the SSLs surroundings, passing them from a few meters to more than one hundred. Based on the Global Ocean Low and Mid Trophic Levels Biomass Hindcast description given by Lehodey and Titauud (2019), the depths provided by the product represent each layer's lower limit. Moreover, the SSLs thickness is known to vary along time and between places (Dietz, 1962; Ariza *et al.*, 2016). Thus, dives stopping between two layers may represent foraging events at the bottom layer. On the other hand, diving deeper than the target layer may give the sharks an advantage by using their countershading to overtake prey from below without being noticed (Klimley, 1994; Heithaus *et al.*, 2002; Sepulveda *et al.*, 2004). Furthermore, dives transcending the LDSL by a considerable distance might be linked with foraging events at a third DSL not described by the environmental model and/or behavioural thermoregulation (Campana *et al.*, 2011; Coffey *et al.*, 2017). Yet, given that the mean SST during deep dives (blue  $22.90 \pm 2.16$ ; mako  $20.32 \pm 3.16$ ) was below the general average (blue  $23.27 \pm 3.03$ ; mako  $22.20 \pm 3.42$ ) the hypothesis of behavioural thermoregulation is less probable. Interestingly, during the day the number of dives per individual passing the LDSL for more than 100m was similar in the two species. Whereas at night the blue sharks did considerably fewer deep dives than mako sharks. These differences might be associated with mako sharks' endothermy, which in theory gives them a physiological advantage for deep diving, (Carey and Teal, 1969; Bernal *et al.*, 2012) or an increased foraging selectivity.

Regarding layers' distance analyses, the negative relationship between the SSL distance and its respective micronekton concentration, along with the non-significant relation of the UDSL, suggests that sharks were foraging at the UDSL as a consequence of low prey availability in the SSL. In comparison, the significant relation observed for the LDSL

suggests that sharks were reaching the LDSL in response to the layer's high prey abundance and not as a reaction to low micronekton concentrations at the upper layer. As discussed, temperature and oxygen levels can be a limiting factor for the vertical movements of top predators (Prince *et al.*, 2010; Bernal *et al.*, 2012; Schlaff, Heupel and Simpfendorfer, 2014; Vedor *et al.*, 2021). Furthermore, due to the large variations of temperature, oxygen, and pressure that sharks have to endure to reach the LDSL depth, foraging at this layer can be a physiological challenge. Still, under higher micronekton concentrations, the increased energy input gain from mesopelagic/bathypelagic prey may compensate for the energy costs associated with deep diving (Goetsch *et al.*, 2018). Stomach analysis from blue and mako sharks revealed the presence of deep-sea fish and cephalopod, such as *Histioteuthis sp.* (Clarke *et al.*, 1996; Maia *et al.*, 2006; Sosa-Nishizaki, 2010; Preti *et al.*, 2012; Galván-Magaña *et al.*, 2013), *Vampyroteuthis infernalis* (Clarke *et al.*, 1996; Sosa-Nishizaki, 2010; Galván-Magaña *et al.*, 2013), *Alepisaurus sp.* (Maia *et al.*, 2006; Vedor *et al.*, unpublished), and *Argyropelecus gigas* (Vedor *et al.*, unpublished) which are probable inhabitants of the LDSL. Moreover, deep dives reaching the LDSL were frequently seen in sharks near the NAC-LCCZ. Such behaviour might be connected to the general preference from cephalopods of the family Histioteuthidae to high productivity regions (Voss, 1969).

Additionally, an abrupt reduction of the blue sharks' distances to the SSL was observed at micronekton concentrations above 49.90 g m<sup>-2</sup>. A similar pattern was previously described in basking sharks (*Cetorhinus maximus*), where the tracked individuals did not produce a defined area-restricted searching behaviour under zooplankton densities below 1 g m<sup>-3</sup>, probably because it was less profitable to filter-feed (Sims and Quayle, 1998). In the present situation, epipelagic concentrations around 49.90 g m<sup>-2</sup> might represent a threshold, above which becomes less advantageous for the blue shark to dive in search of mesopelagic/bathypelagic prey. On the contrary, the mako shark's non-convergent change point model and the frequent dives reaching the mesopelagic layers during nighttime suggest that this species targets non-migrant and/or semi-migrant organisms at the DSL. Even so, stomach analyses from mako sharks have shown large occurrences of epipelagic schooling fish such as *Scomberesox saurus*, *Cololabis saira*, and *Belone belone* (Maia *et al.*, 2006; Preti *et al.*, 2012; Vedor *et al.*, unpublished). Considering mako shark's extreme energetic demands (Wood *et al.*, 2009), the high importance of schooling fish in its diet might be related to their increased accessibility and the mako shark constant

need for food. In other words, the mako shark is likely to consume schooling fish during opportunistic feeding events, whereas mesopelagic/bathypelagic prey is being targeted. Moreover, differences in prey selectivity between the studied species are further supported by the two times stronger effect of both SSL and LDSL micronekton concentrations on blue sharks' maximum depth.

In short, the diel patterns of the animals tracked during this study were coherent with the hypothesis that foraging behaviour is the main responsible for the DVM of apex predatory species. However, it was clear that prey distribution alone was not sufficient to fully explain variations in nDVM. Other environmental factors such as temperature and DO may limit the extent of the vertical movements and impact the time spent at depth. Moreover, although both the studied species appear to be foraging in the SSLs, metabolic and dietetic differences were likely responsible for the observed variation between blue and mako sharks' use of the SSLs. With the blue sharks increased dependence on higher micronekton concentrations being probably connected to a more generalist diet and/or reduced swimming capacity.

## **4.2 Shark conservation in a changing ocean**

As a consequence of global warming and regular nutrient discharges to coastal waters, the ocean's dissolved oxygen content has been declining since at least the middle of the last century (Keeling, Körtzinger and Gruber, 2010; Schmidtko, Stramma and Visbeck, 2017; Breitburg *et al.*, 2018; Levin, 2018; Stramma and Schmidtko, 2019). Ocean deoxygenation is leading to the vertical and horizontal expansion of the world's OMZs with numerous repercussions for the marine biota (Grantham *et al.*, 2004; Stramma *et al.*, 2008, 2011; Ekau *et al.*, 2010; Penn *et al.*, 2018). Because most organisms have a low hypoxic threshold (Vaquer-Sunyer and Duarte, 2008; Ekau *et al.*, 2010), the ongoing expansion of OMZs increases foraging opportunities for apex predators as their target prey is being compressed in shallower waters (Stramma *et al.*, 2011; Vedor *et al.*, 2021). For instance, in this study we detected a significant reduction of the SSLs depth and a superior daytime micronekton concentrations at the SSL compared to the UDSL within the ETA OMZ. In response, the tracked sharks increased their time above the upper layer and reduced their vertical extent. Consequently raising their risk of being captured by longline fisheries with hooks generally deployed between 100 and 300 m (Domingo *et al.*, 2014). A similar behaviour was detected in sharks passing over the NAC-LCCZ, a highly productive area known to be target by both pelagic predators and longline fisheries

(Queiroz *et al.*, 2016, 2019). However, in this case, the reversed micronekton distribution was likely caused by strong advection currents typically seen in frontal systems (Franks, 1992; Graham, Pagès and Hamner, 2001; Olson, 2002).

Large predators are equally sensible to hypoxia and will also undergo vertical habitat compression according to their physiological limits (Stramma *et al.*, 2011; Sims, 2019), as observed in shark M12. As a result, hypoxic tolerant prey might find refuge from predators in deep hypoxic waters forcing these animals to shift diets to possibly less energy-rich prey. Vetter *et al.* (2008) described a potential hypoxic shelter for the jumbo squid, one of the primary prey items found in mako sharks' stomachs captured over the California current (Preti *et al.*, 2012). Still, the jumbo squid performs diel vertical migrations becoming available to prey upon during the night (Vetter *et al.*, 2008). Other animals observed in the stomach contents of the studied species, such as the *Vampyroteuthis infernalis* (Clarke *et al.*, 1996; Sosa-Nishizaki, 2010; Galván-Magaña *et al.*, 2013), not only are adapted to live under low oxygen concentrations but also are permanent residents of the deep sea (Roper and Young, 1975; Hoving and Robison, 2012; Golikov *et al.*, 2019). Consequently, becoming virtually unavailable for blue and mako sharks inside OMZs.

