

MASTER IN MARINE SCIENCES – MARINE RESOURCES
MARINE BIOLOGY AND ECOLOGY

The impact of climate-driven ocean deoxygenation in *Prionace glauca* and *Isurus oxyrinchus*

Luíza Rodrigues Monteiro

M

2025



INSTITUTO DE CIÊNCIAS BIOMÉDICAS ABEL SALAZAR



LUÍZA RODRIGUES MONTEIRO

**THE IMPACT OF OCEAN DEOXYGENATION CAUSED BY
CLIMATE CHANGE IN *PRIONACE GLAUCA* AND *ISURUS
OXYRINCHUS*.**

Dissertação de Candidatura ao grau de Mestre em
Ciências do Mar – Recursos Marinhos submetida ao
Instituto de Ciências Biomédicas de Abel Salazar da
Universidade do Porto.

Orientador – Dr. Nuno Miguel Cabral Queiroz

Categoria – Investigador Principal

Afiliação – CIBIO/InBIO, Centro de Investigação em
Biodiversidade e Recursos Genéticos, Universidade do
Porto.

Co-orientador – Dra. Marisa Graziela Cerqueira Vedor

Categoria – Investigador Júnior

Afiliação – CIBIO/InBIO, Centro de Investigação em
Biodiversidade e Recursos Genéticos, Universidade do
Porto.

Declaração de Honra

Declaro que a presente dissertação é de minha autoria e não foi utilizada previamente noutro curso ou unidade curricular, desta ou de outra instituição. As referências a outros autores (afirmações, ideias, pensamentos) respeitam escrupulosamente as regras da atribuição, e encontram-se devidamente indicadas no texto e nas referências bibliográficas, de acordo com as normas de referenciação. Tenho consciência de que a prática de plágio e autoplágio constitui um ilícito académico.

12 de setembro de 2025

A estudante,

Assinado por: **Luiza Rodrigues
Monteiro**
Num. de Identificação: 32875674
Data: 2025.12.05 18:25:57+00'00'

Agradecimentos

Antes de mais, gostaria de agradecer aos meus orientadores Nuno Queiroz e Marisa Vedor, pela oportunidade e ajuda ao longo deste período de realização da tese. Fazer parte do grupo MOVE por este curto período com certeza foi uma experiência enriquecedora e fez-me aumentar o interesse em compreender e melhorar as minhas capacidades na área da ecologia do movimento.

Aos meus amigos do CIBIO, Mariana, Duda e João, pela amizade e pelos momentos de alívio e partilha de conhecimento ao longo deste ano.

Ao meu namorado, Mário, por me aguentar a falar do R e pelas longas conversas sobre curiosidades dos tubarões. O seu apoio e boleias foram essenciais neste período. Não poderia esquecer de agradecer também à família do Mário pelo constante interesse sobre o tema da tese e pelos almoços de domingo.

À minha irmã, Júlia, por todo o apoio durante estes 5 anos longe da nossa família, apesar das discussões (não constantes), és a pessoa que mais me incentivou ao longo deste processo.

Por fim, um agradecimento especial aos meus pais, que sempre me apoiaram e incentivaram a alcançar os meus objetivos. E mesmo de longe fazem-se mais do que presentes todos os dias, espero poder recompensar-vos por todas as oportunidades que me proporcionaram. Não poderia terminar este agradecimento sem dizer que prometo ao meu pai que vou escutar mais as suas orientações, já que desde o primeiro ano da licenciatura dizia-me para estudar sobre o R.

A todos, os meus mais sinceros, obrigada!

Resumo

A desoxigenação dos oceanos, impulsionada pelas alterações climáticas antropogénicas, representa uma das ameaças mais importantes para os ecossistemas marinhos. As zonas de mínimo oxigénio (ZMOs) estão a expandir-se globalmente, limitando potencialmente o habitat vertical dos predadores pelágicos. Este estudo investigou como as condições hipóxicas afetam os padrões de movimento vertical dos tubarões azuis (*Prionace glauca*) e dos tubarões mako (*Isurus oxyrinchus*).

Tags pop-up de transmissão de arquivo por satélite (PSAT) foram fixadas em tubarões no Oceano Atlântico Norte entre 2009 e 2022. O conjunto de dados compreendeu 26 tubarões azuis e 27 tubarões mako para análise geral, com um subconjunto de 10 tubarões azuis e 11 tubarões mako selecionados para análise detalhada de mergulho. Os dados ambientais de oxigénio foram extraídos do Serviço de Monitorização do Ambiente Marinho Copernicus, com áreas ZMO definidas como águas com concentrações de oxigénio dissolvido inferiores a 3,5 ml/l O₂ a 100 m de profundidade. A análise de mergulho categorizou as fases de mergulho em descida, nível e subida. As análises estatísticas empregaram teste de Wilcoxon Rank-Sum e modelos lineares para explicar a variação individual.

Ambas as espécies demonstraram uma compressão vertical significativa do habitat dentro das ZMO. Os tubarões-azuis apresentaram profundidades máximas diárias de 174 m mais reduzidas em condições hipóxicas, enquanto os tubarões-mako exibiram restrições de profundidade de 140 m e ausência total de mergulhos abaixo de 600 m em condições de ZMO. Os tubarões-azuis demonstraram reduções consistentes de profundidade (~55 m) em todas as fases de mergulho e velocidades de natação reduzidas dentro das ZMO. Os tubarões-mako mostraram respostas dependentes da fase de mergulho, com frequência de mergulho reduzida em águas hipóxicas, sugerindo estratégias de conservação de energia. Ambas as espécies exibiram exploração vertical comprimida dentro das ZMO, com diferenças de profundidade reduzidas entre fases de nível consecutivas.

Este estudo fornece evidências conclusivas de que a desoxigenação dos oceanos restringe significativamente os padrões de movimento vertical dos tubarões azuis e makos. Os padrões consistentes de compressão do habitat demonstram que a disponibilidade de oxigénio atua como um filtro ambiental fundamental, estruturando o comportamento dos predadores. Os tubarões-azuis, como predadores ectotérmicos, exibiram ajustes comportamentais mais pronunciados em várias dimensões, enquanto os tubarões-mako mostraram respostas específicas da espécie, refletindo as suas capacidades endotérmicas e maiores exigências metabólicas. Estas descobertas têm implicações ecológicas

profundas, uma vez que a compressão do habitat pode intensificar a competição interespecífica, aumentando a vulnerabilidade à pesca de superfície. À medida que as alterações climáticas impulsionam a expansão da ZMO a nível global, estas restrições comportamentais tornam-se cada vez mais relevantes para a gestão do ecossistema e as estratégias de conservação destes importantes predadores pelágicos.

Palavras-chave: Zonas de mínimo oxigénio, Movimento vertical, Tubarão azul (*Prionace glauca*), Tubarão mako (*Isurus oxyrinchus*), Compressão do habitat.

Abstract

Ocean deoxygenation, driven by anthropogenic climate change, represents one of the most important threats to marine ecosystems. Oxygen minimum zones (OMZs) are expanding globally, potentially constraining the vertical habitat of pelagic predators. This study investigated how hypoxic conditions affect the vertical movement patterns of blue sharks (*Prionace glauca*) and mako sharks (*Isurus oxyrinchus*).

Pop-up satellite archival transmitting tags (PSAT) were attached to sharks in the North Atlantic Ocean between 2009 and 2022. The dataset comprised 26 blue sharks and 27 mako sharks for general analysis, with a subset of 10 blue sharks and 11 mako sharks selected for detailed dive analysis. Environmental oxygen data were extracted from the Copernicus Marine Environment Monitoring Service, with OMZ areas defined as waters with dissolved oxygen concentrations below 3.5 ml/l O₂ at 100 m depth. The dive analysis categorised dive phases into descent, level, and ascent. Statistical analyses employed Wilcoxon rank sum tests and Linear Models to explain individual variation.

Both species demonstrated significant vertical habitat compression within OMZs. Blue sharks showed maximum daily depths 174 m shallower in hypoxic conditions, while mako sharks exhibited 140 m depth restrictions and a complete absence of dives below 600 m in OMZ conditions. Blue sharks demonstrated consistent depth reductions (~55 m) across all dive phases and reduced swimming speeds within OMZs. Mako sharks showed phase-dependent responses with reduced diving frequency in hypoxic waters, suggesting energy conservation strategies. Both species exhibited compressed vertical exploration within OMZs, with reduced depth differences between consecutive level phases.

This study provides conclusive evidence that ocean deoxygenation significantly constrains the vertical movement patterns of both blue and mako sharks. The consistent patterns of habitat compression demonstrate that oxygen availability acts as a fundamental environmental filter, structuring predator behaviour. Blue sharks, as ectothermic predators, exhibited more pronounced behavioural adjustments across multiple dimensions, while mako sharks showed species-specific responses reflecting their endothermic capabilities and higher metabolic demands. These findings have profound ecological implications, as habitat compression may intensify interspecific competition while increasing vulnerability to surface fisheries. As climate change drives OMZ expansion globally, these behavioural constraints become increasingly relevant for ecosystem management and conservation strategies for these important pelagic predators.

Keywords: Oxygen minimum zones, Vertical movement, Blue shark (*Prionace glauca*), Mako shark (*Isurus oxyrinchus*), Habitat compression.

List of contents

Resumo	v
Abstract	vii
List of contents	viii
List of abbreviations	xiv
1. Introduction	1
1.1 Climate change	1
1.2 Oxygen Minimum Zones	1
1.3 Pelagic predators	4
1.3.1 The Blue shark	5
1.3.2 The Shortfin Mako	6
2. General objectives	8
3. Methods	9
3.1 Tagging	9
3.2 Environmental data extraction	10
3.3 Dataset description	12
3.4 Dive analysis data processing	13
3.5 Statistical analysis	14
4. Results	15
4.1 General Vertical Behaviour Analysis	16
Blue shark:.....	16
Mako shark:	17
4.1.1. Maximum daily depth	19
Blue shark:.....	19
Mako shark:	20
4.1.2 Time-at-Depth (TAD)	22
Blue shark:.....	22
Mako shark:	23
4.1.3 Time-at-Temperature (TAT)	23
Blue shark:.....	24
Mako shark:	25
4.2 Dive analysis	26
4.2.1 General dive metrics	28
4.2.1.1 Number of daily dives	28
Blue shark:	28
Mako shark:	30
4.2.1.2 Mean dive depth	31

Blue shark:	31
Mako shark:	32
4.2.1.3 Dive duration.....	33
Blue shark:	33
Mako shark:	34
4.2.2 Dive Phase Analysis	35
4.2.2.1 Mean depth per step phase.....	35
Blue shark:	35
Mako shark:	36
4.2.2.2 Step phase duration	37
Blue shark:	37
Mako shark:	38
4.2.2.3 Vertical speed per step phases	39
Blue shark:	40
Mako shark:	41
4.2.3 Level Phase Analysis	42
4.2.3.1 Proportion of time in level	42
Blue shark:	42
Mako shark:	44
4.2.3.2 Proportion of level phases	47
Blue shark:	47
Mako shark:	49
4.2.3.3 Depth of level phases	52
Blue shark:	52
Mako shark:	54
4.2.3.4 Depth difference between consecutive level phases	56
Blue shark:	56
Mako shark:	58
5. Discussion	62
Vertical habitat compression in response to oxygen minimum zones	62
Species-specific depth usage patterns.....	62
Thermal habitat adjustments	63
Contrasting diving strategies and behavioural adaptations	63
Dive characteristics and depth selection behaviour	64
Temporal dynamics	64
Dive phase analysis.....	65
Level phase dynamics	65

Physiological basis for species-specific responses	66
Ecological implications and management considerations	67
Study limitations and future path	67
Climate change implications and conservation perspectives	67
6. Conclusion.....	68
6.1 Key findings and hypothesis validation	68
6.2 Species-specific responses and physiological implications	69
6.3 Ecological and Conservation Implications	69
6.4 Limitations and Future Directions	70
6.5 Global Change Context and Management Implications	70
6.6 Final Considerations	70
7. References.....	72
8. Supplementary material.....	81

List of figures

Figure 1: (a) Oxygen concentrations among distinct ocean regions - Hawaii Ocean Time-series (HOT), the northeast subarctic Pacific (NESAP), Saanich Inlet (SI), the eastern tropical South Pacific (ETSP), the Cariaco Basin (CB), the eastern tropical Atlantic (ETA) OMZ, Namibian upwelling (NAM), and the Baltic, Black and Arabian seas. (b) Cross-sectional view of the northeast subarctic Pacific OMZ illustrating oxygen levels from the surface down to the seabed. Upper oxycline: transition from surface waters to the OMZ core. OMZ core: defined by O ₂ concentrations < 20 µmol per kg water. Deep oxycline: transition from the bottom of the OMZ core to abyssal waters. Adapted from (Wright et al., 2012).	2
Figure 2: Illustration of the blue shark (<i>Prionace glauca</i>), highlighting its characteristic morphology. Public domain image, originally published by NOAA, produced by NMFS, E. Hoffmayer, S. Iglésias and R. McAuley, available on Wikimedia Commons.	5
Figure 3: Illustration of the Shortfin Mako shark (<i>Isurus oxyrinchus</i>). Public domain image, originally published by NOAA, produced by NMFS, E. Hoffmayer, S. Iglésias and R. McAuley, available on Wikimedia Commons.	7
Figure 4: MiniPat (PSAT) tag developed by Wildlife Computers, utilised to record depth, temperature, and light level. Image source: Wildlife Computers.	9
Figure 5: Excess monofilament being cut during the attachment of a PSAT (Pop-up Satellite Archival Tag) to the dorsal fin of a shark. Source: Saving the Blue (n.d.). Available at: https://www.savingtheblue.org/sharktags . Photo credit: Annie Guttridge.	10
Figure 6: Example of a daily temperature profile from MATLAB, the red line is the start of the thermocline, and the green line is the end of the thermocline.	11
Figure 7: Example of comparison of data from the same shark for archival data (a) and time series data (b). The archival data, summarised at 5-minute intervals, provides more detailed dive information than the time series data, summarised at 7.5-minute intervals.	13
Figure 8: Depth and temperature over time for blue shark, in relation to the OMZ. In the pink section is represented the time spent inside the OMZ, and in the blue section, the time spent outside the OMZ.	17
Figure 9: Depth and temperature over time for mako shark, spent outside OMZ conditions.	18
Figure 10: Depth and temperature over time for mako shark, spent inside OMZ conditions.	18
Figure 11: A back-to-back histogram illustrating the comparison of the percentage of time spent in each bin (100 m) of maximum depth usage of blue sharks inside (red) and outside (blue) the OMZ.	19
Figure 12: Boxplot illustrating the comparison of the maximum daily depth of blue sharks inside (red) and outside (blue) the OMZ.	20
Figure 13: A back-to-back histogram illustrating the comparison of the percentage of time spent in each bin (100 m) of maximum depth usage of mako sharks inside (red) and outside (blue) the OMZ.	21
Figure 14: Boxplot illustrating the comparison of the maximum daily depth of mako sharks inside (red) and outside (blue) the OMZ.	21
Figure 15: A back-to-back histogram illustrating the comparison of the percentage of time spent in each 50 m depth interval used by blue sharks inside (red) and outside (blue) the OMZ.	22

Figure 16: A back-to-back histogram illustrating the comparison of the percentage of time spent in each 50 m depth interval used by mako sharks inside (red) and outside (blue) the OMZ.	23
Figure 17: A back-to-back histogram illustrating the comparison of the percentage of time spent in each 2°C temperature range used by blue sharks inside (red) and outside (blue) the OMZ.	24
Figure 18: A back-to-back histogram illustrating the comparison of the percentage of time spent in each 2°C temperature range used by mako sharks inside (red) and outside (blue) the OMZ.	26
Figure 19: Geographic tracks of 10 blue sharks (<i>Prionace glauca</i>) recorded in the North Atlantic Ocean. Each colour trajectory represents the horizontal movement of a specific shark. Oxyclines represented by red (1.5 ml/l of O ₂), orange (2.5 ml/l of O ₂), yellow (3.5 ml/l of O ₂) and blue (4.5 ml/l of O ₂) lines at 100 metres from the OMZ of Eastern Tropical Atlantic (ETA).	27
Figure 20: Geographic tracks of 11 mako sharks (<i>Isurus oxyrinchus</i>) recorded in the North Atlantic Ocean. Each colour trajectory represents the horizontal movement of a specific shark. Oxyclines represented by red (1.5 ml/l of O ₂), orange (2.5 ml/l of O ₂), yellow (3.5 ml/l of O ₂) and blue (4.5 ml/l of O ₂) lines at 100 metres from the OMZ of Eastern Tropical Atlantic (ETA).	28
Figure 21: Boxplot illustrating the comparison of the number of daily dives of blue sharks inside (red) and outside (blue) the OMZ.	29
Figure 22: Boxplot illustrating the comparison of the number of daily dives of mako sharks inside (red) and outside (blue) the OMZ.	31
Figure 23: Boxplot illustrating the comparison of mean dive depth of blue sharks inside (red) and outside (blue) the OMZ.	32
Figure 24: Boxplot illustrating the comparison of mean dive depth of mako sharks inside (red) and outside (blue) the OMZ.	33
Figure 25: Boxplot illustrating the comparison of mean daily dive duration of blue sharks inside (red) and outside (blue) the OMZ.	34
Figure 26: Boxplot illustrating the comparison of mean daily dive duration of mako sharks inside (red) and outside (blue) the OMZ.	35
Figure 27: Boxplot illustrating the comparison of mean depth in each step phase of blue sharks inside (red) and outside (blue) the OMZ.	36
Figure 28: Boxplot illustrating the comparison of mean depth in each step phase of mako sharks inside (red) and outside (blue) the OMZ.	37
Figure 29: Boxplot illustrating the comparison of the duration of each step phase in blue sharks inside (red) and outside (blue) the OMZ.	38
Figure 30: Boxplot illustrating the comparison of the duration of each step phase in mako sharks inside (red) and outside (blue) the OMZ.	39
Figure 31: Boxplot illustrating the comparison of the speed in phase A and D in blue sharks inside (red) and outside (blue) the OMZ.	41
Figure 32: Boxplot illustrating the comparison of the speed in phase A and D in mako sharks inside (red) and outside (blue) the OMZ.	42
Figure 33: Boxplot illustrating the comparison of the time in the level phase in blue sharks inside (red) and outside (blue) the OMZ.	43
Figure 34: Map illustrating the proportion of time in the level phase along the blue shark's track, with circles increasing as time in level increases.	44