In the present context of rapidly declining shark populations and ongoing global changes, it is imperative to implement effective conservation and management actions (Baum *et al.*, 2003; Baum and Myers, 2004; Dulvy *et al.*, 2008). Observer programs can provide more accurate catch and discard data, essential for the efficient management of shark populations and, at the same time, improve fishing-records of the more lucrative teleost species (Campana, 2016). Thus, the increase of observer coverage on commercial fishing vessels in national and international fisheries might be the first step for successfully managing shark populations. Secondly, as the ocean conditions continue to change, affecting stock productivity, the implementation of dynamic stock productivity models instead of the traditionally used stationary stock risk models is essential for the sustainable harvesting of fish populations (Britten *et al.*, 2017). Moreover, tracking data provides crucial fisheries-independent information on highly mobile animals' movements and habitat preferences over large spatial and temporal scales. Such information can then be used to assess the species' spatiotemporal susceptibility to fisheries (Queiroz *et al.*, 2019). Likewise, tracking data can be employed to inform population assessments and estimate natural and fishery-induced mortality (Block *et al.*, 2011; Byrne *et al.*, 2017). In this

sense, telemetry studies like the present can largely contribute to the sustainable management and conservation of highly mobile predators by improving our understanding of their ecology.

Beyond the urgent need to improve regulation on shark catches with the introduction of international science-based catch limits or even total catch prohibition of critically endangered species (Dulvy *et al.*, 2008; Campana, 2016), the implementation of marine protected areas (MPAs) in key regions, such as the ETA OMZ and the NAC-LCCZ, can provide essential support for the recovery of shark populations (Game *et al.*, 2009; Worm *et al.*, 2009; Ward-Paige *et al.*, 2012; Birkmanis *et al.*, 2020). Moreover, considering the rapid changing ocean conditions, the implementation of near real-time management strategies, like dynamic MPAs, based on both satellite telemetry and fisheries observer data might help to accomplish conservation goals while supporting economically viable fisheries (Hazen *et al.*, 2018). Sharks' vulnerability to fisheries is influenced by multiple factors, including gear type and depth, bait, time of operation, visibility conditions, and attractors (Cortés *et al.*, 2009). Hence, additional management actions could pass by increasing gear selectivity and the deployment of fishing hooks beyond the sharks' preferred depths (Queiroz *et al.*, 2016). The last might be particularly important over areas with increased permanence at surface waters. Moreover, the use of circle hooks in place of the traditional J-style hooks is known to improve post-release survival with minimal effects on target species' catches (Kerstetter and Graves, 2006a, 2006b). Nevertheless, circle hooks' benefit for shark conservation is debatable due to the increased catchability of some shark species (Ward *et al.*, 2009). Similarly, the banning of wire leaders in pelagic longline fisheries has proved to be an effective way to reduce shark catches while increasing bigeye tuna's catching rates (Ward *et al.*, 2008).

To conclude, during the last two years, critical decisions were made regarding the fate of blue and mako sharks in the Atlantic Ocean, including the implementation of fishing quotas for the blue shark (ICCAT, 2019) and the very recent prohibition of mako shark landings in Portugal and Spain. Nevertheless, the substantial space use overlap between these two species and the longline fishing fleet (Queiroz *et al.*, 2016, 2019) makes their by-catch unavoidable. Moreover, ongoing global changes are altering marine habitats and consequently changing the sharks' space use, often increasing their exposure to pelagic fisheries and possibly reducing their rebound capacity (White, 2008; Stramma *et al.*, 2011; Vedor *et al.*, 2021). Hence, an improved understanding of these species' spatial

ecology patterns is fundamental to implement prompt and adequate management decisions and ensure their preservation.

## 5 Conclusion and future work

The present study highlights the importance of the SSLs as a food source for mesopelagic predators and their influence on these animals' vertical movements. It also suggests the potential use of the oceanographic product Global Ocean Low and Mid Trophic Levels Biomass Hindcast provided by Copernicus as a tool to identify areas of increased fisheries susceptibility. Precisely, areas with inverted daytime micronekton distributions ( $mnkc.SSL > mnkc.UDSL < mnkc.LDSL$ ) and shallower SSLs, which proved to increase the time sharks spent within epipelagic waters and reduce their vertical extent, raising their exposure to pelagic fisheries. Moreover, considering the ongoing expansion of the world's OMZs, some pelagic macropredators might lose their access to highly energetic mesopelagic/bathypelagic prey. Consequently, affecting these species' fitness and possibly their rebound capacity (White, 2008).

Nonetheless, some improvements could be made in order to increase the robustness of the present analyses. For instance, with the combination of animal-borne image records and accelerometers would be possible to identify/verify foraging attempts/success at the SSLs (Nakamura *et al.*, 2011; Papastamatiou, Watanabe, *et al.*, 2018; Watanabe *et al.*, 2019). Likewise, double-tagging the individuals with both ARGOS (Advanced Research and Global Observation Satellite) platform transmitter terminals (PTTs) and PSAT tags would improve the accuracy of the location estimates and consequently allow the extraction of more precise environmental data (Hueter, Tyminski and de la Parra, 2013). Furthermore, improved information on the species-composition and diel patterns of the SSLs would help to better define relationships between the scattering layers and the animals' vertical movements. Finally, future studies concerning blue and mako sharks' diet in the North Atlantic Ocean with higher spatial coverage and area-restricted analyses are equally needed to explain regional differences in these predators' usage of the SSLs.

## 6 References

- Abascal, F. J. et al. (2011) 'Movements and environmental preferences of the shortfin mako, *Isurus oxyrinchus*, in the southeastern Pacific Ocean', *Marine Biology*, 158(5), pp. 1175–1184. doi: 10.1007/s00227-011-1639-1.
- Andrews, K. S. et al. (2009) 'Diel activity patterns of sixgill sharks, *Hexanchus griseus*: the ups and downs of an apex predator', *Animal Behaviour*. Elsevier Ltd, 78(2), pp. 525–

536. doi: 10.1016/j.anbehav.2009.05.027.

Ariza, A. et al. (2016) 'Vertical distribution, composition and migratory patterns of acoustic scattering layers in the Canary Islands', *Journal of Marine Systems*. Elsevier B.V., 157, pp. 82–91. doi: 10.1016/j.jmarsys.2016.01.004.

Barker, M. J. and Schluessel, V. (2005) 'Managing global shark fisheries: Suggestions for prioritizing management strategies', *Aquatic Conservation: Marine and Freshwater Ecosystems*, 15(4), pp. 325–347. doi: 10.1002/aqc.660.

Baum, J. K. et al. (2003) 'Collapse and conservation of shark populations in the Northwest Atlantic', *Science*, 299(5605), pp. 389–392. doi: 10.1126/science.1079777.

Baum, J. K. and Myers, R. A. (2004) 'Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico', *Ecology Letters*, 7(2), pp. 135–145. doi: 10.1111/j.1461-0248.2003.00564.x.

Bennett, A. F. (1985) 'Temperature and muscle', *Journal of Experimental Biology*, 115, pp. 333–344.

Bennett, A. F. (1990) 'Thermal dependence of locomotor capacity', *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, 259(2), pp. 253–258. doi: 10.1152/ajpregu.1990.259.2.r253.

Bernal, D. et al. (2012) 'Energetics, Metabolism, and Endothermy in Sharks and Rays', in Carrier, J. C., Musick, J. A. J., and Heithaus, M. R. (eds) *Biology of Sharks and Their Relatives*. Second Edition. CRC Press, pp. 211–237. doi: 10.5860/choice.50-2067.

Bianchi, D. and Mislan, K. A. S. (2016) 'Global patterns of diel vertical migration times and velocities from acoustic data', *Limnology and Oceanography*, 61(1), pp. 353–364. doi: 10.1002/lno.10219.

Birkmanis, C. A. et al. (2020) 'Shark conservation hindered by lack of habitat protection', *Global Ecology and Conservation*. Elsevier Ltd, 21, p. e00862. doi: 10.1016/j.gecco.2019.e00862.

Block, B. A. et al. (2011) 'Tracking apex marine predator movements in a dynamic ocean', *Nature*. Nature Publishing Group, 475(7354), pp. 86–90. doi: 10.1038/nature10082.

Booth, J. A. T. et al. (2014) 'Patterns and potential drivers of declining oxygen content along the southern California coast', *Limnology and Oceanography*, 59(4), pp. 1127–1138. doi: 10.4319/lo.2014.59.4.1127.

Breitburg, D. et al. (2018) 'Declining oxygen in the global ocean and coastal waters', *Science*, 359(6371). doi: 10.1126/science.aam7240.

Britten, G. L. et al. (2017) 'Extended fisheries recovery timelines in a changing environment', *Nature Communications*. Nature Publishing Group, 8(May 2017), pp. 1–7. doi: 10.1038/ncomms15325.

Burnham, K. P., Anderson, D. R. and Huyvaert, K. P. (2011) 'AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and



comparisons', *Behavioral Ecology and Sociobiology*, 65(1), pp. 23–35. doi: 10.1007/s00265-010-1029-6.

Byrne, M. E. et al. (2017) 'Satellite telemetry reveals higher fishing mortality rates than previously estimated, suggesting overfishing of an apex marine predator', *Proceedings of the Royal Society B: Biological Sciences*, 284(1860). doi: 10.1098/rspb.2017.0658.

Cailliet, G. M., Musick, J. A. and Simpfendorfer, C. A. (2005) 'Ecology and Life History Characteristics of Chondrichthyan Fish', in *Sharks, Rays and Chimaeras: The Status of the Chondrichthyan Fishes*, Status Survey., pp. 12–18.

Camhi, M. D. et al. (2008) 'A Global Overview of Commercial Fisheries for Open Ocean Sharks', in Camhi, M. D., Pikitch, E. K., and Babcock, E. A. (eds) *Sharks of the Open Ocean: Biology, Fisheries and Conservation*. Blackwell Publishing Ltd., pp. 166–192. doi: 10.1002/9781444302516.ch14.

Campana, S. E. et al. (2011) 'Migration pathways, behavioural thermoregulation and overwintering grounds of blue sharks in the Northwest Atlantic', *PLoS ONE*, 6(2). doi: 10.1371/journal.pone.0016854.

Campana, S. E. (2016) 'Transboundary movements, unmonitored fishing mortality, and ineffective international fisheries management pose risks for pelagic sharks in the Northwest Atlantic', *Canadian Journal of Fisheries and Aquatic Sciences*, 73(10), pp. 1599–1607. doi: 10.1139/cjfas-2015-0502.

Campana, S. E., Joyce, W. and Fowler, M. (2010) 'Subtropical pupping ground for a cold-water shark', *Canadian Journal of Fisheries and Aquatic Sciences*, 67(5), pp. 769–773. doi: 10.1139/F10-020.

Carey, F. G., Scharold, J. V. and Kalmijn, A. J. (1990) 'Movements of blue sharks (*Prionace glauca*) in depth and course', *Marine Biology*, 106(3), pp. 329–342. doi: 10.1007/BF01344309.

Carey, F. G. and Teal, J. M. (1969) 'Mako and porbeagle: warm-bodied sharks', 28(2138), pp. 199–204.

Clarke, M. et al. (1996) 'The diet of the blue shark (*Prionace glauca* L.) in Azorean waters', *Life and Marine Sciences*, 14A, pp. 41–56.

Coffey, D. M. et al. (2017) 'Oceanographic drivers of the vertical distribution of a highly migratory, endothermic shark', *Scientific Reports*. Springer US, 7(1), pp. 1–14. doi: 10.1038/s41598-017-11059-6.

Cortés, E. (2000) 'Life History Patterns and Correlations in Sharks', *Reviews in Fisheries Science*, 8(4), pp. 299–344. doi: 10.1080/10408340308951115.

Cortés, E. et al. (2009) 'Ecological risk assessment of pelagic sharks caught in Atlantic pelagic longline fisheries', *Aquatic Living Resources*, 23(1), pp. 25–34. doi: 10.1051/alr/2009044.

Dagorn, L., Bach, P. and Josse, E. (2000) 'Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry', *Marine*

- Biology*, 136(2), pp. 361–371. doi: 10.1007/s002270050694.
- Dietz, R. S. (1962) ‘The Sea’s Deep Scattering Layers’, *Scientific American*, 207(2), pp. 44–50. doi: 10.1038/scientificamerican0862-44.
- Domingo, A. et al. (2014) ‘Longline’, in *ICCAT manual*, pp. 1–48. doi: 10.13140/2.1.1615.8088.
- Dulvy, N. et al. (2014) ‘Extinction risk and conservation of the world’s sharks and rays’, *eLife*, 3, pp. 1–34. doi: 10.7554/eLife.00590.
- Dulvy, N. K. et al. (2008) ‘You can swim but you can’t hide: the global status and conservation of oceanic pelagic sharks and rays’, *Aquatic conservation: Marine and Freshwater Ecosystems*, 18, pp. 459–482.
- Ekau, W. et al. (2010) ‘Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish)’, *Biogeosciences*, 7(5), pp. 1669–1699. doi: 10.5194/bg-7-1669-2010.
- Estes, J. A. et al. (2011) ‘Trophic downgrading of planet earth’, *Science*, 333(6040), pp. 301–306. doi: 10.1126/science.1205106.
- Ferretti, F. et al. (2010) ‘Patterns and ecosystem consequences of shark declines in the ocean’, *Ecology Letters*, 13(8), pp. 1055–1071. doi: 10.1111/j.1461-0248.2010.01489.x.
- Le Fèvre, J. (1987) Aspects of the Biology of Frontal Systems, *Advances in Marine Biology*. doi: 10.1016/S0065-2881(08)60109-1.
- Franks, P. J. S. (1992) ‘Sink or swim: Accumulation of biomass at fronts’, *Marine Ecology Progress Series*, 82, pp. 1–12. doi: 10.3354/meps082001.
- Galuardi, B. (2019) ‘analyzepsat: Microwave Telemetry PSAT analysis’.
- Galván-Magaña, F. et al. (2013) ‘Shark predation on cephalopods in the Mexican and Ecuadorian Pacific Ocean’, *Deep-Sea Research Part II: Topical Studies in Oceanography*. Elsevier, 95, pp. 52–62. doi: 10.1016/j.dsr2.2013.04.002.
- Game, E. T. et al. (2009) ‘Pelagic protected areas: the missing dimension in ocean conservation’, *Trends in Ecology and Evolution*, 24(7), pp. 360–369. doi: 10.1016/j.tree.2009.01.011.
- Goetsch, C. et al. (2018) ‘Energy-rich mesopelagic fishes revealed as a critical prey resource for a deep-diving predator using quantitative fatty acid Signature Analysis’, *Frontiers in Marine Science*, 5(NOV), pp. 1–19. doi: 10.3389/fmars.2018.00430.
- Golikov, A. V. et al. (2019) ‘The first global deep-sea stable isotope assessment reveals the unique trophic ecology of Vampire Squid *Vampyroteuthis infernalis* (Cephalopoda)’, *Scientific Reports*, 9(1), pp. 1–13. doi: 10.1038/s41598-019-55719-1.
- Graham, W. M., Pagès, F. and Hamner, W. M. (2001) ‘A physical context for gelatinous zooplankton aggregations: A review’, *Hydrobiologia*, 451, pp. 199–212. doi: 10.1023/A:1011876004427.