Figure 35: Boxplot illustrating the comparison of the time in the level phase in mako sharks inside (red) and outside (blue) the OMZ.	45
Figure 36: Map illustrating the proportion of time in the level phase along the mako shark's track inside the OMZ.	46
Figure 37: Map illustrating the proportion of time in the level phase along the mako shark's track outside the OMZ.	46
Figure 38: Boxplot illustrating the comparison of the proportion of the level phase in relation to the other phases in blue sharks inside (red) and outside (blue) the OMZ.	48
Figure 39: Map illustrating the proportion of level phases along the blue shark's track, with circles increasing as the proportion of level phases increases.	48
Figure 40: Boxplot illustrating the comparison of the proportion of the level phase in relation to the other phases in mako sharks inside (red) and outside (blue) the OMZ.	50
Figure 41: Map illustrating the proportion of the level phase along the mako shark's track inside the OMZ.	51
Figure 42: Map illustrating the proportion of the level phase along the mako shark's track outside the OMZ.	51
Figure 43: Boxplot illustrating the comparison of the mean depth of levels in blue sharks inside (red) and outside (blue) the OMZ.	53
Figure 44: Map illustrating the mean depth of level along the blue shark's track, with circle sizes decreasing as the depth of level is shallower.	53
Figure 45: Boxplot illustrating the comparison of the mean depth of levels in mako sharks inside (red) and outside (blue) the OMZ.	54
Figure 46: Map illustrating the mean depth of the level phase along the mako shark's track inside the OMZ.	55
Figure 47: Map illustrating the mean depth of the level phase along the mako shark's track outside the OMZ.	56
Figure 48: Boxplot illustrating the comparison of the difference in the depth of consecutive levels in blue sharks inside (red) and outside (blue) the OMZ, focusing on the upper layers of the water column.	57
Figure 49: Boxplot illustrating the comparison of the difference in the depth of consecutive levels in blue sharks inside (red) and outside (blue) the OMZ.	57
Figure 50: Map illustrating the difference in depth of consecutive levels along the blue shark's track, with circle sizes decreasing as the depth of the level is shallower.	58
Figure 51: Boxplot illustrating the comparison of the difference in the depth of consecutive levels in mako sharks inside (red) and outside (blue) the OMZ, focusing on the upper layers of the water column.	59
Figure 52: Boxplot illustrating the comparison of the difference in the depth of consecutive levels in mako sharks inside (red) and outside (blue) the OMZ.	60
Figure 53: Map illustrating the mean difference in depth of consecutive levels along the mako shark's track inside the OMZ.	61
Figure 54: Map illustrating the mean difference in depth of consecutive levels along the mako shark's track outside the OMZ.	61

List of abbreviations

AWERB	Animal Welfare Ethical Review Body
CMEMS	Copernicus Marine Environmental Monitoring Service
DSL	Deep scattering layer
DO	Dissolved Oxygen
EBUS	Eastern Boundary Upwelling System
ELG	Exponential Leap-forward Gradient
ETA	Eastern Tropical Atlantic
ID	Individual
IUCN	International Union for the Conservation of Nature
LM	Linear Model
LMM	Linear Mixed Models
MBA	Marine Biological Association
m	Meters
n.d.	No data
NEEC	North Equatorial Countercurrent
NEUC	North Equatorial Undercurrent
OMZ	Oxygen Minimum Zone
PSAT	Pop-up Satellite Archival Transmitting Tags
SST	Sea Surface Temperature
TAD	Time at Depth
TAT	Time at Temperature

1. Introduction

1.1 Climate change

Anthropogenic climate change is one of the greatest threats to marine ecosystems (IPCC, 2021). The increase in greenhouse gas concentrations in the atmosphere in recent years, particularly CO₂, has resulted in major changes in global climate patterns. In recent decades, the oceans have stored approximately 93% of the Earth's excess thermal energy (IPCC, 2013). This abundant absorption of thermal energy has resulted in numerous transformations in ocean systems, including increased sea surface temperature (SST), ocean acidification, alterations in circulation patterns, and reduced dissolved oxygen levels (Gruber, 2011).

Ocean warming exerts a direct influence on the capacity of water masses to retain oxygen. This phenomenon can be attributed to the fact that an increase in SST leads to a reduction in the solubility of oxygen (Garcia-Soto et al., 2021). Moreover, the decline in oceanic oxygen levels is concomitant with diminished ventilation of deeper waters, due to increased stratification of the upper ocean layer induced by warming (Keeling et al., 2010; M. C. Long et al., 2016; Schmidtke et al., 2017).

These interconnected processes have resulted in a decline in oxygen concentration in the open ocean since at least the mid-20th century (Breitburg et al., 2018; Diaz & Rosenberg, 2008; Keeling et al., 2010; Stramma, C. Johnson, et al., 2008). Ocean deoxygenation manifests through two main mechanisms: reduced oxygen solubility in heated surface waters, and decreased oxygen transfer from the atmosphere to the water column due to increased stratification (Gilly et al., 2013; Keeling et al., 2010).

Although deoxygenation is a global phenomenon, there are ocean regions where oxygen concentrations are naturally much lower. These areas, known as oxygen minimum zones (OMZs), have exhibited substantial expansion in geographical extent, representing a growing concern for marine ecosystems and the species that depend on these habitats (Limburg et al., 2020; Ma et al., 2021).

1.2 Oxygen Minimum Zones

Oxygen minimum zones (OMZs) are characterised by low dissolved oxygen (DO) concentrations and are mostly found in tropical oceans (Limburg et al., 2020; Stramma et al., 2010; Zhou et al., 2022). In the Eastern Boundary Upwelling Systems (EBUS), these zones represent one of the most productive biomes in the ocean but are at risk due to ocean deoxygenation. The formation and maintenance of OMZs result from a complex interplay of oceanographic processes, including wind-driven upwelling that brings oxygen-poor waters

from the ocean interior to coastal areas, thermal stratification of surface waters, reduced ventilation, high primary production, and intense mesopelagic microbial respiration (Chan et al., 2025; da Costa et al., 2024; Diaz & Rosenberg, 2008). The OMZs are widespread, encompassing around 8% of the global ocean surface (Figure 1a). Within these zones, dissolved oxygen decreases with depth until reaching a minimum, before rising again, thereby creating a hypoxic layer, commonly located between 200 and 800 metres, known as the OMZ core (Figure 1b) (Stramma et al., 2008; Gilly et al., 2013).

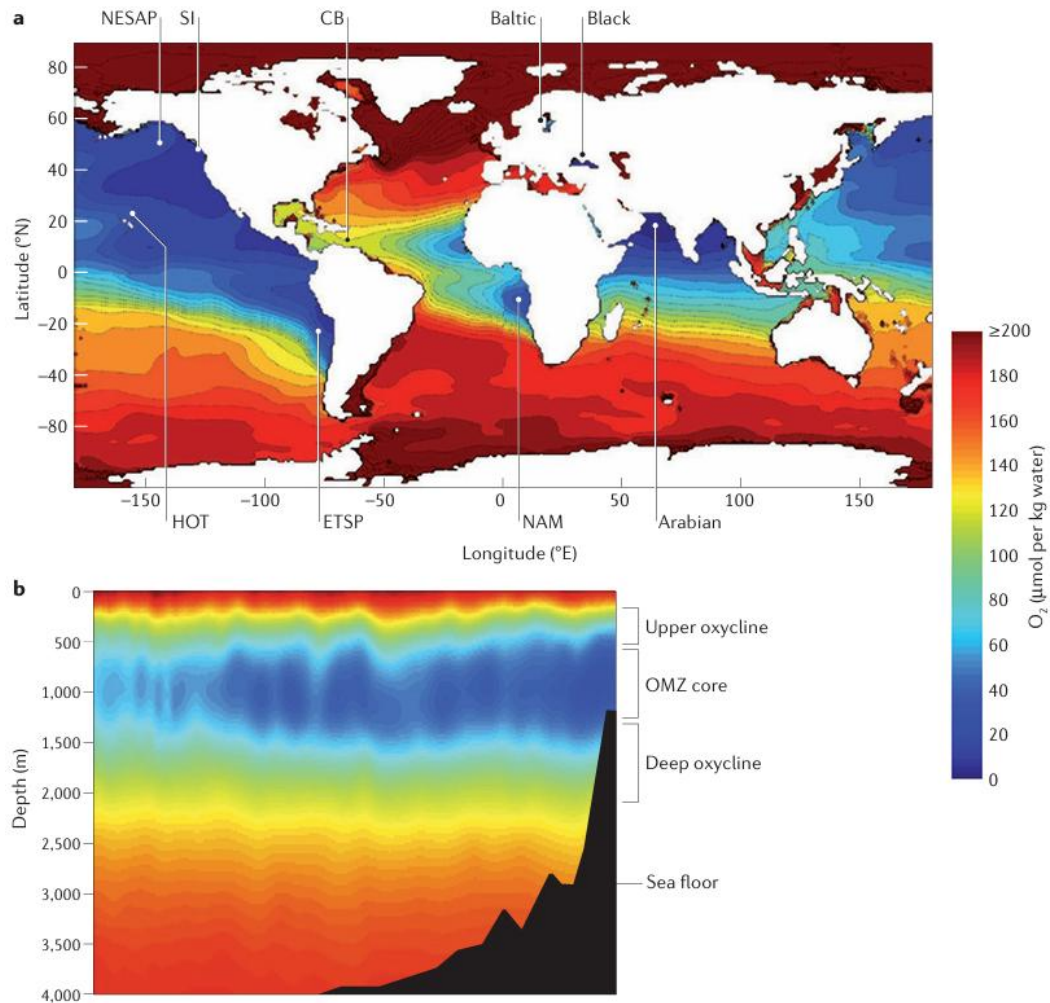


Figure 1: (a) Oxygen concentrations among distinct ocean regions - Hawaii Ocean Time-series (HOT), the northeast subarctic Pacific (NESAP), Saanich Inlet (SI), the eastern tropical South Pacific (ETSP), the Cariaco Basin (CB), the eastern tropical Atlantic (ETA) OMZ, Namibian upwelling (NAM), and the Baltic, Black and Arabian seas. (b) Cross-sectional view of the northeast subarctic Pacific OMZ illustrating oxygen levels from the surface down to the seabed. Upper oxycline: transition from surface waters to the OMZ core. OMZ core: defined by O₂ concentrations $< 20 \mu\text{mol per kg water}$. Deep oxycline: transition from the bottom of the OMZ core to abyssal waters. Adapted from (Wright et al., 2012).

The ecological consequences of these hypoxic zones have been discussed for a variety of taxa (Ekau et al., 2010; Gilly et al., 2013). At the ecosystem level, different species with varying oxygen tolerance levels experience differential success, leading to parallel

changes in community structure and trophic dynamics (Gilly et al., 2013). The upper boundary zone of OMZs plays an important ecological role, as large quantities of micronekton, particularly krill and myctophid fish, seek refuge from predators in these low-oxygen environments during daylight hours (Gilly et al., 2013). These organisms aggregate in layers that are detectable by sonar, often forming a deep scattering layer (DSL) near the upper and lower boundaries of OMZs (Bertrand et al., 2010; Cornejo & Koppelman, 2006; Gilly et al., 2013; Koslow et al., 2011).

Since dissolved oxygen is crucial for maintaining the vast majority of marine animal life, decreasing DO levels can result in widespread mortality or avoidance of affected areas (Chan et al., 2008; Diaz & Rosenberg, 2008; Stramma et al., 2012). The expansion of the OMZ could pose several threats to marine ecosystems, including the vertical habitat compression for pelagic fish with high oxygen demands, such as tunas and billfishes, which increases their vulnerability to overfishing (Prince et al., 2010; Stramma et al., 2012; Vedor, Queiroz, et al., 2021; Whitney et al., 2007). Consequently, changes in the vertical distributions of predators and prey can have local and regional ecological impacts in areas with OMZs.

Future projections indicate that OMZs are particularly vulnerable to the effects of ocean warming across different layers, especially in subsurface waters (200-1,000 metres depth), where OMZs mainly occur. Long-term studies predict continued increases in sea temperatures due to projected climate warming by the end of the century, with consequent expansions in regional and global OMZ areas (Zhou et al., 2022), and with model projections showing reductions in DO levels of 1% to 7% by 2100 (Keeling et al., 2010; Stramma, et al., 2008a).

A specific example of these dynamics can be observed in the OMZ of the northeast tropical Atlantic, specifically of the coast of Cabo Verde. This system is characterised by a layer of water with low DO concentrations located between approximately 300 and 600 meters depth, with the lowest concentrations occurring between 400 and 500 metres (Brandt et al., 2010; Stramma, et al., 2008b). This OMZ is the result of a combination of high surface biological production, which increases oxygen demand at depth, and limited ocean ventilation to intermediate layers (Brandt et al., 2010; Karstensen et al., 2008). The core of this OMZ is located in the “shadow zone” at the eastern boundary, where the lowest oxygen values reach approximately 40 $\mu\text{mol kg}^{-1}$ (Luyten et al., 1983; Stramma et al., 2008b).

The region’s primary oxygen supply comes from subsurface currents, including the North Equatorial Countercurrent (NEEC) and the North Equatorial Undercurrent (NEUC), which transport more oxygenated water to the OMZ during autumn and summer. However, ventilation weakens during winter and spring, with reduced circulation below 300 metres,

thereby maintaining hypoxic conditions (Stramma et al., 2008b). The North Atlantic OMZ is considered hypoxic compared to other OMZs, such as those in the Pacific, and these hypoxic conditions have serious consequences for the ecosystem. Oxygen levels strongly influence the vertical distribution of pelagic fauna in the region, with in situ observations revealing that numerous taxonomic groups avoid the deeper, oxygen-depleted waters and instead congregate above the OMZ, suggesting a habitat compression effect with potential ecological implications for predators (Hoving et al., 2020).

1.3 Pelagic predators

Many characteristics of pelagic predators, such as long generation times, slow growth rates, and low reproduction rates (Camhi et al., 1998; Collette et al., 2011), can make them susceptible to overexploitation and extinction (Bornatowski et al., 2018; Dulvy et al., 2014). Pelagic predators in the food chain are important because they occupy high positions in marine food chains and play a key role in regulating lower trophic level species, thereby influencing the structure and functioning of marine ecosystems through direct (predation) and indirect (competition) ecological interactions (Ferretti et al., 2010; Heithaus et al., 2008; Navia et al., 2016). They can exert top-down effects on marine food webs, and their reduction can alter the structure and functioning of ecosystems (Bornatowski et al., 2018; Ferretti et al., 2010).

Sharks are the top predators in virtually all marine ecosystems (Cortés, 1999). These animals face several anthropogenic threats, such as intentional fishing (when the shark is the target), due to the growth of the shark fin soup market, a sophisticated dish in Asian cuisine (Dulvy et al., 2014; Fields et al., 2018; Worm et al., 2013), and bycatch (when the shark is not the target) (Porcher & Darvell, 2022). Studies show that pelagic sharks are the main suppliers to the fin market. In addition, they represent substantial bycatch in several fisheries and are frequently caught by longliners, drift nets, purse seine nets, and bottom trawlers (Porcher & Darvell, 2022). Combined with their low productivity and slow population recovery rates, sharks cannot tolerate high mortality rates (Myers & Worm, 2003), which contributes to their global decline.

An observational study (Ferretti et al., 2010) suggested that an increase in fishing effort coincided with a decline in large apex-predatory sharks, as well as an increase in smaller sharks, rays, mammals, and turtles. This growth in the number of mesopredators can be partially explained by reduced mortality from predation and risk effects, and in some instances, led to increased pressure on prey species, such as invertebrates, teleost fish and even seagrasses (Ferretti et al., 2010). This demonstrates the need for top predators in food chains for the ecosystem to function properly.

1.3.1 The Blue shark

The Blue shark (Figure 2) is one of the most abundant pelagic sharks, with a global distribution in tropical and temperate waters (Watanabe et al., 2021). In general, ocean waters are less productive and exhibit lower biodiversity when compared to coastal areas (Camhi et al., 2008). However, there are areas of high productivity in the open ocean (Worm et al., 2003), usually associated with marine fronts (Lucifora et al., 2012) or physiographic structures such as seamounts (Morato et al., 2010; Worm et al., 2003). Oceanographic conditions have been demonstrated to induce seasonal variations in areas of high productivity, which can often result in migration of species inhabiting these regions over long distances (Queiroz et al., 2010). Furthermore, Queiroz et al. (2012) found that female blue sharks displayed fidelity to regions characterised by the presence of thermal fronts. Their diet consists of a variety of prey, including teleosts, cephalopods, and pelagic crustaceans found in the water column (Markaida & Sosa-Nishizaki, 2010).

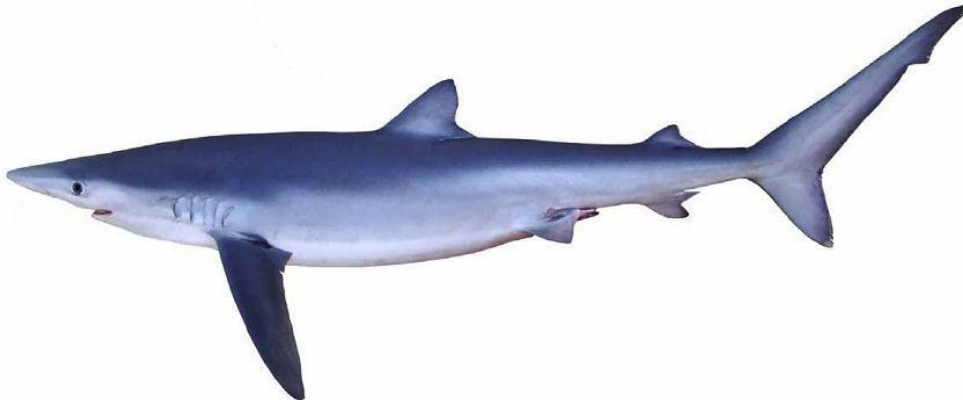


Figure 2: Illustration of the blue shark (Prionace glauca), highlighting its characteristic morphology. Public domain image, originally published by NOAA, produced by NMFS, E. Hoffmayer, S. Iglésias and R. McAuley, available on Wikimedia Commons.

Regarding its vertical behaviour, the blue shark has been observed to dive from the surface to the bathypelagic zone, with a maximum recorded depth of 1,706 metres (Queiroz et al., 2017). Despite being classified as ectothermic, large variations in water are experienced, with temperatures reaching above 25°C and dropping to below 5°C (Campana et al., 2011; Queiroz et al., 2012; Stevens et al., 2010). Additionally, studies verified diel behaviour in blue sharks, characterised by shallower nocturnal dives, while during the daylight hours, blue sharks tend to remain at greater depths, a behaviour consistent with the vertical migration of prey species (Mas et al., 2024; Queiroz et al., 2010, 2012; Stevens et al., 2010).

It is one of the most frequently caught sharks on a global scale (Camhi et al., 2008; S. Clarke et al., 2014; Druon et al., 2022). It is also one of the main species in the global trade in shark fins and meat (Cardeñosa et al., 2022; Dent & Clarke, 2015). It accounts for

around 90% of the worldwide catch of elasmobranchs (Da Silva et al., 2021), and the blue shark provides more fins for the fin trade than any other species (S. C. Clarke et al., 2006). Moreover, blue sharks are frequently bycatch by longline fisheries (Oliver et al., 2015). In the North Atlantic Ocean, it has been demonstrated that blue sharks are at elevated risk of exposure to fishing activities due to their distribution overlapping with important fishing zones (Queiroz et al., 2019). Consequently, the global blue shark population is regarded as near threatened according to the IUCN Red List, with a declining population trend (Rigby et al., 2019).