- Gramacy, R. B. and Taddy, M. (2010) ‘Categorical Inputs, Sensitivity Analysis, Optimization and Importance Tempering with *tgp* Version 2, an R Package for Treed Gaussian Process Models.’, *Journal of Statistical Software*, 33(6), pp. 1–48. Available at: <https://www.jstatsoft.org/v33/i06/>.
- Grantham, B. A. et al. (2004) ‘Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific’, *Nature*, 429(6993), pp. 749–754. doi: 10.1038/nature02605.
- Harcourt, R. et al. (2019) ‘Animal-borne telemetry: An integral component of the ocean observing toolkit’, *Frontiers in Marine Science*, 6(326), pp. 1–21. doi: 10.3389/fmars.2019.00326.
- Härdle, W. K. and Simar, L. (2015) *Applied Multivariate Statistical Analysis, Fourth Edition*. doi: 10.1007/978-3-662-45171-7.
- Hartig, F. (2020) ‘DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models’. Available at: <http://florianhartig.github.io/DHARMA/>.
- Hays, G. C. (2003) ‘A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations’, *Hydrobiologia*, 503, pp. 163–170. doi: 10.1023/B:HYDR.0000008476.23617.b0.
- Hazen, E. L. et al. (2018) ‘A dynamic ocean management tool to reduce bycatch and support sustainable fisheries’, *Science Advances*, 4(5), pp. 1–8. doi: 10.1126/sciadv.aar3001.
- Heithaus, M. R. et al. (2002) ‘Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem’, *Marine Biology*, 140(2), pp. 237–248. doi: 10.1007/s00227-001-0711-7.
- Heithaus, M. R. et al. (2008) ‘Predicting ecological consequences of marine top predator declines’, *Trends in Ecology and Evolution*, 23(4), pp. 202–210. doi: 10.1016/j.tree.2008.01.003.
- Heupel, M. R. et al. (2014) ‘Sizing up the ecological role of sharks as predators’, *Marine Ecology Progress Series*, 495, pp. 291–298. doi: 10.3354/meps10597.
- Holland, K. N., Brill, R. W. and Chang, R. K. C. (1990) ‘Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregating devices’, *Fishery Bulletin*, 88(3), pp. 493–507.
- Hoving, H. J. T. and Robison, B. H. (2012) ‘Vampire squid: Detritivores in the oxygen minimum zone’, *Proceedings of the Royal Society B: Biological Sciences*, 279(1747), pp. 4559–4567. doi: 10.1098/rspb.2012.1357.
- Hueter, R. E., Tyminski, J. P. and de la Parra, R. (2013) ‘Horizontal Movements, Migration Patterns, and Population Structure of Whale Sharks in the Gulf of Mexico and Northwestern Caribbean Sea’, *PLoS ONE*, 8(8). doi: 10.1371/journal.pone.0071883.
- Hussey, N. E. et al. (2015) ‘Aquatic animal telemetry: A panoramic window into the underwater world’, *Science*, 348(6240), p. 1255642. doi: 10.1126/science.1255642.

ICCAT (2019) '26th Regular Meeting of the International Commission for the Conservation of Atlantic Tunas (Palma de Mallorca, Spain)'. Available at: <https://www.iccat.int/en/Meetings.asp>.

Johnson, D. S., London, J. and Wilson, K. (2015) 'crawl: Fit Continuous-Time Correlated Random Walk Models to Animal Movement Data'.

Johnston, I. A. and Temple, G. K. (2002) 'Thermal plasticity of skeletal muscle phenotype in ectothermic vertebrates and its significance for locomotory behaviour', *Journal of Experimental Biology*, 205(15), pp. 2305–2322.

Jonsen, I. D., Flemming, J. M. and Myers, R. A. (2005) 'Robust state-space modeling of animal movement data', *Ecology*, 86(11), pp. 2874–2880. doi: 10.1890/04-1852.

Keeling, R. F., Körtzinger, A. and Gruber, N. (2010) 'Ocean deoxygenation in a warming world', *Annual Review of Marine Science*, 2(1), pp. 199–229. doi: 10.1146/annurev.marine.010908.163855.

Kerstetter, D. W. and Graves, J. E. (2006a) 'Effects of circle versus J-style hooks on target and non-target species in a pelagic longline fishery', *Fisheries Research*, 80(2–3), pp. 239–250. doi: 10.1016/j.fishres.2006.03.032.

Kerstetter, D. W. and Graves, J. E. (2006b) 'Survival of white marlin (*Tetrapturus albidus*) released from commercial pelagic longline gear in the western North Atlantic', *Fishery Bulletin*, 104(3), pp. 434–444.

Kitagawa, T. et al. (2006) 'Thermal adaptation of Pacific bluefin tuna *Thunnus orientalis* to temperate waters', *Fisheries Science*, 72(1), pp. 149–156. doi: 10.1111/j.1444-2906.2006.01129.x.

Klevjer, T. A. et al. (2016) 'Large scale patterns in vertical distribution and behaviour of mesopelagic scattering layers', *Scientific Reports*. Nature Publishing Group, 6(1), pp. 1–11. doi: 10.1038/srep19873.

Klevjer, T. A., Torres, D. J. and Kaartvedt, S. (2012) 'Distribution and diel vertical movements of mesopelagic scattering layers in the Red Sea', *Marine Biology*, 159(8), pp. 1833–1841. doi: 10.1007/s00227-012-1973-y.

Klimley, A. P. (1994) 'The Predatory Behavior of the White Shark', *American Scientist*. The Scientific Research Society, 82(2), pp. 122–133. Available at: <http://www.jstor.org/stable/29775147>.

Klimley, A. P. et al. (2002) 'Movements and swimming behavior of three species of sharks in La Jolla Canyon, California', *Environmental Biology of Fishes*, 63(2), pp. 117–135. doi: 10.1023/A:1014200301213.

Lam, C. H., Nielsen, A. and Sibert, J. R. (2008) 'Improving light and temperature based geolocation by unscented Kalman filtering', *Fisheries Research*, 91(1), pp. 15–25. doi: 10.1016/j.fishres.2007.11.002.