Another cause that adds to the threats to the blue shark is ocean deoxygenation, as OMZs expand due to global warming, which may result in changes in distribution patterns to more superficial water to avoid deeper waters with low oxygen levels (Vedor, Queiroz, et al., 2021). This has the potential to increase the species' vulnerability to surface fishing, including techniques such as surface longline fishing, which are typically conducted at depths above the OMZs (Vedor, Queiroz, et al., 2021). A study conducted on blue sharks utilised mercury isotopes to verify the vertical compression of the habitat. The research study made a comparison between mercury isotopes in sharks from normoxic waters in the northeast Atlantic and those from the world's largest and shallowest OMZ, located in the northeast Pacific (Le Croizier et al., 2022). The study found that blue sharks in the OMZ area exhibited a reduction in foraging depth of approximately 200 metres, suggesting that the OMZ may influence the feeding and foraging patterns of this species (Le Croizier et al., 2022).

1.3.2 The Shortfin Mako

Isurus oxyrinchus, the shortfin mako shark (Figure 3), is a large pelagic predator with a global distribution, found in tropical and temperate waters. It inhabits depths from the surface to at least 1,064 metres and is typically found in pelagic regions, though it is occasionally encountered in coastal waters where the continental shelf is narrow (Abascal et al., 2011; Compagno, 2001; Francis et al., 2019; Mucientes et al., 2012; Rogers et al., 2015; Santos et al., 2021; Vaudo et al., 2017). It is one of the fastest fish in the sea. This ambush predator that feeds on pelagic prey such as cephalopods and teleosts, and like other members of the lamnid family, it is considered endothermic (Camhi et al., 2008; Compagno, 2001; Díez et al., 2015; Maia et al., 2006). In the Atlantic Ocean, the Gulf Stream, the North Atlantic Current/Labrador Current convergence zone, the Azores, the Mid-Atlantic Ridge area, and the upwelling zone off the northwest coast of Africa (where the Cabo Verde OMZ is located) have been identified as areas of high use for the shortfin mako shark (Queiroz et al., 2016, 2019).



Figure 3: Illustration of the Shortfin Mako shark (Isurus oxyrinchus). Public domain image, originally published by NOAA, produced by NMFS, E. Hoffmayer, S. Iglésias and R. McAuley, available on Wikimedia Commons.

In terms of vertical movement, a study in the western North Atlantic found that maximum depths ranged from 28 to 866 metres, with maximum temperatures between 23.3 and 31.1 °C and minimum temperatures between 5.2 and 11.8 °C (Vaudo et al., 2016). The study hypothesised that temperature is the primary environmental factor influencing the movement ecology of this species. Temperatures between 10 and 15 °C represent the lower temperature limit for mako sharks, limiting their maximum depth and range to the north. The study also considered that the upper limit of the depth distribution appears to be thermally limited, with mako sharks avoiding waters above 27°C (Vaudo et al., 2016).

Other studies have also suggested that oxygen levels may influence the maximum depth limit of pelagic fish (Braun et al., 2015; Prince & Goodyear, 2006). In the south-eastern Pacific Ocean, mako sharks' dives mostly ended at depths corresponding to an oxygen concentration of 3 ml l⁻¹ (Abascal et al., 2011), and in the California region, mako sharks rarely descended to depths with oxygen concentrations below 2 ml l⁻¹ (Vetter et al., 2008). This vertical restriction in habitat caused by oxygen can make pelagic fish, including mako sharks, more vulnerable to surface fishing gear (Prince & Goodyear, 2006).

According to the Red List of the International Union for Conservation of Nature (IUCN), the global population of shortfin mako sharks is considered endangered (Rigby et al., 2018), and fishing is among its main threats. It is one of the most important species caught by pelagic longline and gillnet fisheries, which mainly target swordfish and tuna in the Atlantic Ocean, second only to the blue shark (Campana et al., 2005; Coelho et al., 2012; Mejuto et al., 2017).

2. General objectives

This study aims to investigate the vertical movement patterns of *Prionace glauca* and *Isurus oxyrinchus* in relation to normoxic and hypoxic zones, as well as to verify any changes in their behaviour in these two oxygen conditions.

A second objective is to analyse the phases of their dives, paying particular attention to their structure. To achieve this, the dives extracted from satellite archival tags were categorised into three phases: descent, level, and ascent. The resulting dataset was then compiled for further dive analysis (see methods section 3.4).

By fulfilling these goals, the research hopes to provide answers to two primary questions:

- Does hypoxia alter the vertical behaviour of blue and mako sharks?
- Can the frequency, duration, and depth of dive phases be affected by hypoxia?

The present study will explore the effects of hypoxia on the vertical behaviour of the two most commonly fished pelagic predator species in the Atlantic: the blue shark (an exothermic species) and the mako shark (an endothermic species). The main hypothesis is that low oxygen conditions may affect the behaviour of these large predators, altering their habitat use and making them more susceptible to surface fishing.

This study is important because it contributes to our understanding of how the behaviour of these pelagic predators can be affected by low oxygen levels. In addition to being classified as high-trophic species, which is of paramount importance to the ecosystem's proper functioning, it is imperative to comprehend the consequences of ocean deoxygenation, a phenomenon that has been expanding as a result of global warming.

This project is also aligned with the United Nations Global Sustainable Development Goals: Goal 14 (Life Below Water) and Goal 13 (Climate Action). Goal 14 aims to preserve and sustainably use the oceans and their resources. By investigating the behavioural effects of global warming on marine ecosystems it lends support to Goal 13, which calls for urgent action against climate change and its impacts.

3. Methods

3.1 Tagging

The shark tagging process took place in the North Atlantic, specifically near the Azores and Cabo Verde, between 2009 and 2022. All sharks were tagged with pop-up satellite archival transmitting tags (PSAT), in particular the MiniPat model developed by Wildlife Computers (Redmond, WA, USA) (Figure 4). These tags combined archival and Argos satellite technology to track the large-scale movement and behaviour of aquatic animals. The tags recorded depth, external temperature, and light level. The data is recorded and summarised for transmission to Argos satellites when tags are released on a predefined date. Additionally, these tags can be physically recovered, enabling access to the complete archive.



Figure 4: MiniPat (PSAT) tag developed by Wildlife Computers, utilised to record depth, temperature, and light level. Image source: Wildlife Computers.

In the Azores region, the sharks were tagged on the surface using a small auxiliary vessel, and in other offshore regions of the North Atlantic, tagging was carried out in a main research vessel. In both regions, the sharks were captured using fishing gear.



Figure 5: Excess monofilament being cut during the attachment of a PSAT (Pop-up Satellite Archival Tag) to the dorsal fin of a shark. Source: Saving the Blue (n.d.). Available at: <https://www.savingtheblue.org/sharktags>. Photo credit: Annie Guttridge.

The tags were attached to the base of the first dorsal fin using a flexible, silicone-coated monofilament tether, which was inserted through a small hole made in the shark's fin (Figure 5). This method was designed to ensure the security of the tag while minimising impact on the animal.

It is imperative to note that all tagging procedures comply with national animal welfare regulations and have been approved by the ethics committee of the Marine Biological Association (MBA) and the Animal Welfare Ethical Review Body (AWERB) in the United Kingdom.

3.2 Environmental data extraction

To extract the oxygen data, the methodology of Vedor et al. (2021) was used, and the monthly modelled oxygen data values (0.25° spatial resolution) were obtained from Copernicus Marine Environmental Monitoring Service (CMEMS, <https://marine.copernicus.eu/>), Global Ocean Biogeochemistry Hindcast (Product ID: GLOBAL_MULTIYEAR_BGC_001_029). Concentrations of DO were extracted from the surface to 2000m depth, and to account for the spatial inaccuracy surrounding actual individual geolocations, oxygen data were averaged for 1.25° in latitude and 0.75° in longitude (5 x 3 pixel grid) around each shark position.

For spatial analysis of shark movements, an OMZ area in the eastern tropical Atlantic (ETA) was defined as the waters with DO concentrations below 3.5 ml/l O₂ at depths shallower than 100 m (general depth of the thermocline in the ETA). The definition of the ETA OMZ area under consideration was adopted based on its prior utilisation in related studies, wherein it was identified as the DO level that has been demonstrated to induce

stress in large tropical pelagic fishes (Prince et al., 2010; Stramma et al., 2012; Vedor, Queiroz, et al., 2021). Therefore, when DO levels above 100 m were less than 3.5 ml/l O₂, tracked sharks were deemed to be within the OMZ area.

The methodology for extracting the thermocline followed Klöcker et al. (2025), which employed the exponential leap-forward gradient (ELG) method (Chu & Fan, 2017) to identify and characterise the mixed layer and thermocline in temperature profiles. The identification of the thermocline was achieved through the generation of daily temperature profiles from CMEMS, Global Ocean Physics Reanalysis (Product ID: GLOBAL_MULTIYEAR_PHY_001_030) model data. Temperature data were extracted for each shark location using the same methodology applied for oxygen extraction, following Vedor et al. (2021). Temperature profiles were obtained at 1-meter depth intervals from the surface to 1200 m depth, with a 3-day moving window applied to account for temporal variability. The geometric mean of temperatures within each specified window was calculated, producing a final profile representing the lowest depth over the 3-day period. The ELG method was applied to the respective daily temperature profiles using MATLAB (MathWorks) (Figure 6). This conservative approach was selected as it provides a more accurate representation of actual ocean conditions experienced by the sharks.

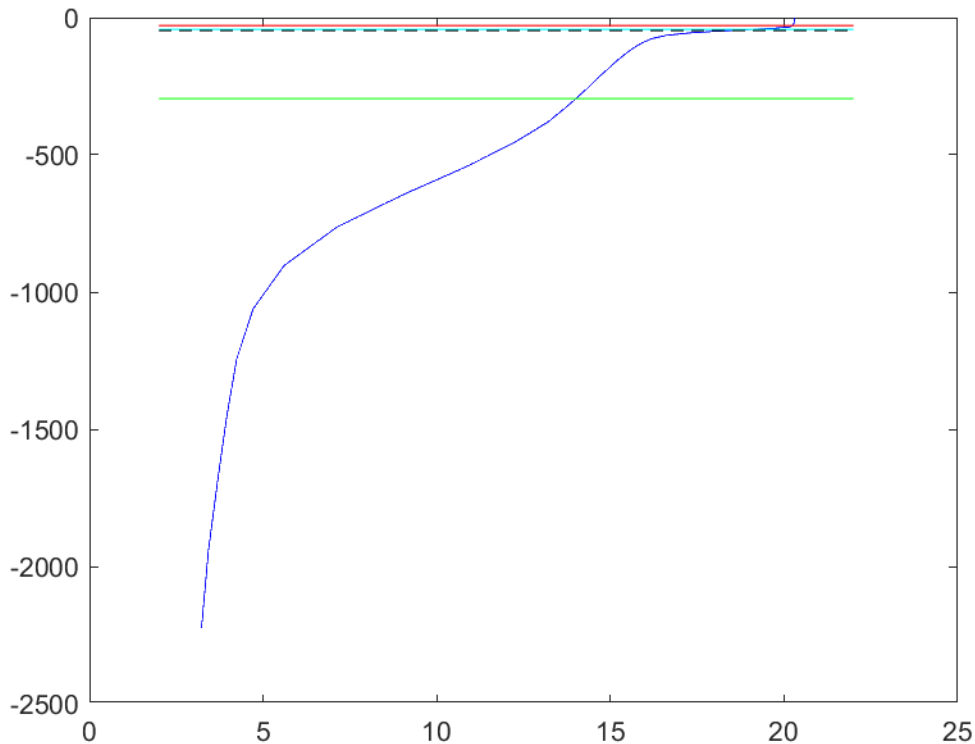


Figure 6: Example of a daily temperature profile from MATLAB, the red line is the start of the thermocline, and the green line is the end of the thermocline.

3.3 Dataset description

The dataset for all sharks is divided by species, with 26 blue sharks and 27 mako sharks from 2009 to 2022 (see summary tables S1 and S2 in Supplementary material). For these individuals, maximum depths were verified in relation to the OMZ.

For a subset of 9 blue sharks and 11 mako sharks, time series data were used, which summarise depth and temperature every 5 or 7.5 minutes (available from 2017 onwards), and time at depth (TAD) and time at temperature (TAT) were verified in relation to the OMZ.

The dive analysis dataset was composed of 10 blue sharks from 2009 to 2022 and 11 mako sharks from 2010 to 2022 (see summary tables S3 and S4 in Supplementary material). The selection of these individuals was made on the basis that they had more dives and better data quality. This was due to the occurrence of data recording and satellite transmission gaps.

It is also important to note that tags of 6 sharks were recovered: 4 blue sharks (bl_nq107085; bl_nq85693; bl_nq96036 and bl_pa98174) and 2 mako sharks (mk_dws164449; mk_dws86408). For these sharks, the complete archival dataset was obtained with higher resolution, with data recorded at one-second intervals. For the remaining sharks, the analysis was performed using data transmitted by satellite, time series data, which were summarised at intervals of every 5 minutes or 7.5 minutes (Figure 7). Even the data from retrieved tags, archival data, when summarised every 5 minutes, show differences in data quality compared to time series data summarised and transmitted by satellite.

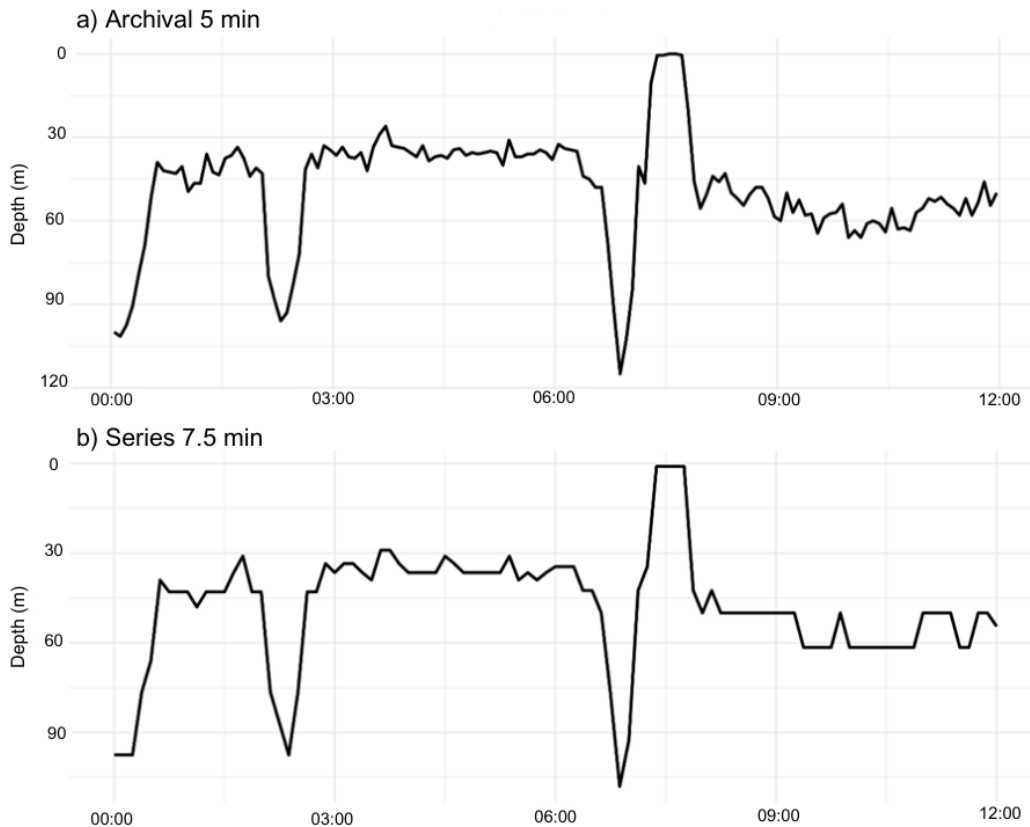


Figure 7: Example of comparison of data from the same shark for archival data (a) and time series data (b). The archival data, summarised at 5-minute intervals, provides more detailed dive information than the time series data, summarised at 7.5-minute intervals.

3.4 Dive analysis data processing

The initial procedure undertaken with the sharks selected for dive analysis (see summary tables S3 and S4 in Supplementary material) involved the utilisation of the software employed in Humphries et al. (2010). This software utilised an analysis of vertical variation to identify movement steps, i.e., it monitored the points at which the animal's behaviour underwent significant changes in depth. In order to accomplish this objective, a methodology known as the split moving-window analysis was employed. This technique enables the segmentation of the dive time series into consistent behavioural discontinuities in the pattern of vertical space use. Each resulting section was then converted into a series of consecutive vertical displacements (steps). Following the definition of the steps, the dive phases were classified as:

- Descent (D): where the vertical variation is negative;
- Level (L): where the vertical speed is zero or lower than the median of the general dive speed for each shark;
- Ascent (A): where the vertical variation is positive.

Once the phases of the dive have been identified, it is necessary to characterise each dive individually. To this end, the daily thermocline data previously extracted (see methods section 3.2) were utilised, and specific criteria were applied during the classification of individual dives, namely:

1. The descent phase or the immediately preceding descent phase must begin at a point located above the start of the thermocline;
2. The descent phase must exceed or be equal to 50 depth (long descent);
3. The end of the dive is defined when the end ascent phase passes back over the thermocline.

Subsequent cleaning steps removed dives with gaps greater than 15 minutes and dives with overlapping time periods from the analysis.

As previously mentioned, there is a difference in how tags summarise data transmitted via satellite (time series) compared to data derived from recovered tags (archival) (see methods section 3.3). In an attempt to reduce these discrepancies in data resolution and structure, the methodology proposed by Oosthuizen et al. (2025) was utilised. This methodology analysed different metrics to identify “wiggles”, defined as small undulations in the dive profile that may be associated with foraging behaviour in marine animals.

In this study, wiggles were used as a complementary tool in the analysis of level phases, defined as periods in which the animal's vertical velocity approaches zero, indicating permanence at a relatively constant depth. This approach enables the integration of time series data with archival data, given that both wiggles and levels represent exploratory movements within a layer of the water column. To ensure consistency between individuals and adjust the sensitivity of wiggle detection, a threshold based on the median of each animal's general vertical velocity was applied. This approach enables the analysis to be tailored to each shark's specific diving profile, thereby enhancing the robustness of behavioural pattern identification.

Finally, the data were organised into daily summaries in order to preserve the temporal structure of the data and enable the identification of vertical movement patterns, respecting the principles of autocorrelation and ensuring replicability in subsequent statistical analyses.

3.5 Statistical analysis

To investigate whether oxygen minimum zones (OMZs) alter shark behaviour, appropriate statistical tests for the non-parametric data structure were applied, conducted separately for each species (*Prionace glauca* and *Isurus oxyrinchus*).

Initially, the Wilcoxon rank-sum test was employed to compare behavioural differences between "inside" (in) and "outside" (out) OMZ conditions. This non-parametric test is suitable for comparing two independent samples when assumptions of normality are not met.

Simple Linear Models (LMs) were used to assess direct relationships between OMZ condition (in vs. out) and shark behaviour when data independence could be assumed. Furthermore, Linear Mixed Models (LMMs) were applied to capture the hierarchical structure of the data. The LMMs included OMZ condition (in vs. out) as a fixed effect and individual (shark ID) as a random effect. When preliminary analyses indicated a significant influence of temporal variation, day was additionally included as a random effect. This approach allowed for simultaneous modelling of the effects of interest (OMZ condition) whilst controlling for variability between individuals and, when necessary, between days.

LMMs are particularly appropriate for this type of data, as they allow for: (i) capturing the natural heterogeneity in individual shark behaviour; (ii) controlling for pseudoreplication resulting from multiple observations per individual; (iii) avoiding inflation of statistical significance; and (iv) providing more robust and generalisable estimates of OMZ effects on shark behaviour.

All analyses were conducted using R software (R Core Team, version 4.4.2, 2024). Data manipulation was performed using the dplyr and lubridate packages, whilst graphical visualisation employed ggplot2 and patchwork. Statistical analyses utilised the stats package for Shapiro-Wilk and Wilcoxon rank-sum tests, car for Levene's test, lme4 and lmerTest for linear mixed models, and emmeans for calculating marginal means and contrasts. Spatial data processing and visualisation were performed using the sf, lwgeom, naturalearth, and naturalearthdata packages.

4. Results

This section presents the analysis of fundamental behavioural metrics for understanding the vertical behaviour of blue sharks (*Prionace glauca*) and mako sharks (*Isurus oxyrinchus*) in relation to oxygen minimum zones (OMZs). The results are organised into two complementary analytical approaches, which differ in temporal resolution and the number of individuals analysed.

The first analysis examines general vertical behaviour using data from 26 blue sharks and 27 mako sharks for maximum daily depth analysis. For Time-at-Depth (TAD) and Time-at-Temperature (TAT) analysis, a subset of 9 blue sharks and 11 mako sharks was used, as these metrics require series data that are only available from 2017 onwards.

This approach focuses on broad vertical distribution metrics in relation to the presence or absence of OMZ conditions.

The second analysis provides a more detailed characterisation of diving behaviour (dive analysis) using a subset of 10 blue sharks and 11 mako sharks (see summary tables S3 and S4 in Supplementary material). This more detailed resolution analysis is structured into three hierarchical levels:

General dive analyses, which include the number of daily dives, mean dive depth, and dive duration.

Dive phases analyses (step phases), which encompass mean depth per step phase, step phase duration, and vertical speed during step phases.

Specific analyses of ‘Level’ phases, which comprise the proportion of time in “Level” phases, proportion of “Level” phases, depth of “Level” phases, and depth difference between consecutive “Level” phases.

All analyses were conducted with the objective of identifying vertical behavioural changes potentially associated with exposure to hypoxic conditions, testing the hypothesis that the presence of OMZs significantly influences the vertical movement patterns of these pelagic shark species.

4.1 General Vertical Behaviour Analysis

The general vertical movement patterns of blue sharks and mako sharks reveal distinct species-specific behaviours and responses to environmental conditions, particularly in relation to OMZ. The temporal tracking data demonstrate considerable variability in depth utilisation strategies between species and across different oceanographic conditions.

Blue shark:

To demonstrate the movement patterns of blue sharks, the blue shark 164443 (Figure 8) was analysed to illustrate the dynamic vertical behaviour of this species over a four-month tracking period (January to May 2017). This blue shark demonstrates a wide use of vertical range, with regular excursions from surface waters to depths greater than 1000 metres. Its diving behaviour shows clear temporal variation, with an intensification of deep-diving activity in March and April, when the animal consistently accessed depths of 800-1,200 metres in cold water masses (5-10 °C). Of particular importance is the animal's exposure to contrasting oxygen conditions in the OMZ throughout the tracking period. During the initial phase (January-February), the shark predominantly operated inside OMZ conditions, exhibiting more compressed vertical behaviour and occasionally diving below 500 metres. Temperatures ranged from approximately 10 to 25 degrees within a more restricted depth range.

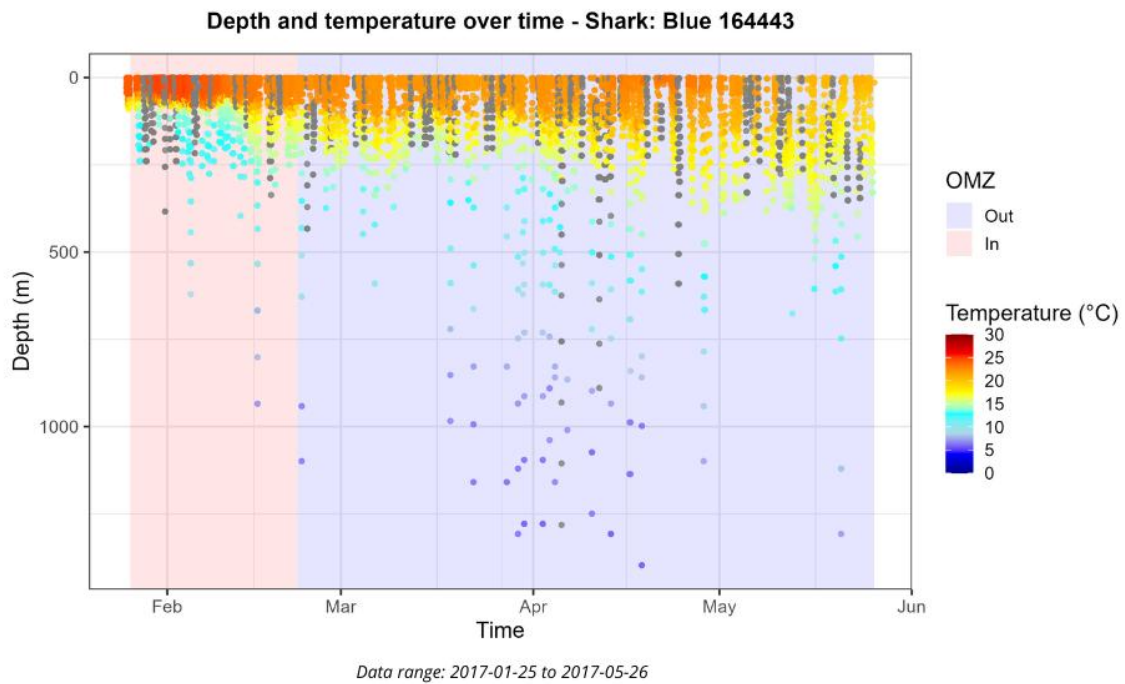


Figure 8: Depth and temperature over time for blue shark, in relation to the OMZ. In the pink section is represented the time spent inside the OMZ, and in the blue section, the time spent outside the OMZ.

Mako shark:

As there were no mako sharks inside and outside the OMZ during the tracking period, one shark was visualised outside (Figure 9) the OMZ and another inside (Figure 10).

The mako shark 202895 (Figure 9), tracked from June to October 2021, exhibited a more restricted vertical distribution, utilising depths between 0 and 500 metres during the entire tracking period. This individual remained consistently outside OMZ conditions, showing regular patterns of diving from the surface to upper mesopelagic zones, typically accessing water temperatures between 10 and 25 °C.

In contrast, the mako shark 164448 (Figure 10), which was tracked during April to June 2018, exhibited more restricted vertical behaviour while operating inside OMZ conditions throughout the tracking period. This individual exhibits limited deep diving activity, rarely exceeding 300 metres in depth, and uses more superficial waters with temperatures ranging from over 25°C to approximately 10°C. The restricted vertical distribution indicates the potential for behavioural modifications when operating in persistent hypoxic conditions.

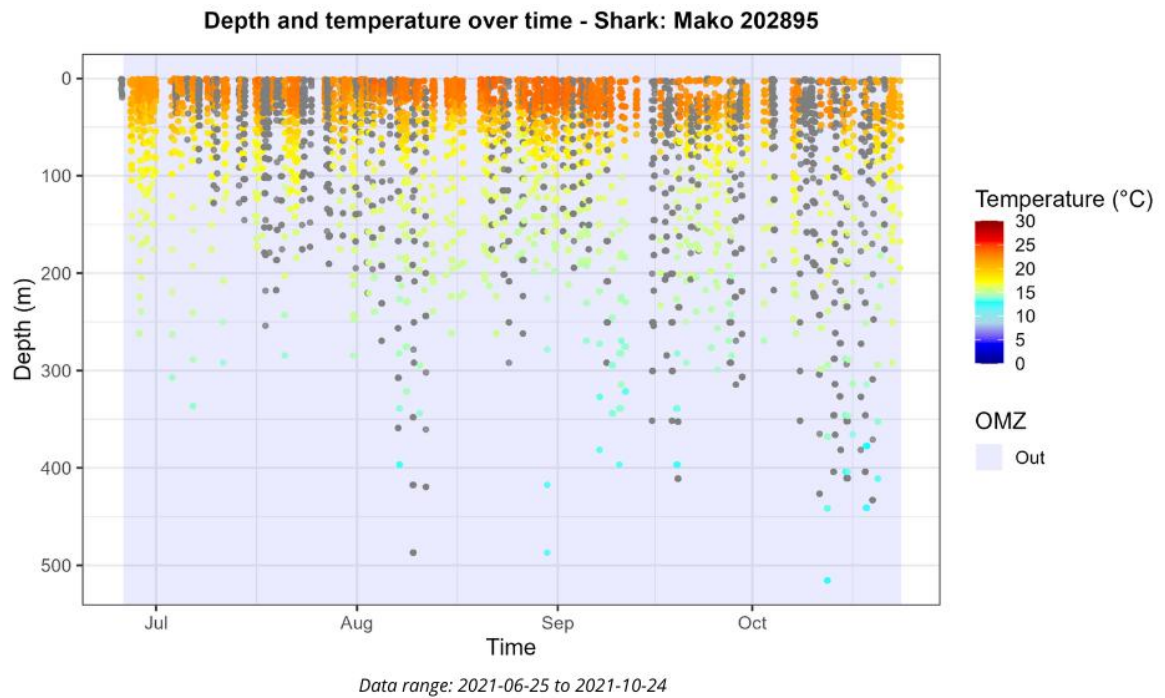


Figure 9: Depth and temperature over time for mako shark, spent outside OMZ conditions.

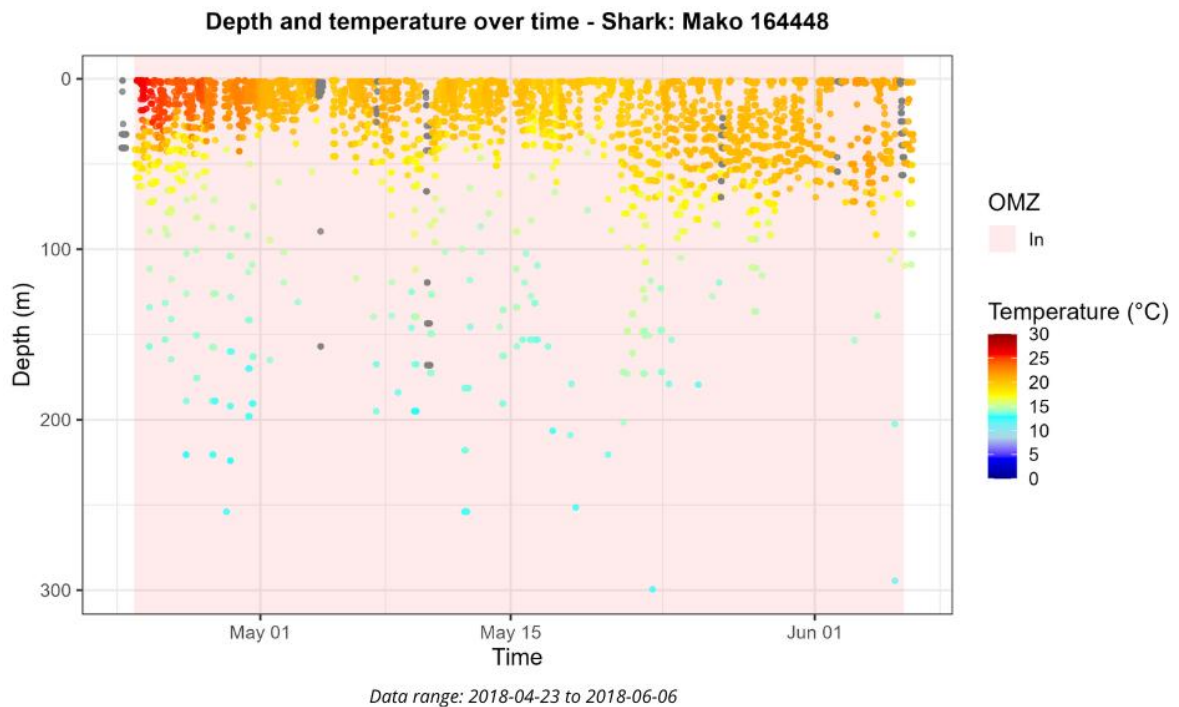


Figure 10: Depth and temperature over time for mako shark, spent inside OMZ conditions.

For a better analysis of the differences inside and outside the OMZ in blue sharks and makos, the following topics cover specific metrics to improve understanding of these differences.

4.1.1. Maximum daily depth

Blue shark:

The analysis of maximum daily depth data for blue sharks ($n = 26$) revealed significant behavioural differences between normoxic conditions (Out OMZ) and hypoxic conditions (In OMZ). Visual inspection of the data shows an apparent change in depth utilisation patterns, with blue sharks demonstrating reduced maximum depths when encountering OMZ conditions (Figures 11 and 12).

The depth usage patterns (Figure 11) distribution illustrates a pronounced increase in time spent at intermediate depths (100-300 m) when in OMZ conditions, accompanied by a corresponding decrease in deeper water usage (300-600+ m).

To account for individual variation amongst sharks, a Linear Mixed Model (LMM) was applied with shark ID as a random effect. This analysis provided quantitative estimates of the behavioural response, revealing that blue sharks reached maximum depths that were, on average, 174.4 metres shallower under low oxygen conditions (In OMZ) compared to high oxygen conditions (Out OMZ) ($p = 9.85 \times 10^{-9}$). By controlling inter-individual variability, this model ensured that the observed difference was attributable to oxygen conditions rather than individual behavioural preferences, confirming the robustness of the oxygen effect (full output results in Figure S1 at Supplementary figures).

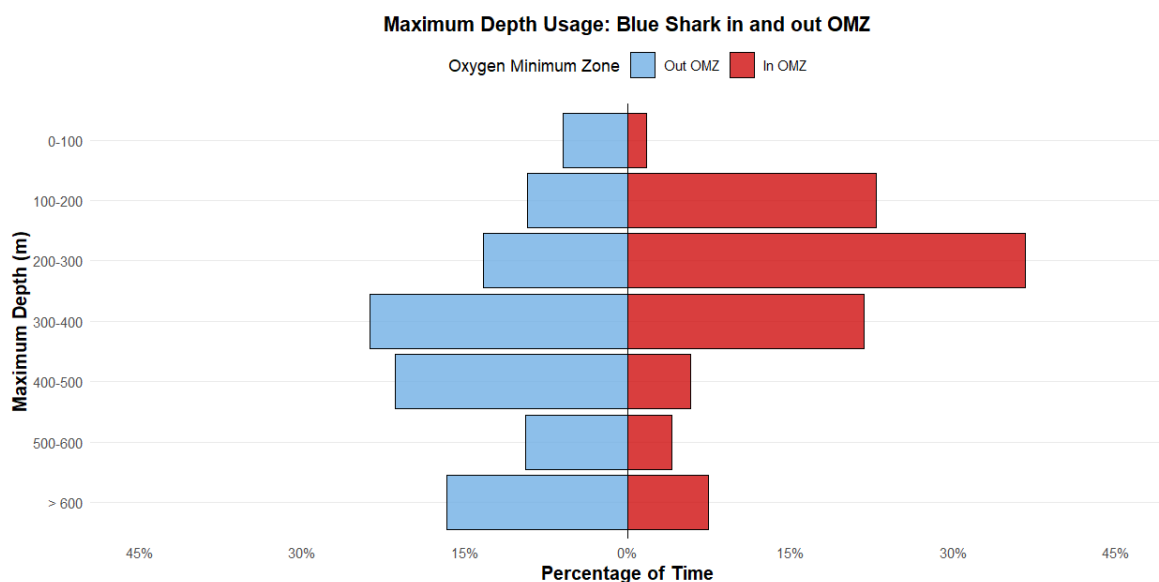


Figure 11: A back-to-back histogram illustrating the comparison of the percentage of time spent in each bin (100 m) of maximum depth usage of blue sharks inside (red) and outside (blue) the OMZ.

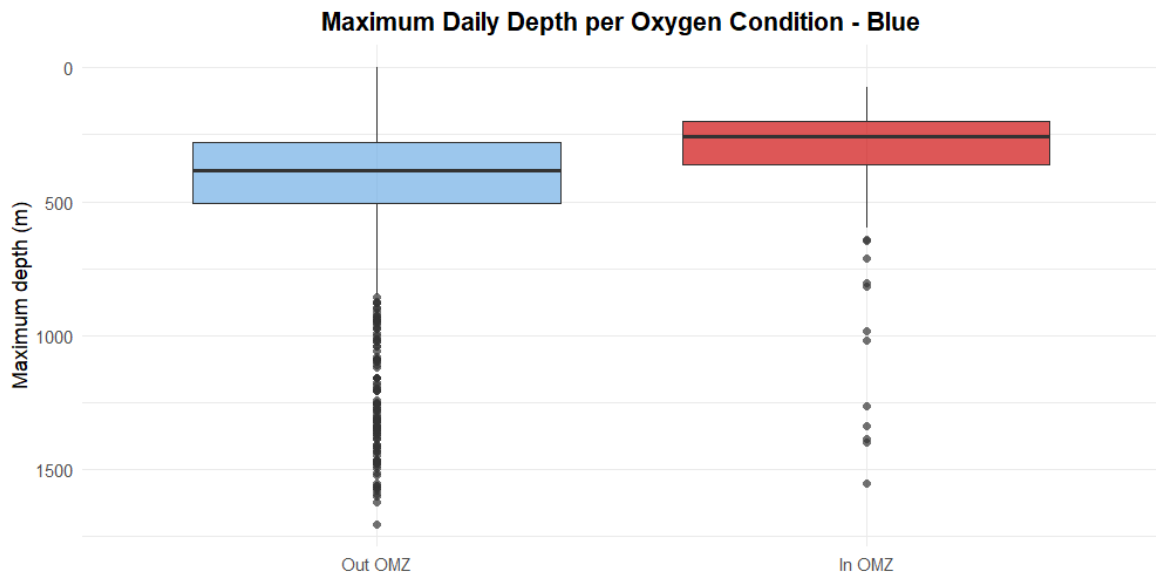


Figure 12: Boxplot illustrating the comparison of the maximum daily depth of blue sharks inside (red) and outside (blue) the OMZ.