- Lehodey, P. and Titaud, O. (2019) ‘Global Production Centre GLOBAL\_REANALYSIS\_BIO\_001\_033’, pp. 1–27.
- Levin, L. A. (2018) ‘Manifestation, drivers, and emergence of open ocean deoxygenation’, *Annual Review of Marine Science*, 10, pp. 229–260. doi: 10.1146/annurev-marine-121916-063359.
- Li, W. and Liu, Z. (2011) ‘A method of SVM with normalization in intrusion detection’, *Procedia Environmental Sciences*, 11, pp. 256–262. doi: 10.1016/j.proenv.2011.12.040.
- Lindeløv, J. K. (2020) ‘mcp: An R Package for Regression with Multiple Change Points’, *OSF Preprints*. doi: 10.31219/osf.io/fzqxv.
- Lutjeharms, J. R. E., Walters, N. M. and Allanson, B. R. (1985) ‘Oceanic frontal systems and biological enhancement.’, *Antarctic nutrient cycles and food webs*, pp. 11–21. doi: 10.1007/978-3-642-82275-9\_3.
- Maia, A. et al. (2006) ‘Food habits of the shortfin mako, *Isurus oxyrinchus*, off the southwest coast of Portugal’, *Environmental Biology of Fishes*, 77(2), pp. 157–167. doi: 10.1007/s10641-006-9067-7.
- McClatchie, S. et al. (2010) ‘Oxygen in the Southern California Bight: Multidecadal trends and implications for demersal fisheries’, *Geophysical Research Letters*, 37(19), pp. 1–6. doi: 10.1029/2010GL044497.
- Nakamura, I. et al. (2011) ‘Yo-yo vertical movements suggest a foraging strategy for tiger sharks *Galeocerdo cuvier*’, *Marine Ecology Progress Series*, 424, pp. 237–246. doi: 10.3354/meps08980.
- Nakano, H. et al. (2003) ‘Acoustic tracking of bigeye thresher shark *Alopias superciliosus* in the eastern Pacific Ocean’, *Marine Ecology Progress Series*, 265, pp. 255–261. doi: 10.3354/meps265255.
- Nandintsetseg, D. et al. (2019) ‘Challenges in the conservation of wide-ranging nomadic species’, *Journal of Applied Ecology*, 56(8), pp. 1916–1926. doi: 10.1111/1365-2664.13380.
- Nasby-Lucas, N. et al. (2009) ‘White shark offshore habitat: A behavioral and environmental characterization of the eastern pacific shared offshore foraging area’, *PLoS ONE*, 4(12). doi: 10.1371/journal.pone.0008163.
- Norheim, E., Klevjer, T. A. and Aksnes, D. L. (2016) ‘Evidence for light-controlled migration amplitude of a sound scattering layer in the Norwegian Sea’, *Marine Ecology Progress Series*, 551, pp. 45–52. doi: 10.3354/meps11731.
- Olson, D. et al. (1994) ‘Life on the Edge: Marine Life and Fronts’, *Oceanography*, 7(2), pp. 52–60. doi: 10.5670/oceanog.1994.03.
- Olson, D. B. (2002) ‘Biophysical dynamics of ocean fronts’, in *The Sea*, 12, pp. 187–218.
- Papastamatiou, Y. P., Watanabe, Y. Y., et al. (2018) ‘Activity seascapes highlight central place foraging strategies in marine predators that never stop swimming’, *Movement*

*Ecology*, 6(1), pp. 1–15. doi: 10.1186/s40462-018-0127-3.

Papastamatiou, Y. P., Iosilevskii, G., et al. (2018) ‘Optimal swimming strategies and behavioral plasticity of oceanic whitetip sharks’, *Scientific Reports*. Springer US, 8(1), pp. 1–12. doi: 10.1038/s41598-017-18608-z.

Penn, J. L. et al. (2018) ‘Temperature-dependent hypoxia explains biogeography and severity of end-Permian marine mass extinction’, *Science*, 362(6419). doi: 10.1126/science.aat1327.

Preti, A. et al. (2008) ‘Feeding habits of the bigeye thresher shark (*Alopias superciliosus*) sampled from the California-based drift gillnet fishery’, *California Cooperative Oceanic Fisheries Investigations Reports*, 49, pp. 202–211.

Preti, A. et al. (2012) ‘Comparative feeding ecology of shortfin mako, blue and thresher sharks in the California Current’, *Environmental Biology of Fishes*, 95(1), pp. 127–146. doi: 10.1007/s10641-012-9980-x.

Prince, E. D. et al. (2010) ‘Ocean scale hypoxia-based habitat compression of Atlantic istiophorid billfishes’, *Fisheries Oceanography*, 19(6), pp. 448–462. doi: 10.1111/j.1365-2419.2010.00556.x.

Queiroz, N. et al. (2012) ‘Spatial Dynamics and Expanded Vertical Niche of Blue Sharks in Oceanographic Fronts Reveal Habitat Targets for Conservation’, *PLoS ONE*, 7(2). doi: 10.1371/journal.pone.0032374.

Queiroz, N. et al. (2016) ‘Ocean-wide tracking of pelagic sharks reveals extent of overlap with longline fishing hotspots’, *PNAS*, 113(6). doi: 10.1073/pnas.1510090113.

Queiroz, N. et al. (2019) ‘Global spatial risk assessment of sharks under the footprint of fisheries’, *Nature*, 572(7770), pp. 461–466. doi: 10.1038/s41586-019-1444-4.

Roper, C. F. E. and Young, R. E. (1975) ‘Vertical distribution of pelagic cephalopods’, *Smithsonian Contributions to Zoology*, (209), pp. 1–51. doi: 10.5479/si.00810282.209.

Schlaff, A. M., Heupel, M. R. and Simpfendorfer, C. A. (2014) ‘Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review’, *Reviews in Fish Biology and Fisheries*, 24(4), pp. 1089–1103. doi: 10.1007/s11160-014-9364-8.

Schmidtko, S., Stramma, L. and Visbeck, M. (2017) ‘Decline in global oceanic oxygen content during the past five decades’, *Nature*. Nature Publishing Group, 542(7641), pp. 335–339. doi: 10.1038/nature21399.

Schmiing, M. et al. (2013) ‘Predictive habitat modelling of reef fishes with contrasting trophic ecologies’, *Marine Ecology Progress Series*, 474, pp. 201–216. doi: 10.3354/meps10099.

Seibel, B. A. (2011) ‘Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones’, *Journal of Experimental Biology*, 214(2), pp. 326–336. doi: 10.1242/jeb.049171.

Sepulveda, C. A. et al. (2004) ‘Movement patterns, depth preferences, and stomach temperatures of free-swimming juvenile mako sharks, *Isurus oxyrinchus*, in the Southern

- California Bight', *Marine Biology*, 145(1), pp. 191–199. doi: 10.1007/s00227-004-1356-0.
- Sepulveda, C. A., Graham, J. B. and Bernal, D. (2007) 'Aerobic metabolic rates of swimming juvenile mako sharks, *Isurus oxyrinchus*', *Marine Biology*, 152(5), pp. 1087–1094. doi: 10.1007/s00227-007-0757-2.
- Sims, D. W. et al. (2005) 'Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark', *Journal of Animal Ecology*, 74(4), pp. 755–761. doi: 10.1111/j.1365-2656.2005.00971.x.
- Sims, D. W. et al. (2006) 'Hunt warm, rest cool: Bioenergetic strategy underlying diel vertical migration of a benthic shark', *Journal of Animal Ecology*, 75(1), pp. 176–190. doi: 10.1111/j.1365-2656.2005.01033.x.
- Sims, D. W. (2010) 'Tracking and Analysis Techniques for Understanding Free-Ranging Shark Movements and Behavior', in Carrier, J. C., Musick, J. A., and Heithaus, M. R. (eds) *Sharks and Their Relatives II: Biodiversity, Adaptive Physiology, and Conservation*. CRC Press, pp. 351–392. doi: 10.1201/9781420080483.
- Sims, D. W. and Quayle, V. A. (1998) 'Selective foraging behaviour of basking sharks on zooplankton in a small-scale front', *Nature*, 393(6684), pp. 460–464. doi: 10.1038/30959.
- Sosa-Nishizaki, O. (2010) 'Food and feeding habits of the blue shark *Prionace glauca* caught off Ensenada, Baja California, Mexico, with a review on its feeding', *Journal of the Marine Biological Association of the United Kingdom*, 90, pp. 977–994. doi: 10.1017/S0025315409991597.
- Spaet, J. L. Y. et al. (2017) 'Extensive use of mesopelagic waters by a Scalloped hammerhead shark (*Sphyrna lewini*) in the Red Sea', *Animal Biotelemetry*. BioMed Central, 5(1), pp. 1–12. doi: 10.1186/s40317-017-0135-x.
- Stramma, L. et al. (2008) 'Expanding oxygen-minimum zones in the tropical oceans', *Science*, 320(5876), pp. 655–658. doi: 10.1126/science.1153847.
- Stramma, L. et al. (2011) 'Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes', *Nature Climate Change*. Nature Publishing Group, 2(1), pp. 33–37. doi: 10.1038/nclimate1304.
- Stramma, L. and Schmidtko, S. (2019) 'Global evidence of ocean deoxygenation', in Laffoley, D. and Baxter, J. M. (eds) *Ocean deoxygenation: Everyone's problem. Causes, impacts, consequences and solutions*. IUCN, pp. 25–36.
- Teo, S. L. H. et al. (2007) 'Annual migrations, diving behavior, and thermal biology of Atlantic bluefin tuna, *Thunnus thynnus*, on their Gulf of Mexico breeding grounds', *Marine Biology*, 151(1), pp. 1–18. doi: 10.1007/s00227-006-0447-5.
- Vaquier-Sunyer, R. and Duarte, C. M. (2008) 'Thresholds of hypoxia for marine biodiversity', *PNAS*, 105(40), pp. 15452–15457. doi: 10.1073/pnas.0803833105.
- Vedor, M. et al. (2021) 'Climate-driven deoxygenation elevates fishing vulnerability for the ocean's widest ranging shark', *eLife*, 10, pp. 1–29. doi: 10.7554/elife.62508.

- Vetter, R. et al. (2008) 'Predatory interactions and niche overlap between Mako Shark, *Isurus oxyrinchus*, and jumbo squid, *Dosidicus gigas*, in the California current', *California Cooperative Oceanic Fisheries Investigations Reports*, 49(May 2014), pp. 142–156.
- Voss, N. A. (1969) 'A Monograph of the Cephalopoda of the North Atlantic. The Family Histioteuthidae', (67).
- Wallman, H. L. and Bennett, W. A. (2006) 'Effects of parturition and feeding on thermal preference of Atlantic stingray, *Dasyatis sabina* (Lesueur)', *Environmental Biology of Fishes*, 75(3), pp. 259–267. doi: 10.1007/s10641-006-0025-1.
- Ward-Paige, C. A. et al. (2012) 'Recovery potential and conservation options for elasmobranchs', *Journal of Fish Biology*, 80(5), pp. 1844–1869. doi: 10.1111/j.1095-8649.2012.03246.x.
- Ward, P. et al. (2008) 'Large-scale experiment shows that nylon leaders reduce shark bycatch and benefit pelagic longline fishers', *Fisheries Research*, 90(1–3), pp. 100–108. doi: 10.1016/j.fishres.2007.09.034.
- Ward, P. et al. (2009) 'The effects of circle hooks on bycatch and target catches in Australia's pelagic longline fishery', *Fisheries Research*, 97(3), pp. 253–262. doi: 10.1016/j.fishres.2009.02.009.
- Watanabe, Y. Y. et al. (2019) 'Hunting behaviour of white sharks recorded by animal-borne accelerometers and cameras', *Marine Ecology Progress Series*, 621. doi: 10.3354/meps12981.
- White, T. C. R. (2008) 'The role of food, weather and climate in limiting the abundance of animals', *Biological Reviews*, 83(3), pp. 227–248. doi: 10.1111/j.1469-185X.2008.00041.x.
- Wilson, R. P. (1992) 'Estimation of location: global coverage using light intensity', in *Wildlife Telemetry: Remote Monitoring and Tracking of Animals*. Ellis Horwood. Available at: <http://ci.nii.ac.jp/naid/10018066932/en/> (Accessed: 18 January 2020).
- Wood, A. D. et al. (2009) 'Recalculated diet and daily ration of the shortfin mako (*Isurus oxyrinchus*), with a focus on quantifying predation on bluefish (*Pomatomus saltatrix*) in the northwest Atlantic Ocean', *Fishery Bulletin*, 107(1), pp. 76–88.
- Worm, B. et al. (2009) 'Rebuilding Global Fisheries', *Science*, 325(5940), pp. 578–585. doi: 10.1126/science.1173146.
- Worm, B. et al. (2013) 'Global catches, exploitation rates, and rebuilding options for sharks', *Marine Policy*. Elsevier, 40(1), pp. 194–204. doi: 10.1016/j.marpol.2012.12.034.
- Žydelis, R. et al. (2011) 'Dynamic habitat models: Using telemetry data to project fisheries bycatch', *Proceedings of the Royal Society B: Biological Sciences*, 278(1722), pp. 3191–3200. doi: 10.1098/rspb.2011.0330.



# Annexes

## Supporting Tables

**Table A1** Summary of TAD models. Models' intercepts are not represented.

	<b>Estimate</b>	<b>Std. Error</b>	<b>p-value</b>	<b>R^2 Efron</b>
<b>Blue</b>	0.0425	0.0040	<2e-16	18.93%
<b>Mako</b>	0.0202	0.0033	1.59e-09	6.98%

**Table A2** Summary of time weighted mean depth models. Models' intercepts are not represented.

		<b>Estimate</b>	<b>Std. Error</b>	<b>p-value</b>	<b>R^2 Efron</b>	
<b>Blue</b>	<b>SSL</b>	Day	0.0090	0.0011	<2e-16	8.44%
		Night	0.0118	0.0013	<2e-16	10.71%
	<b>UDSL</b>	Day	0.0030	0.0004	<2e-16	8.44%
		Night	0.0039	0.0004	<2e-16	10.70%
	<b>LDSL</b>	Day	0.0011	0.0002	2.67e-10	5.93%
		Night	0.0015	0.0002	5.2e-12	7.91%
<b>Mako</b>	<b>SSL</b>	Day	0.0135	0.0016	<2e-16	9.28%
		Night	0.0096	0.0018	1.79e-07	6.37%
	<b>UDSL</b>	Day	0.0045	0.0005	<2e-16	9.28%
		Night	0.0032	0.0006	1.66e-07	6.40%
	<b>LDSL</b>	Day	0.0021	0.0002	<2e-16	10.99%
		Night	0.0014	0.0003	5.42e-07	5.22%

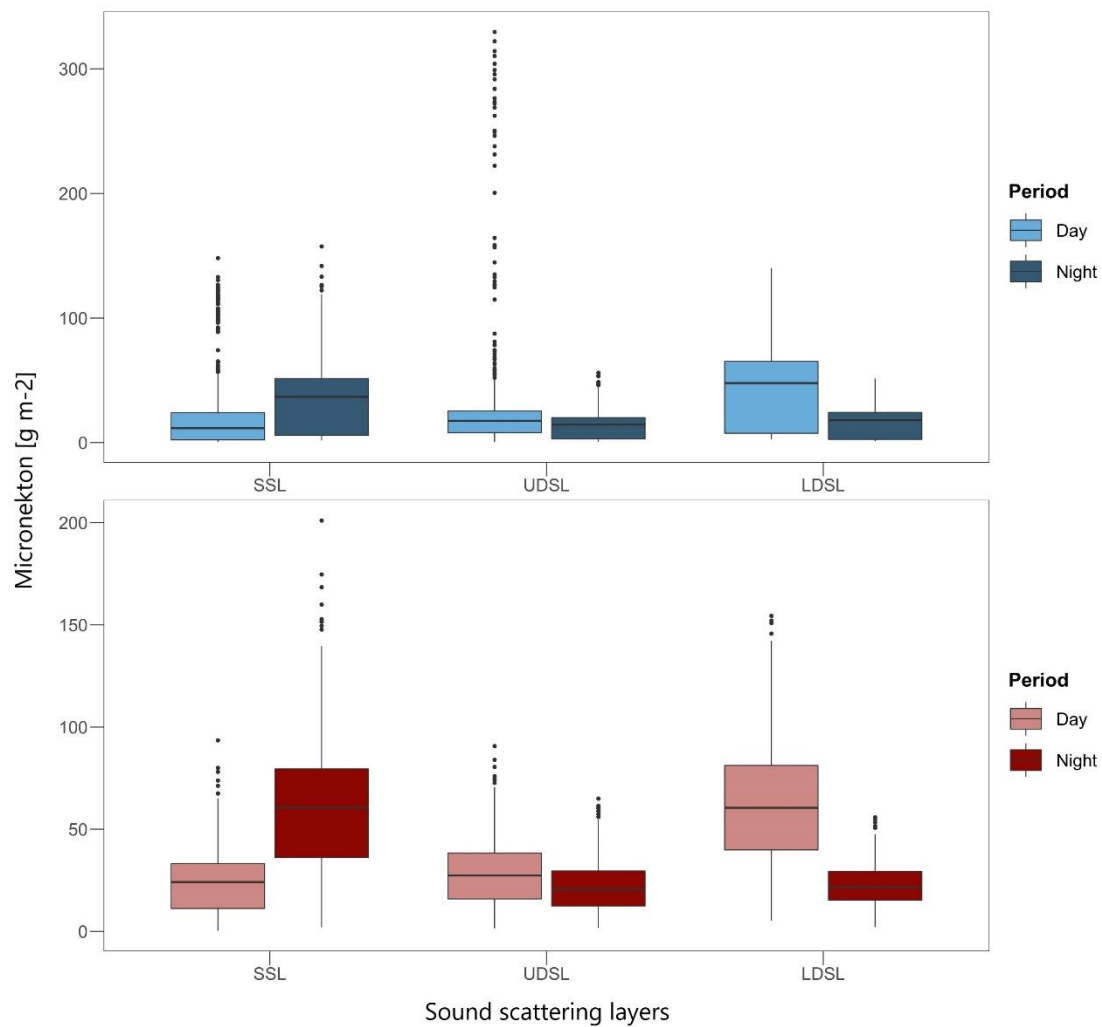
**Table A3** Summary of layers' distance models. Models' intercepts are not represented.