Mako shark:

The analysis of maximum daily depth data for mako sharks ($n = 27$) revealed significant behavioural responses to varying oxygen conditions. The depth usage patterns (Figure 13) demonstrate distinct distributional differences between high oxygen (Out OMZ) and reduced oxygen (In OMZ) conditions, with mako sharks exhibiting notable shifts in their vertical habitat usage.

Visual analysis of the depth usage distribution reveals that mako sharks showed increased utilisation of intermediate depths (100-300 m) when encountering OMZ conditions, with a marked expansion of time spent in the 100-200 m and 200-300 m depth ranges. Conversely, utilisation of deeper waters (> 400 m) was substantially reduced under hypoxic conditions, with complete absence of activity in the deepest category (> 600 m) when in OMZ. This pattern suggests a compression of the available vertical habitat range under oxygen-limited conditions.

The boxplot comparison (Figure 14) illustrates the distributional differences in maximum daily depths between the two oxygen conditions. Whilst both conditions show considerable variability, there is a clear upward shift in the median maximum depth when mako sharks are inside the OMZ, indicating consistently shallower diving behaviour under hypoxic conditions.

Statistical analysis confirmed these visual observations. The Linear Mixed Model, which included individual shark ID as a random effect to control for inter-individual variation, estimated that on days with reduced oxygen availability, mako sharks reached maximum depths that were, on average, 140 m shallower than on days with normal oxygen levels (coefficient = -140.08 ± 49.57 m; $p = 0.0056$) (full output results in Figure S2 at

Supplementary figures). This result demonstrates a statistically significant constraint on maximum diving depth under hypoxic conditions.

Collectively, these results demonstrate that reduced oxygen availability is associated with significant limitations on the maximum depths achieved by mako sharks. In contrast to high oxygen conditions that permit substantially deeper dives, hypoxic environments constrain mako sharks to shallower portions of the water column.

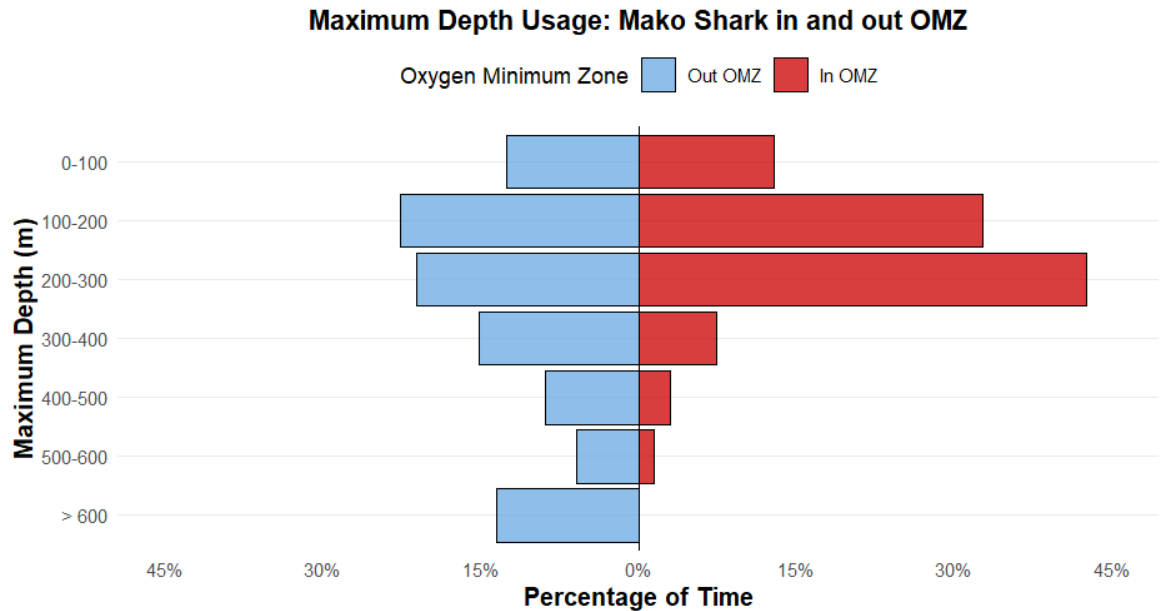


Figure 13: A back-to-back histogram illustrating the comparison of the percentage of time spent in each bin (100 m) of maximum depth usage of mako sharks inside (red) and outside (blue) the OMZ.

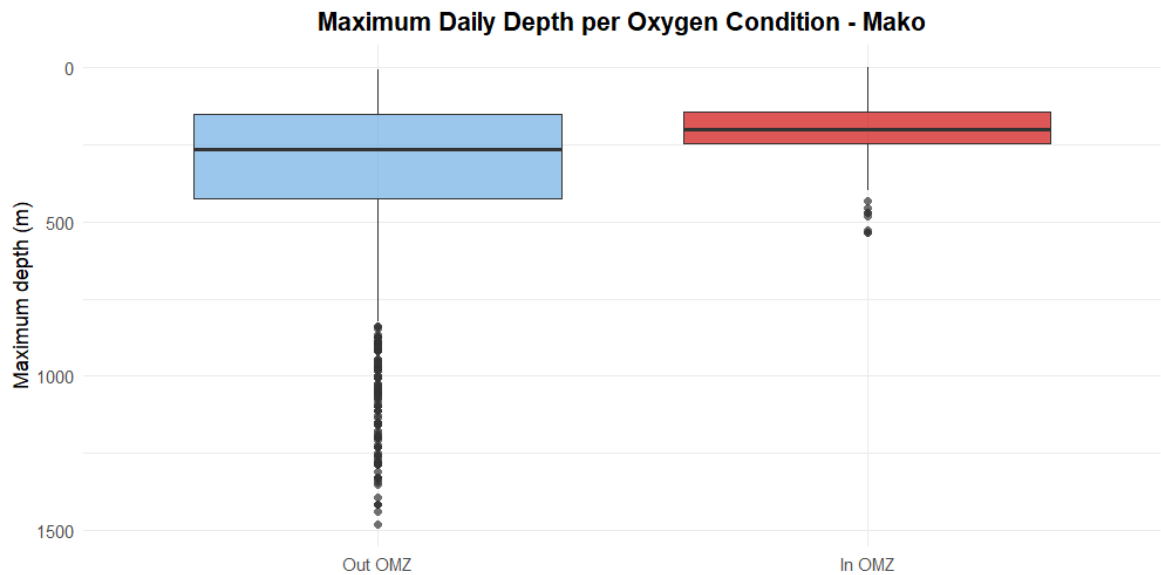


Figure 14: Boxplot illustrating the comparison of the maximum daily depth of mako sharks inside (red) and outside (blue) the OMZ.

4.1.2 Time-at-Depth (TAD)

The time-at-depth (TAD) was evaluated to determine whether significant differences in the distribution of the percentage of time spent inside and outside the OMZ across different depth intervals, the Wilcoxon test for independent samples was performed. This non-parametric test was selected due to the non-normal distribution of the data and the presence of tied values across multiple depth bins. Only bins containing a minimum of three observations per OMZ conditions were included in the statistical analysis to ensure adequate statistical power.

Blue shark:

The analysis of blue sharks ($n = 9$) revealed statistically significant differences in the upper and intermediate water column layers. Specifically, significant differences were observed in the 0-50 m depth bin ($p = 0.046$), 50-100 m bin ($p < 0.001$), and 100-150 m bin ($p = 0.003$). These findings indicate that blue sharks exhibit differential time allocation behaviour in response to the presence of the OMZ within these shallower and intermediate depths. In contrast, at greater depths (150-400 m), no significant differences were observed ($p > 0.05$), which suggests that the OMZ has less influence on the amount of time blue sharks spend at these depths (full output results in Figure S3 at Supplementary figures).

Depth bins exceeding 400 m were not analysed statistically due to a lack of observations, reflecting the lower use of these depths by the individuals studied. However, it is important to note that blue sharks do not spend time at these depths within the OMZ (Figure 15), which could restrict their use of the deeper layers due to lower oxygen availability.

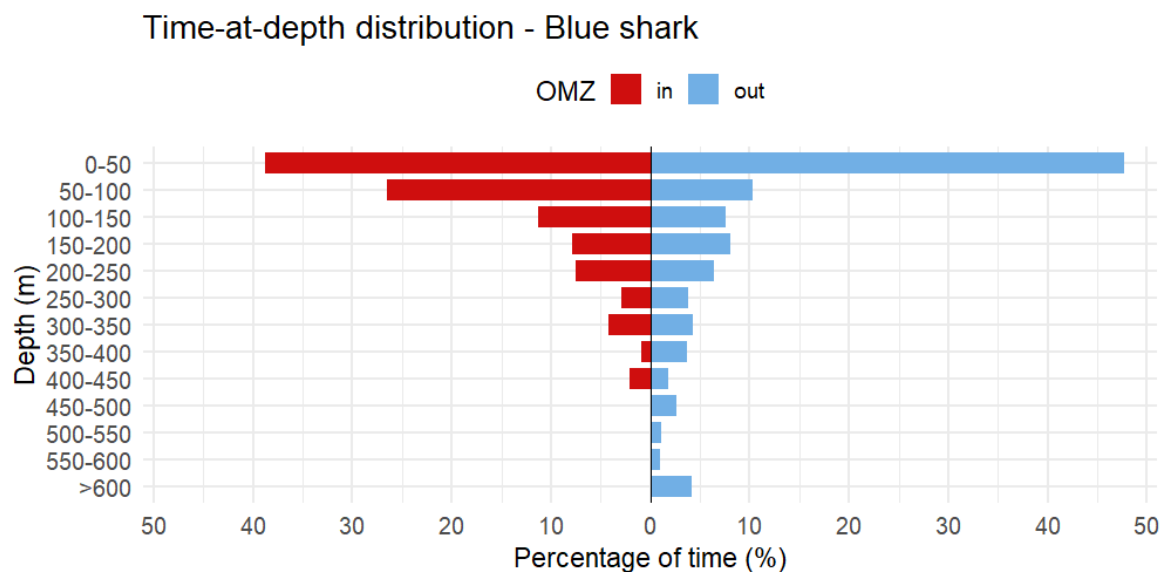


Figure 15: A back-to-back histogram illustrating the comparison of the percentage of time spent in each 50 m depth interval used by blue sharks inside (red) and outside (blue) the OMZ.

Mako shark:

The results of mako sharks ($n = 11$) demonstrated that there were no statistically significant differences in the percentage of time allocated inside and outside the OMZ across all depth ranges analysed ($p > 0.05$ for all bins; full output results in Figure S4 at Supplementary figures). These findings suggest that mako sharks do not exhibit differentiated time allocation behaviour in relation to the presence of the OMZ at any of the depth ranges examined (Figure 16).

In summary, the analysis reveals that the presence of the OMZ does not significantly influence the depth distribution of mako sharks. Habitat use across depth ranges appears largely unaffected by oxygen availability. Notably, it is also important to note that in the 450-500 and >600 m bins, there was no presence of sharks in these deeper bins.

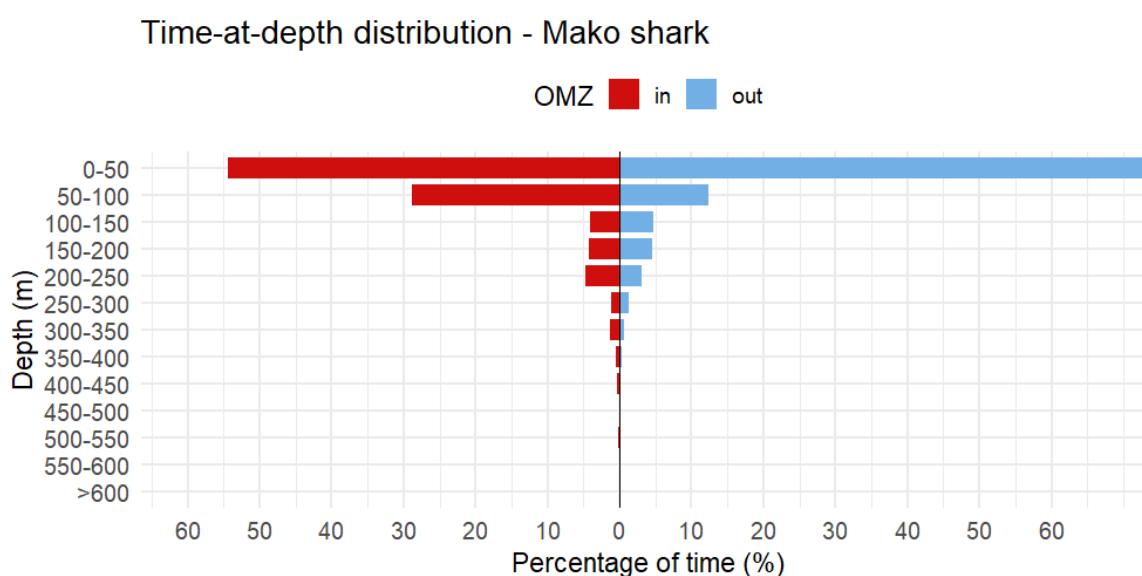


Figure 16: A back-to-back histogram illustrating the comparison of the percentage of time spent in each 50 m depth interval used by mako sharks inside (red) and outside (blue) the OMZ.

4.1.3 Time-at-Temperature (TAT)

The analysis of sharks' temporal distribution as a function of water temperature revealed distinct behavioural patterns between individuals operating within and outside the OMZ. For each temperature bin, the percentage of time spent within specific thermal ranges was compared between "in" (inside OMZ) and "out" (outside OMZ) groups using the Wilcoxon rank-sum test. This non-parametric approach was selected as appropriate for data with unknown distribution characteristics and robust performance in the presence of tied values.

Blue shark:

The results of blue sharks ($n = 9$) demonstrate statistically significant differences across specific temperature ranges, indicating that blue sharks exhibit thermal habitat selection influenced by OMZ presence. Significant differences were observed in the 11-13 °C ($p < 0.05$), 13-15 °C ($p < 0.05$), 17-19 °C ($p < 0.05$), and 21-23 °C ($p < 0.05$) temperature bins, revealing that sharks modify their thermal habitat use in response to oxygen availability within these intermediate temperature ranges (full output results in Figure S5 at Supplementary figures).

The remaining temperature bins showed no statistically significant differences ($p > 0.05$), indicating relatively similar thermal utilisation patterns inside and outside the OMZ for these conditions. Notably, extreme thermal ranges (both coldest $< 9^{\circ}\text{C}$ and warmest $> 25^{\circ}\text{C}$) demonstrated limited utilisation regardless of OMZ presence, reflecting the species' thermal tolerance boundaries and habitat preferences.

A visual analysis of temperature distribution patterns (Figure 17) reveals that sharks demonstrate a pronounced preference for warmer waters ($> 15^{\circ}\text{C}$) when operating outside the OMZ boundaries. The most substantial behavioural differences occur in the range of 17 to 25 °C, where sharks spend considerably more time in these warmer thermal environments when not constrained by the OMZ. Conversely, when operating in OMZ waters, sharks demonstrate a greater preference for colder temperature ranges (11-17 °C) outside the OMZ for the same temperature range, suggesting potential thermoregulatory adaptations or prey-seeking behaviour in hypoxic conditions.

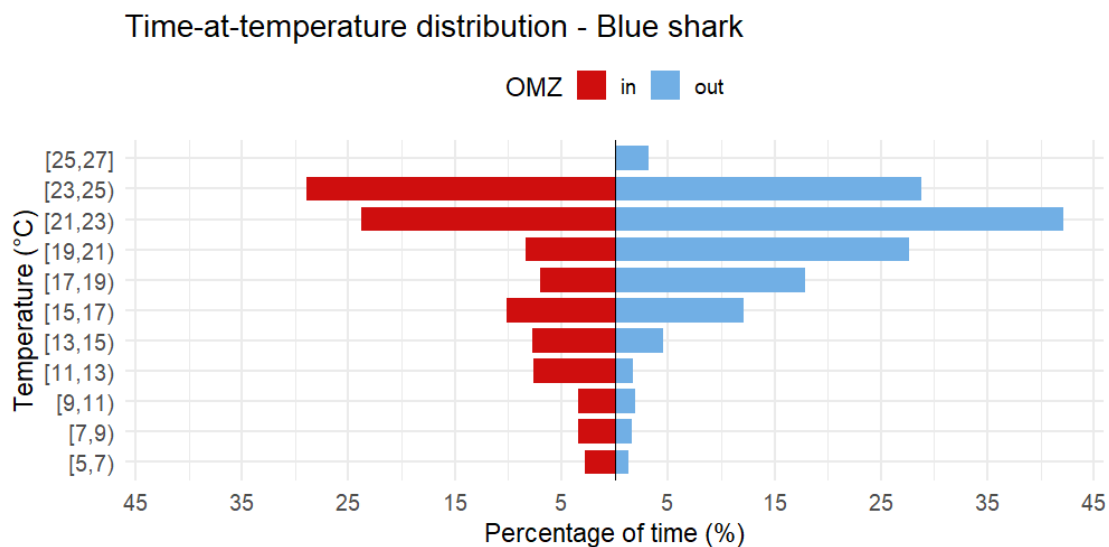


Figure 17: A back-to-back histogram illustrating the comparison of the percentage of time spent in each 2°C temperature range used by blue sharks inside (red) and outside (blue) the OMZ.

Mako shark:

The results of mako sharks ($n = 11$) revealed thermal responses to OMZ presence, with statistically significant differences observed in specific temperature ranges. Significant differences were detected in the 15-17 °C temperature bin ($p = 0.008$) and the 21-23 °C temperature bin ($p < 0.001$), indicating that OMZ presence substantially influences mako shark thermal habitat selection within these intermediate temperature ranges.

In contrast, several temperature ranges showed no statistically significant differences between conditions inside and outside the OMZ: 17-19 °C ($p = 0.285$), 19-21 °C ($p = 0.799$), 23-25 °C ($p = 0.263$) and 25-27 °C ($p = 0.327$). These results indicate that, within these temperature ranges, the presence of the OMZ has minimal influence on the habitat selection of the mako shark, suggesting physiological tolerance or behavioural flexibility within these temperature limits (full output results in Figure S6 at Supplementary figures).

A visual analysis of temperature distribution patterns (Figure 18) reveals distinct thermal usage strategies in waters inside and outside the OMZ. Within the significant 15-17 °C range, mako sharks demonstrate reduced residence time in waters within the OMZ. Meanwhile, in the 21-23 °C range, sharks exhibit a pronounced preference for warmer thermal environments when outside the OMZ boundaries, spending considerably more time in these thermal conditions when oxygen availability is not limiting.

The broader pattern of thermal utilisation demonstrates that mako sharks access a wide temperature range (9-27 °C), with peak activity concentrated in the 17-25 °C temperature range. Notably, the species exhibits substantial use of warmer waters (> 19 °C) when operating outside the OMZ, with visually noticeable differences in the upper-temperature ranges (21-27 °C), although only the 21-23 °C range reaches statistical significance.

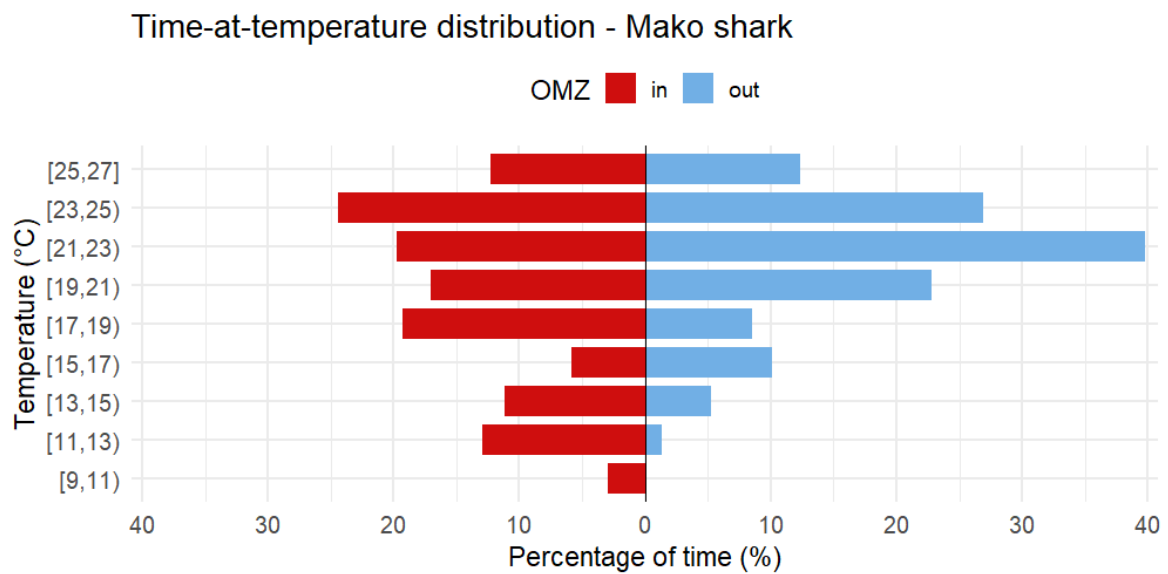


Figure 18: A back-to-back histogram illustrating the comparison of the percentage of time spent in each 2°C temperature range used by mako sharks inside (red) and outside (blue) the OMZ.

4.2 Dive analysis

This section presents a comprehensive analysis of diving behaviour and associated diving phases for both mako sharks and blue sharks tracked in the North Atlantic Ocean. The dataset covers satellite tracking records from 2009 to 2022, and this data will be analysed in relation to the OMZ.

The sharks analysed were tagged in two main regions of the North Atlantic: the Azores archipelago and the Cape Verde Islands (see Figures 19 and 20). These locations were chosen to study the movement ecology of the species in important areas of their Atlantic distribution, including the oxygen minimum zone (OMZ) in the eastern tropical Atlantic (ETA).

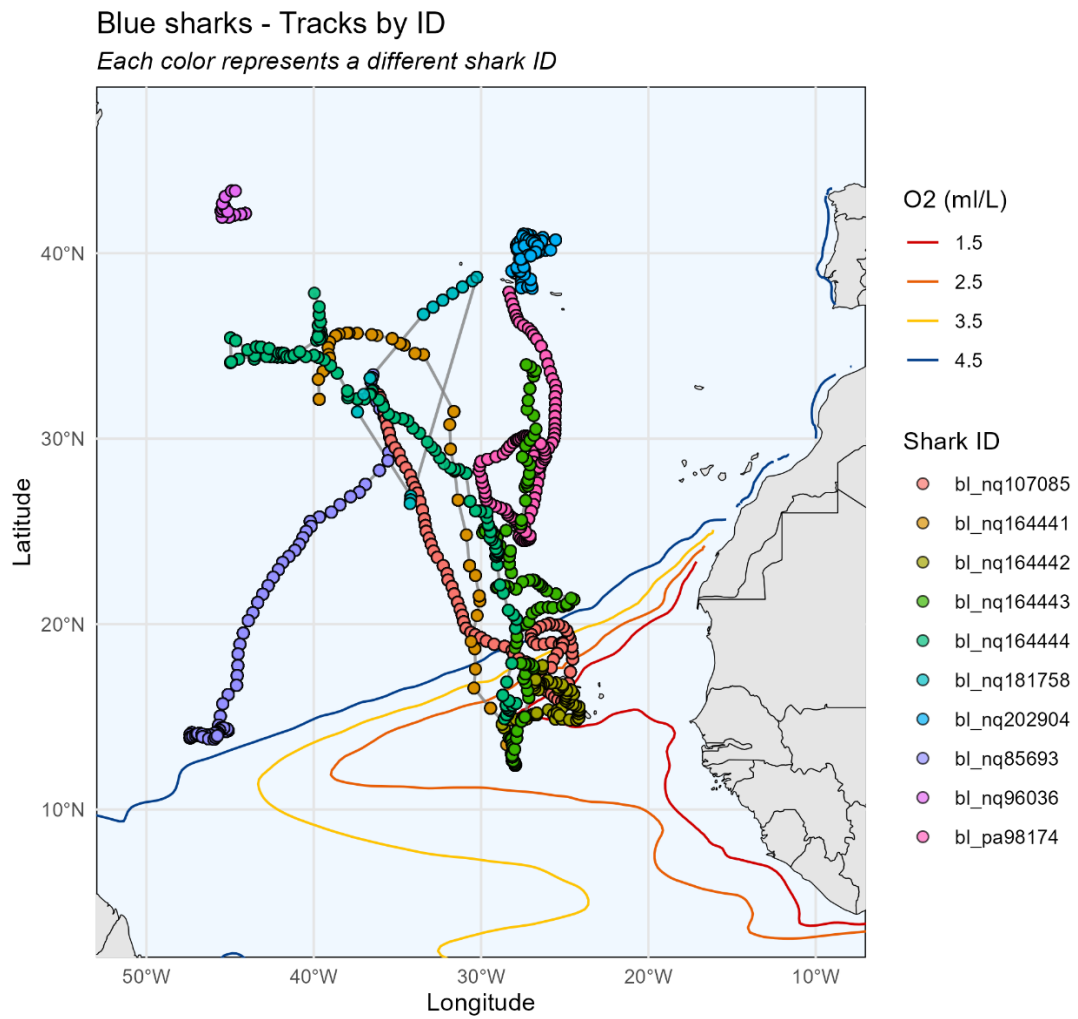


Figure 19: Geographic tracks of 10 blue sharks (*Prionace glauca*) recorded in the North Atlantic Ocean. Each colour trajectory represents the horizontal movement of a specific shark. Oxyclines represented by red (1.5 ml/l of O₂), orange (2.5 ml/l of O₂), yellow (3.5 ml/l of O₂) and blue (4.5 ml/l of O₂) lines at 100 metres from the OMZ of Eastern Tropical Atlantic (ETA).

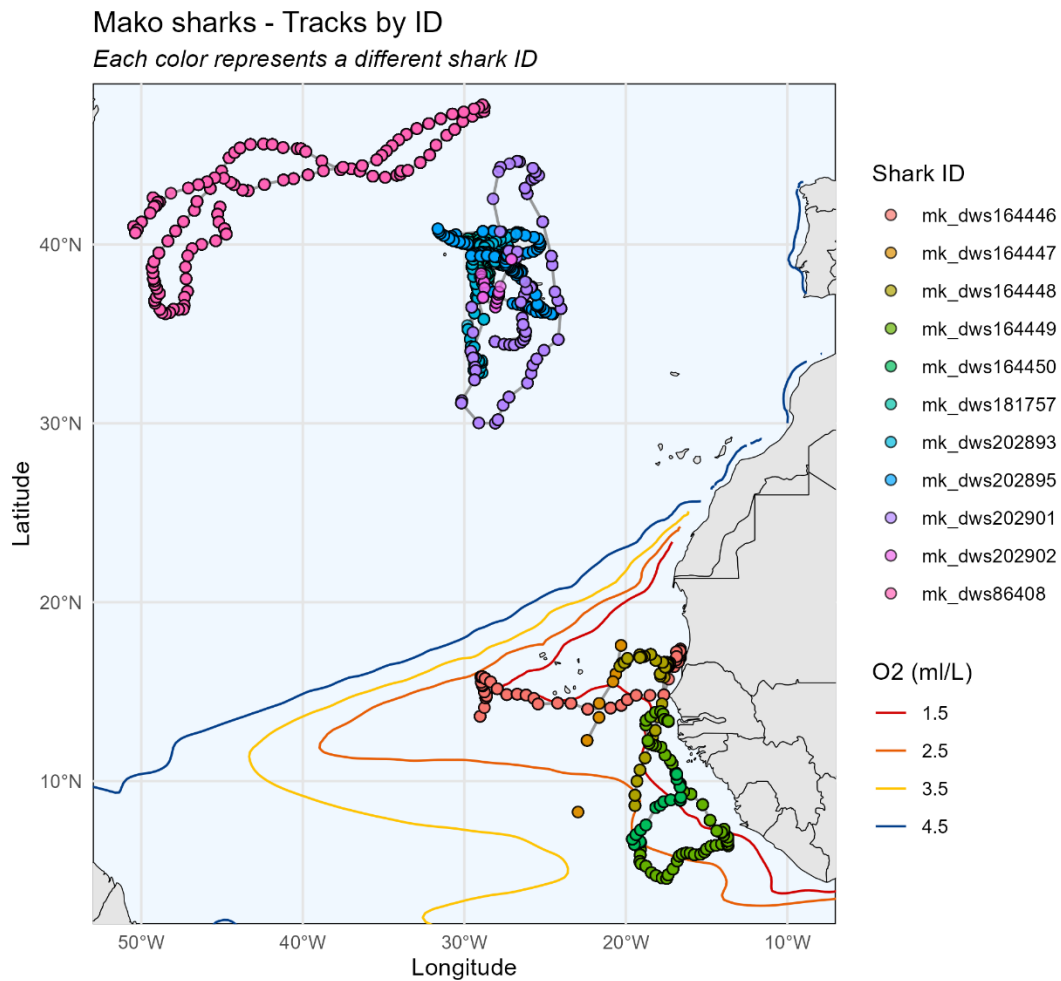


Figure 20: Geographic tracks of 11 mako sharks (*Isurus oxyrinchus*) recorded in the North Atlantic Ocean. Each colour trajectory represents the horizontal movement of a specific shark. Oxyclines represented by red (1.5 ml/l of O₂), orange (2.5 ml/l of O₂), yellow (3.5 ml/l of O₂) and blue (4.5 ml/l of O₂) lines at 100 metres from the OMZ of Eastern Tropical Atlantic (ETA).

4.2.1 General dive metrics

4.2.1.1 Number of daily dives

To assess the daily number of dives under conditions inside and outside the OMZ, a linear model was fitted to evaluate the significance of differences between the two conditions.

Blue shark:

The initial analysis of blue sharks was conducted using the simple linear model, treating the OMZ condition as a categorical predictor. The model estimated a mean diving frequency of 9.14 dives per day for sharks within OMZ waters, with sharks outside the OMZ exhibiting only a marginal increase of 0.048 additional dives ($p = 0.934$) (full output results in Figure S7 at Supplementary figures).

The box plot distribution (Figure 21) illustrates the overlap in diving frequency ranges between the two conditions. Blue sharks within OMZ waters demonstrated a median daily diving frequency of approximately 8 dives, with an interquartile range spanning 5-12 dives per day. Conversely, sharks operating outside OMZ boundaries exhibited a slightly higher median frequency of approximately 9 dives daily, with a broader interquartile range of 4-14 dives. Both conditions showed substantial individual variation in diving behaviour, with some individuals reaching up to 25 dives per day within OMZ waters.

However, by incorporating individual shark ID as a controlling factor, significant OMZ effects of the OMZ were revealed, previously masked by inter-individual variation. This model demonstrated that when individual behaviours are taken into account, sharks exhibited significantly higher diving frequencies within OMZ waters, with a mean reduction of 3.46 dives per day when operating outside OMZ boundaries ($p < 2e-16$) (full output results in Figure S8 at Supplementary figures).

The increased diving frequency within OMZ waters, revealed when controlling for individual effects, suggests that blue sharks may intensify their vertical movement patterns when encountering oxygen-limited environments. This behavioural response may reflect several adaptive strategies, including increased foraging effort to locate prey aggregates associated with OMZ boundaries, as well as temperature, or physiological compensation mechanisms to maintain metabolic efficiency under hypoxic stress.

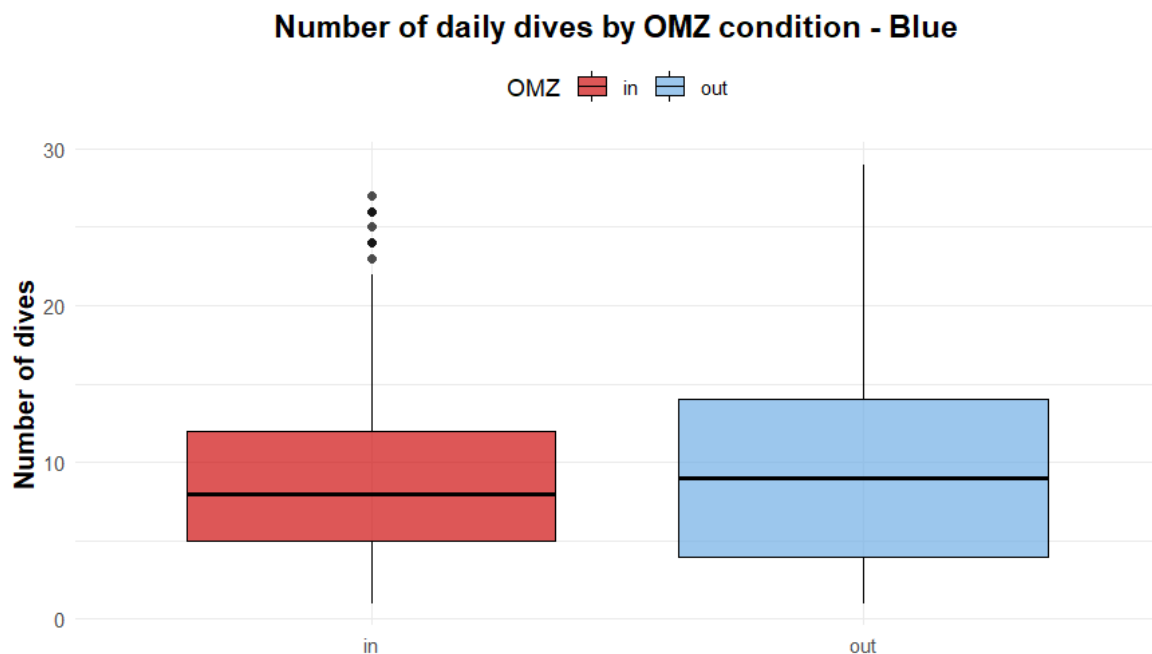


Figure 21: Boxplot illustrating the comparison of the number of daily dives of blue sharks inside (red) and outside (blue) the OMZ.

Mako shark:

In relation to mako sharks, the box plot analysis (Figure 22) illustrates pronounced differences in dive frequency patterns between the two environmental conditions. Mako sharks in OMZ waters demonstrated a lower average dive frequency of approximately 3 dives per day, with a compressed interquartile range ranging from 2 to 5 dives per day. In contrast, sharks operating outside the OMZ exhibited higher diving activity, with a median frequency of approximately 4 dives per day and a wider interquartile range extending from 2 to 7 dives. Some individuals in well-oxygenated waters showed notably increased diving activity, reaching up to 16 dives per day, suggesting that certain sharks intensify their diving behaviour when outside the OMZ.

A simple linear regression model, estimating that mako sharks perform 1.00 additional dive per day when operating outside OMZ boundaries compared to within OMZ waters ($p = 0.000183$). However, the model's low explanatory power ($R^2 = 0.02189$) indicated that the OMZ condition accounts for only 2% of the total variance in daily diving frequency, suggesting the influence of additional factors on diving behaviour (full output results in Figure S9 at Supplementary figures).

To address this limitation, a linear mixed-effects model incorporating individual shark identification as a control variable was employed. This approach revealed an enhanced OMZ effect, with sharks exhibiting 2.26 additional dives per day when outside the OMZ boundaries, after accounting for individual differences. The individual identification variable demonstrated significant effects across multiple sharks, confirming substantial inter-individual variation in diving behaviour that masks population-level responses when uncontrolled (full output results in Figure S10 at Supplementary figures).

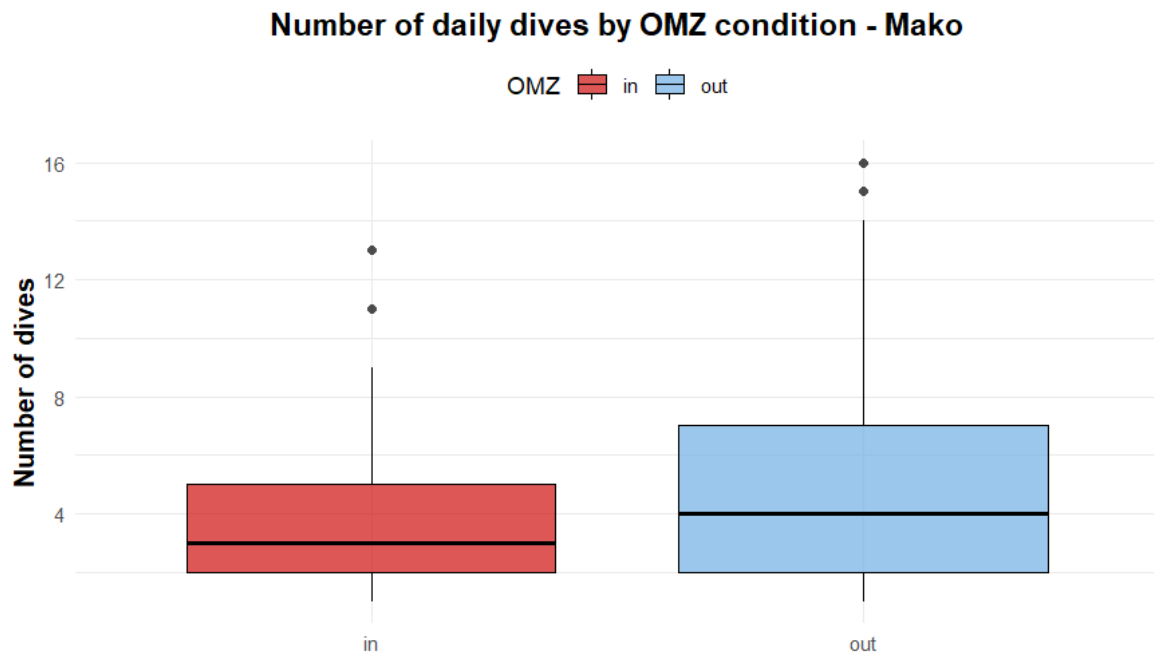


Figure 22: Boxplot illustrating the comparison of the number of daily dives of mako sharks inside (red) and outside (blue) the OMZ.

4.2.1.2 Mean dive depth

Differences in mean dive depth between regions inside and outside the OMZ were evaluated using the Wilcoxon rank-sum test, a non-parametric method, appropriate considering the non-normal data distribution and heterogeneity of variances.