		<b>Estimate</b>	<b>Std. Error</b>	<b>p-value</b>	<b>R^2 Efron</b>
<b>Blue</b>	<b>SSL</b>	-0.0151	0.0012	<2e-16	4.22%
	<b>UDSL</b>	0.0008	0.0019	0.6910	0.01%
	<b>LDSL</b>	-0.0050	0.0004	<2e-16	13.81%
<b>Mako</b>	<b>SSL</b>	-0.0028	0.0014	0.0454	0.42%
	<b>UDSL</b>	-0.0029	-1.4260	0.1540	0.15%
	<b>LDSL</b>	-0.0037	0.0005	2.34e-14	5.81%

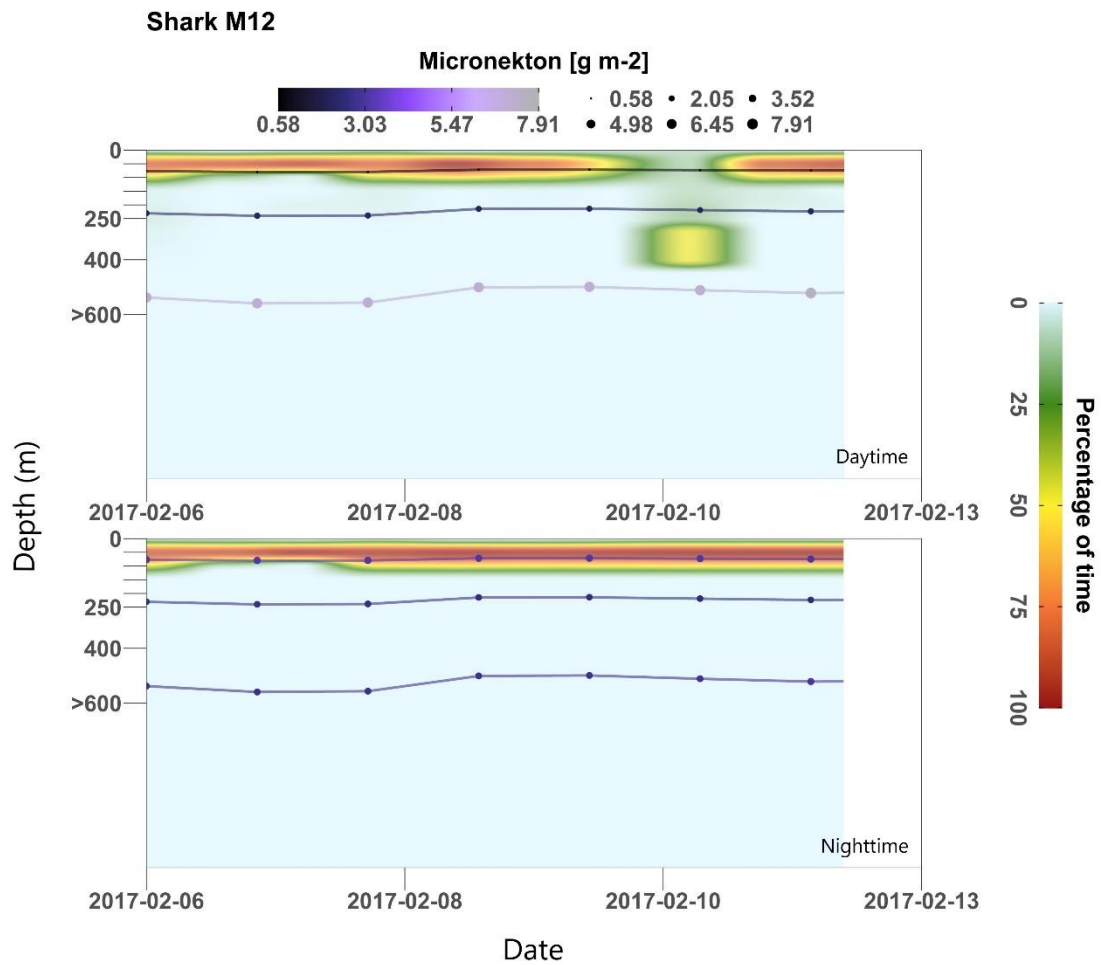
**Table A4** Summary of change point models

	name	mean	lower	upper	Rhat	n.eff
Blue	cp_1	49.90	49.52	50.48	1.00	39113
	int_1	5.32	5.28	5.35	1.00	91983
	int_2	4.14	3.82	4.43	1.00	84544
	sigma_1	137.88	135.51	140.26	1.00	92062
Mako	cp_1	44.51	12.44	102.78	1.87	101
	int_1	5.39	5.29	5.50	1.33	264
	int_2	4.99	5.04	5.31	1.52	775
	sigma_1	137.71	135.23	140.18	1.00	94892