Blue shark:

The analysis of blue shark mean dive depth revealed significant behavioural differences in vertical habitat usage between OMZ and non-OMZ environments. The Wilcoxon rank-sum test demonstrated a statistically significant difference in mean dive depths between the two oxygen conditions ($p < 2.2 \times 10^{-16}$), indicating depth-selection behaviour in response to oxygen availability (full output results in Figure S11 at Supplementary figures).

Analysis of the box plot distribution (Figure 23) reveals distinct depth utilisation patterns between OMZ conditions. Blue sharks inside OMZ waters demonstrated consistently shallower diving behaviour, with a median dive depth of approximately 90 m and a compressed interquartile range spanning 70-110 m. The restricted depth distribution within OMZ conditions suggests constrained vertical habitat use, possibly due to physiological limitations imposed by hypoxic stress.

In contrast, sharks outside the OMZ exhibited deeper diving behaviour, with a median depth of approximately 140 m and a wider interquartile range extending from 100-160 m. The expanded depth range and deeper median values indicate increased use of the

vertical habitat when oxygen availability is not limiting. Notably, the deepest dives, reaching 300-350 m, occurred exclusively outside the OMZ, demonstrating the species' capacity for extensive vertical movements when physiological constraints are not reduced.

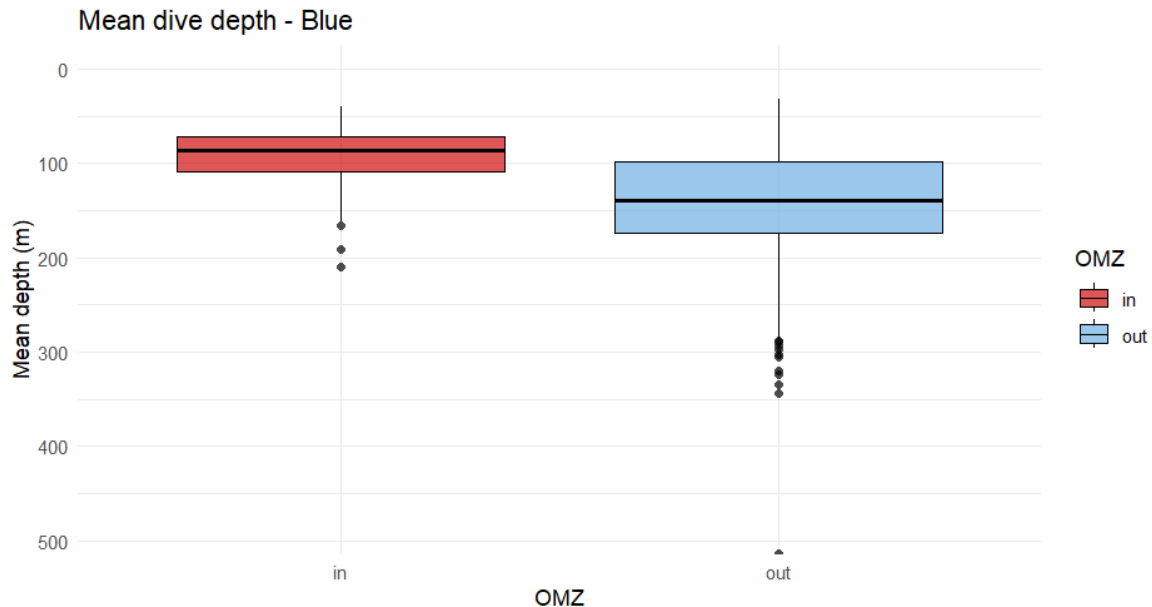


Figure 23: Boxplot illustrating the comparison of mean dive depth of blue sharks inside (red) and outside (blue) the OMZ.

Mako shark:

In relation to mako sharks, analysis of mean dive depth revealed significant differences in vertical habitat usage patterns between environments inside and outside the OMZ. The Wilcoxon rank-sum test demonstrated a statistically significant difference in mean dive depths between oxygen conditions ($p = 5,01 \times 10^{-16}$), suggesting that mako sharks exhibit pronounced depth-selection behaviour in response to oxygen availability (full output results in Figure S12 at Supplementary figures).

Analysis of the box plot distribution (Figure 24) reveals contrasting depth usage strategies between OMZ conditions. Mako sharks inside OMZ waters demonstrated relatively shallow diving behaviour, with a median dive depth of approximately 80 m and a compressed interquartile range spanning 65-100 m. The narrow depth distribution within OMZ conditions suggests restricted vertical habitat use, consistent with behavioural avoidance of hypoxic environments.

Conversely, sharks outside OMZ boundaries exhibited substantially deeper diving behaviour, with a median depth of approximately 120 m and a broader interquartile range extending from 80-160 m. This represents roughly a 40 m difference in median dive depths between oxygen conditions, indicating an expansion of vertical habitat when oxygen restrictions do not exist. Analysing the extreme values, within the OMZ, the values were

limited to approximately 200 m depth, whereas sharks outside the OMZ boundaries demonstrated a wider capacity for deep diving, with atypical values reaching 300-400 m depth more frequently, demonstrating the species' ability to frequently dive deep when oxygen conditions are not limiting.

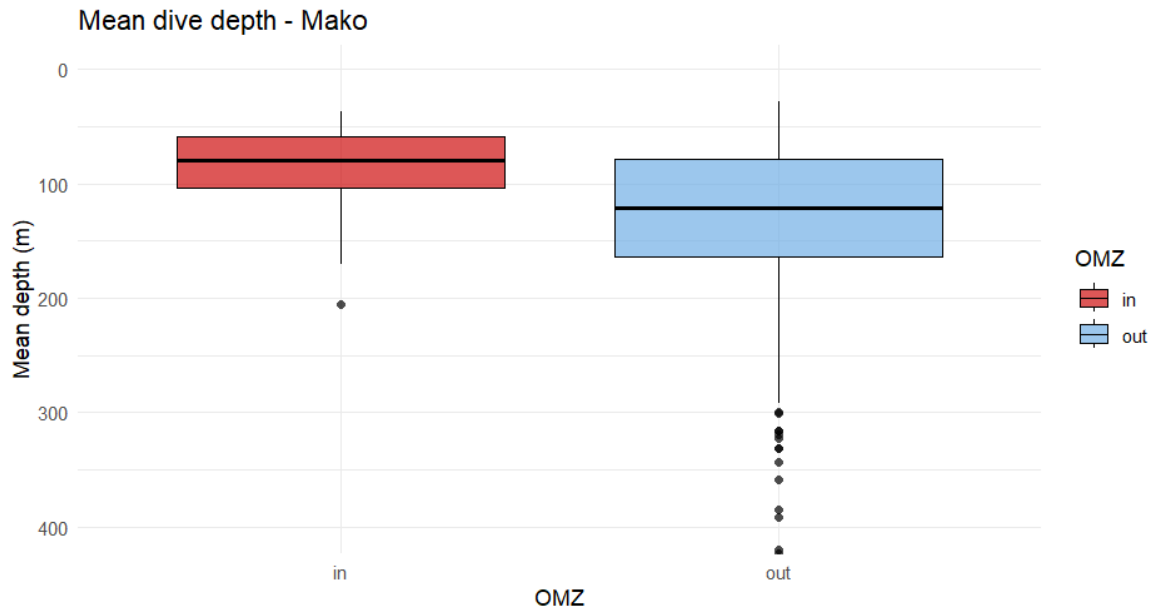


Figure 24: Boxplot illustrating the comparison of mean dive depth of mako sharks inside (red) and outside (blue) the OMZ.

4.2.1.3 Dive duration

Differences in dive duration were investigated by analysing mean daily dive duration in relation to oxygen availability within and outside the OMZ. A linear mixed-effects model incorporating the individual shark identity as a random effect was implemented to control for inter-individual variation, providing a more precise estimation of the impacts of the OMZ.

Blue shark:

Analysis of the mean daily dive duration in blue sharks indicated no significant differences between dives inside and outside the OMZ. The linear mixed model, which incorporates the random effect of individual (ID) to account for repeated dives, indicated no significant effect of OMZ on mean dive duration, with the impact of being outside the OMZ estimated at 0.045 hours (approximately 2.7 minutes), which was not significant ($t = 0.47$) (full output results in Figure S13 at Supplementary figures). These results suggest that the presence of OMZ does not consistently influence the daily dive duration of blue sharks.

As illustrated in Figure 25, the boxplot displays the distribution of mean daily dive duration for blue sharks both inside and outside the OMZ. The median dive durations appear similar between the two conditions, with both showing comparable interquartile ranges. Whilst some extreme values are present in both groups, particularly longer dive durations extending beyond 6 hours outside the OMZ, the overall distributions demonstrate

substantial overlap, supporting the conclusion that OMZ presence does not substantially alter dive behaviour patterns in blue sharks.

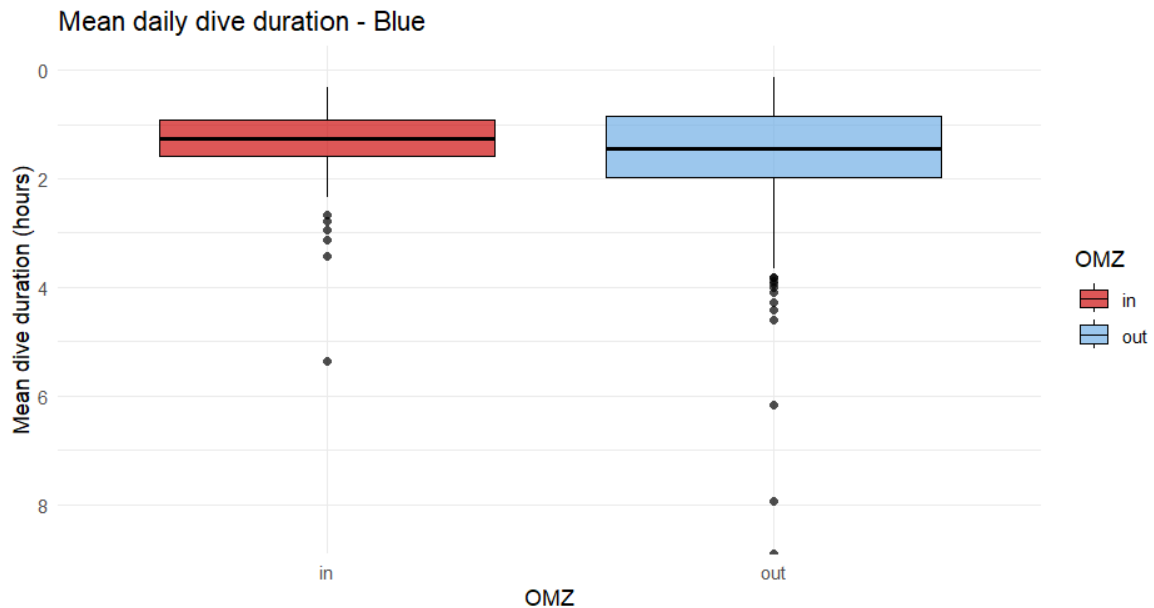


Figure 25: Boxplot illustrating the comparison of mean daily dive duration of blue sharks inside (red) and outside (blue) the OMZ.

Mako shark:

Regarding mako sharks, the linear mixed model considered the variability between individuals (ID as a random effect) and indicated that dives outside the OMZ were, on average, 1.96 hours shorter than dives within the OMZ. However, the effect of the OMZ on the LMM did not reach robust statistical significance ($t = -1.427$), possibly due to high variability among individuals (full output results in Figure S14 at Supplementary figures).

As demonstrated in Figure 26, the boxplot reveals a visual distinction in mean daily dive duration patterns between mako sharks diving inside and outside the OMZ. Dives within the OMZ exhibit longer median durations (approximately 2-3 hours) compared to those outside the OMZ (less than 1 hour). The distribution within the OMZ shows considerably greater variability, with numerous extreme values extending to over 20 hours, whilst dives outside the OMZ display a more constrained distribution with most values concentrated below 10 hours. This pattern corroborates a trend towards longer dive durations within the OMZ. Nonetheless, the substantial individual variability may explain the lack of robust statistical significance in the mixed-effects model.

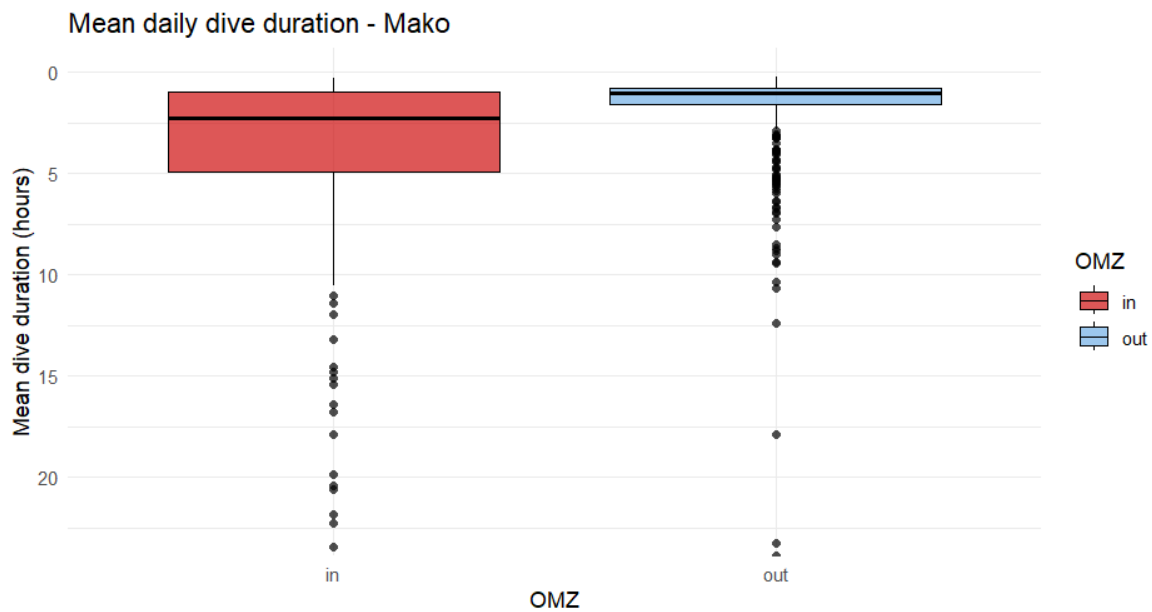


Figure 26: Boxplot illustrating the comparison of mean daily dive duration of mako sharks inside (red) and outside (blue) the OMZ.

4.2.2 Dive Phase Analysis

4.2.2.1 Mean depth per step phase

The analysis of mean depth was performed by comparing the differences between the mean depth inside and outside the OMZ throughout the different step phases. The LMM was employed to incorporate the repeated data structure, thereby controlling for variability between individuals and between days through random effects. In addition, the adjusted means (emmeans) calculated from the mixed model were analysed to estimate and interpret the differences between groups, with confidence intervals ensuring the robustness of the inferences more accurately.

Blue shark:

Analysis of mean depth within and outside the OMZ across different step phases in blue sharks revealed significant differences between the two OMZ conditions. The LMM showed that the step phase and position relative to the OMZ both significantly influenced mean depth. Fixed effects estimates revealed that individuals outside the OMZ exhibited mean depths approximately 55 m greater than those inside the OMZ ($p < 0.0001$), irrespective of step phase (full output results in Figure S15 at Supplementary figures).

Model-adjusted means calculated using estimated marginal means (emmeans) corroborated these consistent differences across all phases. For each phase, individuals outside the OMZ demonstrated significantly greater depths than those within the OMZ, with confidence intervals excluding zero, thereby reinforcing the statistical significance of these findings (full output results in Figure S16 at Supplementary figures). This pattern is clearly

illustrated in the boxplot analysis (Figure 27), showing consistently deeper mean depths for the “out” condition (blue boxes) than for the “in” condition (red boxes) across phases A, D, and L, with minimal overlap between the interquartile ranges.

These findings indicate that the OMZ exerts a robust constraining effect on individual diving behaviour, with a consistent difference of approximately 55 m between “in” and “out” conditions. Importantly, this effect remains consistent across different step phases, even after controlling for individual and daily variability. The boxplot visualisation further demonstrates the consistency of this pattern, with the “out” condition consistently showing both deeper median values and broader depth ranges, suggesting that individuals exploit greater depth ranges when outside OMZ constraints.

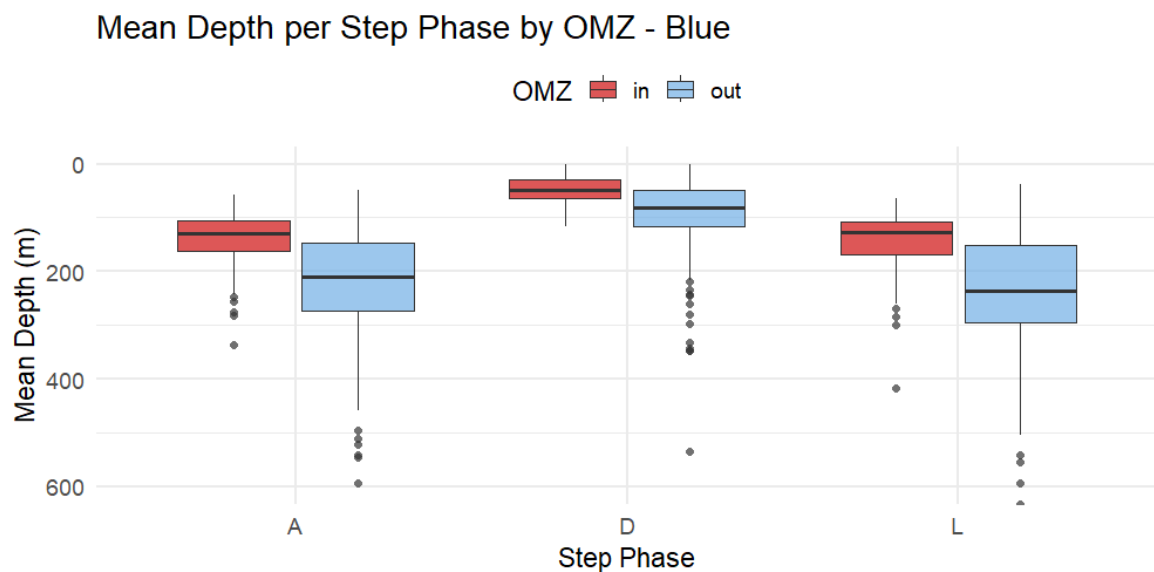


Figure 27: Boxplot illustrating the comparison of mean depth in each step phase of blue sharks inside (red) and outside (blue) the OMZ.

Mako shark:

Analysis of mean depth in mako sharks revealed phase-dependent differences depending on the step phase and the sharks' position relative to the OMZ (inside or outside).

The LMM was fitted, incorporating random effects for individual ID and day. The model revealed significant effects of both OMZ conditions and step phase on diving behaviour. Individuals outside the OMZ exhibited mean depths approximately 39 m greater than those observed within the OMZ ($p = 0.0049$) when considering all phases combined (full output results in Figure S17 at Supplementary figures).