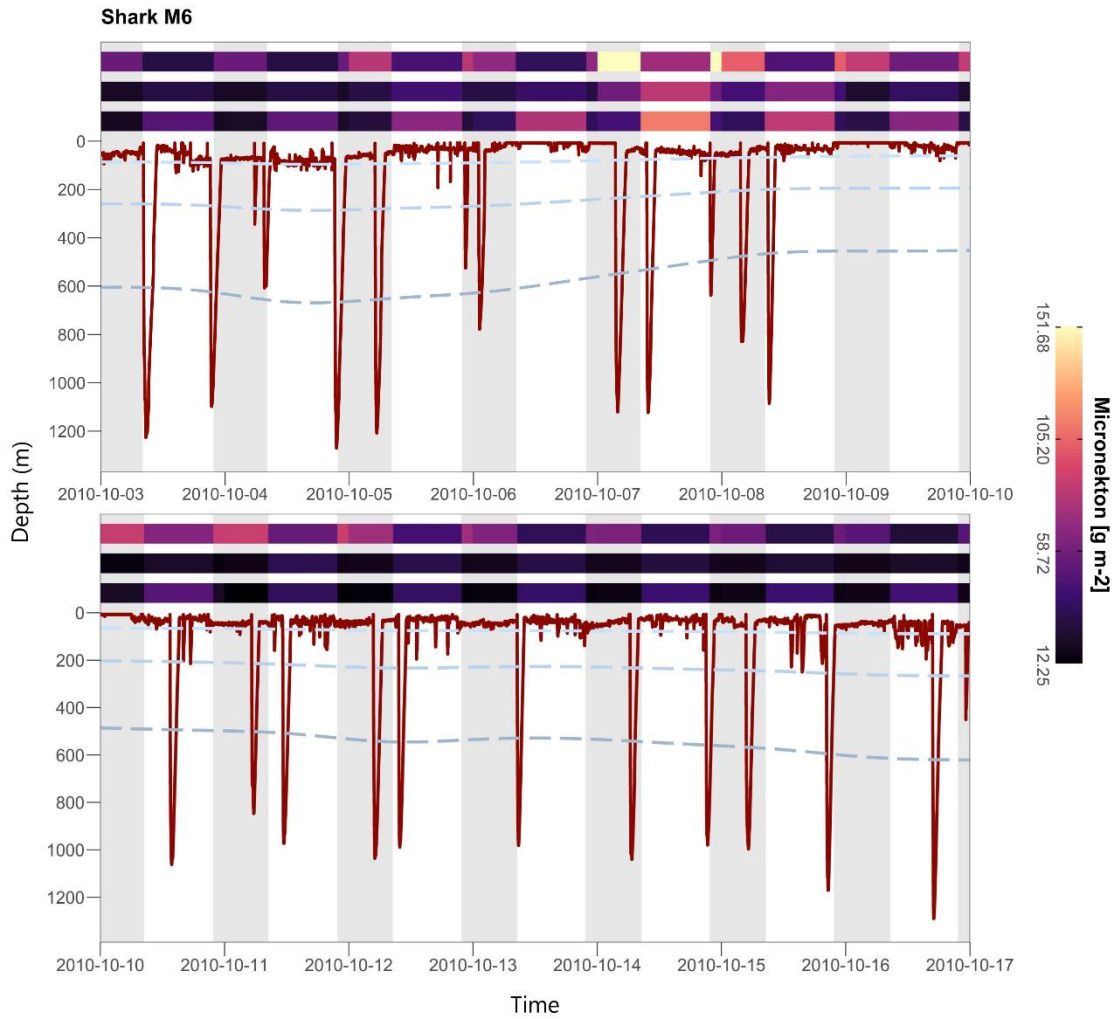
## Supporting Figures



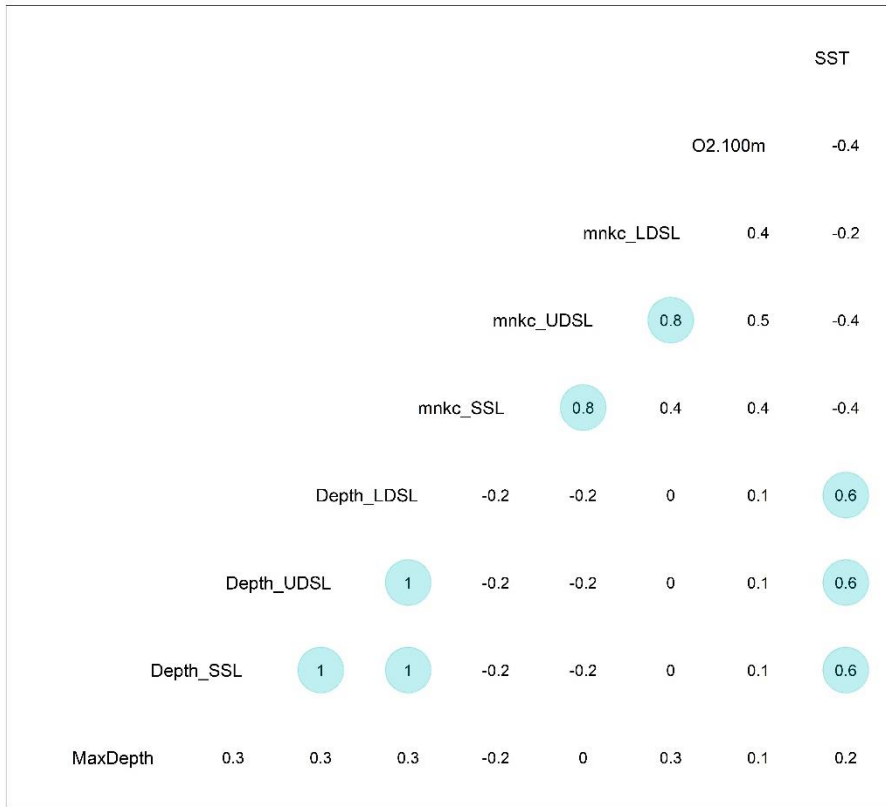
**Figure A1** Boxplot of micronekton concentrations experienced by the tracked individuals. Boxes are colour-coded by species (blue - *Prionace glauca*, red – *Isurus oxyrinchus*). Daytime and nighttime are represented by light and dark colours, respectively.



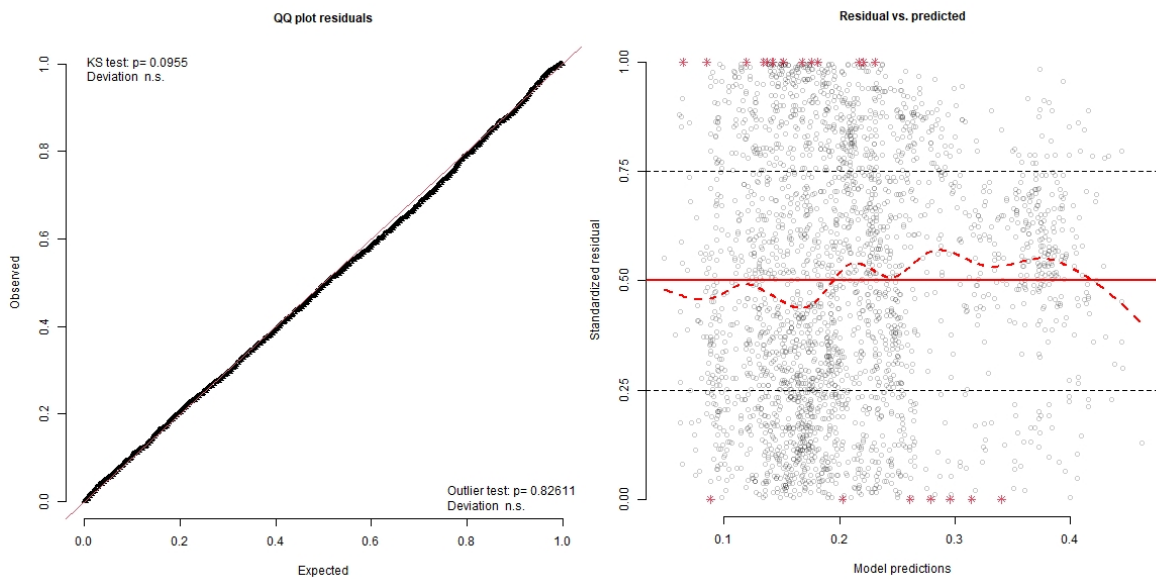
**Figure A2** Shark M12 daytime and nighttime TAD time series. Dotted lines represent the three sound scattering layers coloured and sized according to the micronekton concentration. Dot size is directly proportional to micronekton concentrations.



**Figure A3** Two-weeks interval from shark M6 archival time series. Dashed lines represent the smoothed depth of the three sound scattering layers. Top stripes are coloured according to the micronekton concentration at each layer, stripes' arrangement corresponds to the scattering layers' order. Grey shades indicate nighttime obtained via suncalc R package.



**Figure A4** Spearman’s correlation matrix. Circles highlight Coefficients of  $\rho < -0.5$  and  $> 0.5$



**Figure A5** DHARMA residual diagnostic plots from the maximum depth model.