Model-adjusted means, calculated using estimated marginal means (emmeans), showed consistent and significant differences ($p = 0.003$) between the “in” and “out” conditions across all phases. During phase A, individuals outside the OMZ demonstrated mean depths of approximately 177 m compared with 138 m within the OMZ. In phase L, average depths of 146 m (outside) versus 107 m (inside) reinforced the significant

difference (full output results in Figure S18 at Supplementary figures). Meanwhile, phase D revealed average depths of 63 m (outside) versus 24 m (inside), but with considerable overlap between the interquartile ranges of both conditions. This pattern is evident in the box plot analysis (Figure 28), which shows a distinct separation between the “inside” (red) and “outside” (blue) conditions in phases A and L, but a notable convergence during phase D.

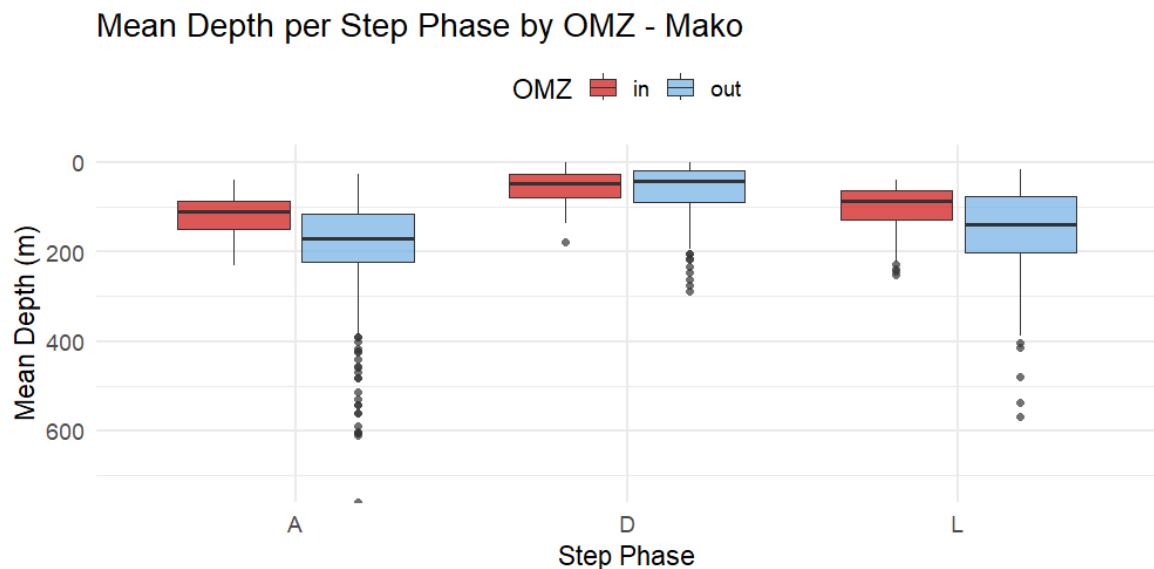


Figure 28: Boxplot illustrating the comparison of mean depth in each step phase of mako sharks inside (red) and outside (blue) the OMZ.

4.2.2.2 Step phase duration

To analyse the average duration of the sharks' step phases in relation to the OMZ (inside or outside), linear mixed-effects models were employed, incorporating random effects for individuals and days. Additionally, estimated marginal means (emmeans) were calculated from the models to obtain adjusted comparisons with confidence intervals, providing a robust framework for interpreting group differences.

Blue shark:

Analysis of mean step phase duration in blue sharks revealed consistent effects of OMZ presence across all phases examined. The LMM demonstrated that the effect of OMZ positioning was remarkably consistent across phases: mean phase duration increased by approximately 98 seconds across all activity phases when sharks were outside the OMZ compared to within it (full output results in Figure S19 at Supplementary figures). This uniform effect is clearly illustrated in the boxplot analysis (Figure 29), which demonstrates consistently higher median durations and broader interquartile ranges for the “out” condition (blue boxes) relative to the “in” condition (red boxes) across phases A and D. Regarding

phase L, the interquartile do not show a considerable difference in size between the “in” and “out” conditions, but their extreme values outside the OMZ reach long durations. In contrast, the medians outside the OMZ are lower than inside, requiring a more detailed analysis of phase L for a better understanding of the effects of the OMZ in this phase.

According to the model-adjusted means (emmeans), outside the OMZ, sharks spend considerably more time in all phases, with consistent confidence intervals that do not significantly overlap with the values obtained within the OMZ (full output results in Figure S20 at Supplementary figures). The box plot further illustrates this pattern, with the “outside” condition consistently exhibiting higher median values and greater variability, as evidenced by the extended whiskers and numerous extreme values, particularly in phases A and L. The consistency of the OMZ effect across all phases reinforces the interpretation that the OMZ exerts a general restrictive influence on behavioural patterns, possibly limiting vertical exploration or requiring adjustments in activity cycles.

These findings indicate that the OMZ significantly and consistently impacts the duration of blue shark diving phases, with individuals spending substantially longer in each behavioural state when unconstrained by low-oxygen conditions. Whilst individual variability between sharks remains a relevant factor in behavioural analysis, the OMZ effect represents a robust environmental influence that transcends individual differences and can affect fundamental aspects of diving behaviour.

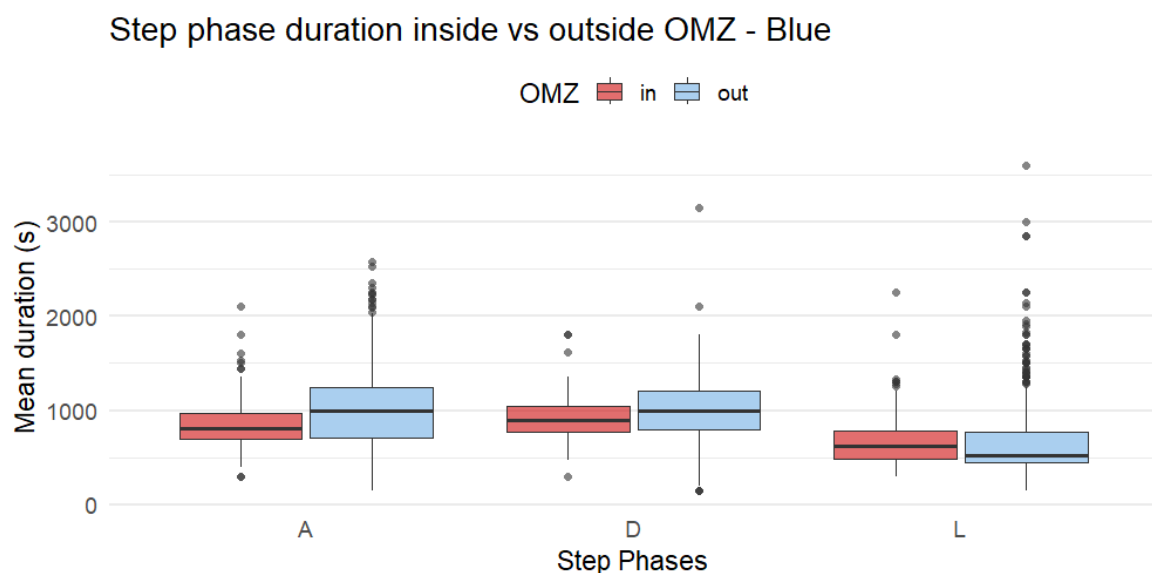


Figure 29: Boxplot illustrating the comparison of the duration of each step phase in blue sharks inside (red) and outside (blue) the OMZ.

Mako shark:

Analysis of mean diving phase duration in mako sharks indicated marked differences between phases, but not between environments inside (in) and outside (out) the

OMZ. The linear mixed-effects model, incorporating day and ID, with adjusted mean estimates (emmeans), indicated that whilst mean mean durations were consistently greater outside the OMZ, these differences were not statistically significant in any phase (A: 918 s in vs 989 s out, $p = 0.356$; D: 698 s in vs 769 s out, $p = 0.356$; L: 516 s in vs 587 s out, $p = 0.356$) (full output results in Figure S21 and S22 at Supplementary figures).

This pattern is reflected in the boxplot analysis (Figure 30), which shows considerable overlap between the interquartile ranges of “in” (red) and “out” (blue) conditions across all phases. Whilst the “out” condition consistently exhibits slightly higher median values and more extensive upper whiskers with numerous extreme values, particularly in phase L, the substantial overlap between the central distributions supports the non-significant differences identified by the mixed-effects model. These findings suggest that mako sharks appear to maintain stable phase durations, regardless of oxygen availability.

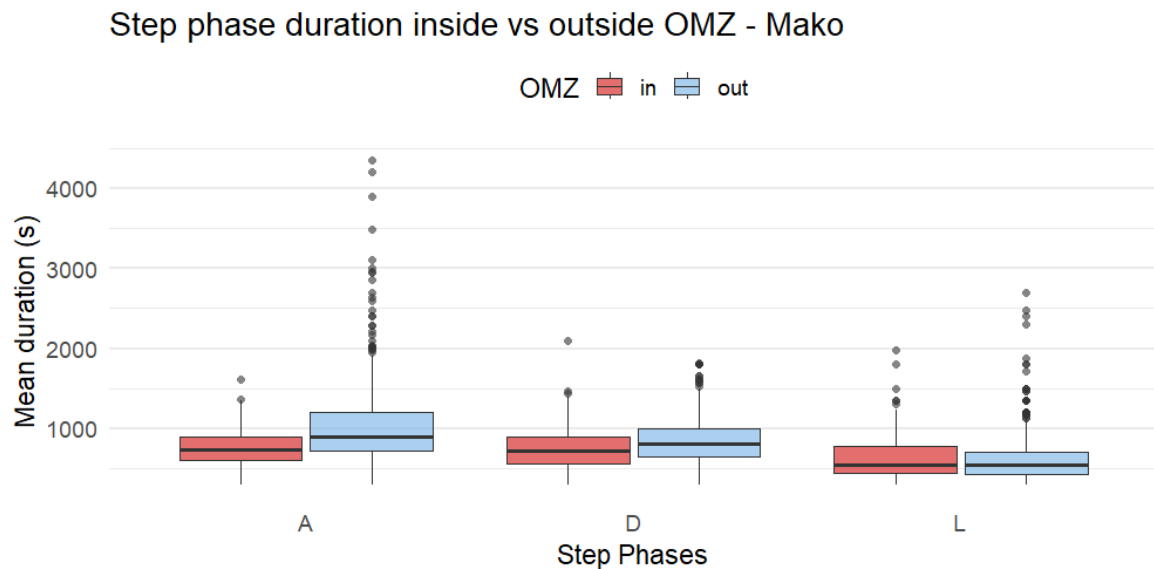


Figure 30: Boxplot illustrating the comparison of the duration of each step phase in mako sharks inside (red) and outside (blue) the OMZ.

4.2.2.3 Vertical speed per step phases

To analyse the vertical speed per step phases, only the ascent (A) and descent (D) phases were included in the analysis, as the level phases have speeds equal to zero or very close to zero. The linear mixed-effects models were fitted, incorporating random effects for individual sharks and days to account for repeated measures and hierarchical data structure. Estimated marginal means (emmeans) were then derived from the models to obtain adjusted comparisons between groups with confidence intervals, ensuring robust and interpretable estimates.

Blue shark:

Analysis of mean speed during different step phases revealed significant differences between areas within and outside the OMZ. During the ascent phase (A), blue sharks exhibited significantly greater mean swimming speeds outside the OMZ (0.122 m/s) compared to within the OMZ (0.084 m/s). This difference was corroborated by linear mixed-effects modelling, which indicated a significant effect of OMZ condition on swimming speed during this phase (emmeans: difference in-out = -0.0378 m/s, $p < 0.0001$) (full output results in Figure S23 and S24 at Supplementary figures).

Similarly, during the descent phase (D), blue sharks moved considerably faster outside the OMZ (0.142 m/s) than within the OMZ (0.104 m/s). The linear mixed-effects models confirmed this significant difference (emmeans: difference in-out = -0.0378 m/s, $p < 0.0001$). These findings are clearly illustrated in the boxplot analysis (Figure 31), which demonstrates consistently higher median speeds and broader speed ranges for the “out” condition (blue boxes) relative to the “in” condition (red boxes) across both phases A and D. The visual representation shows minimal overlap between the interquartile ranges of the two conditions, reinforcing the statistical significance of the observed differences.

The boxplot further reveals that swimming speeds outside the OMZ exhibit greater variability, as evidenced by extended whiskers and numerous extreme values, particularly pronounced in phase D, where speeds reach up to 0.9 m/s. In contrast, speeds within the OMZ remain more constrained, with tighter distributions and fewer extreme values. This pattern suggests that OMZ conditions not only reduce mean diving speeds but also limit the range of speeds that sharks can sustain.

These results indicate that, irrespective of movement phase, OMZ presence is consistently associated with reduced swimming speeds in blue sharks. The observed effect was robust across linear mixed-effects models, which accounted for variability between individuals and observation days. The consistency of the speed reduction (approximately 0.038 m/s) across both ascent and descent phases suggests a uniform physiological or behavioural constraint imposed by low-oxygen conditions on locomotory performance.

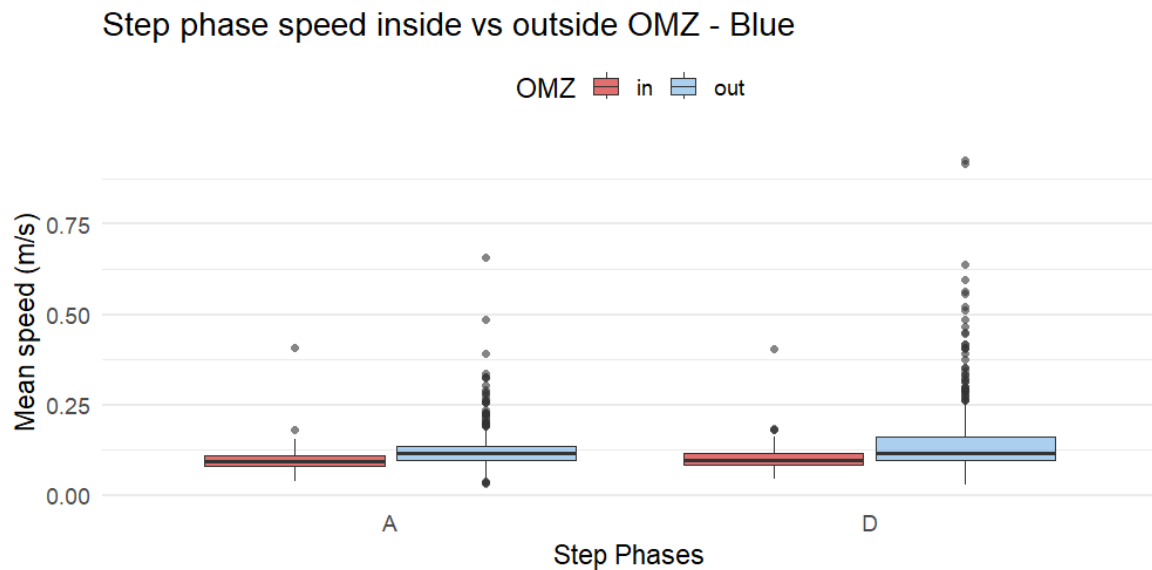


Figure 31: Boxplot illustrating the comparison of the speed in phase A and D in blue sharks inside (red) and outside (blue) the OMZ.

Mako shark:

Analysis of mean swimming speed during ascent (A) and descent (D) phases revealed distinct patterns in relation to OMZ presence in mako sharks. Linear mixed-effects modelling confirmed that descent speeds were significantly faster than ascent speeds (Phase D: 0.034 m/s, $p < 2 \times 10^{-16}$), irrespective of position relative to the OMZ (full output results in Figure S25 at Supplementary figures).

Although the OMZ effect did not achieve conventional statistical significance (OMZout: 0.0388 m/s, $p \approx 0.069$), estimated means suggested that makos tend to move more rapidly outside the OMZ during both phases (full output results in Figure S26 at Supplementary figures). This pattern is evident in the boxplot analysis (Figure 32), which demonstrates consistently higher median speeds for the “out” condition (blue boxes) compared to the “in” condition (red boxes) across both phases A and D. The visual representation shows separation between the central tendencies of the two conditions, with the “out” condition exhibiting broader interquartile ranges and more extensive upper whiskers, particularly pronounced during phase D where numerous extreme values extend beyond 0.4 m/s.

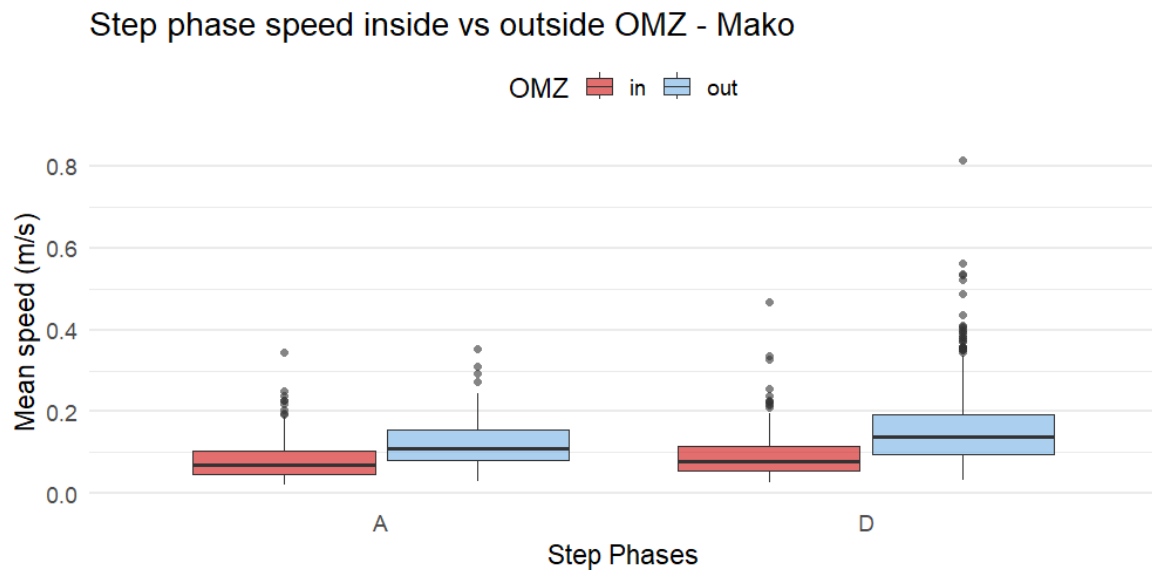


Figure 32: Boxplot illustrating the comparison of the speed in phase A and D in mako sharks inside (red) and outside (blue) the OMZ.

4.2.3 Level Phase Analysis

Level phase analyses were performed separately to obtain a higher resolution of OMZ impacts during this phase. The level phase represents a particularly important behavioural state, as it is often associated with foraging activities, in which sharks maintain relatively stable depths while presumably searching for prey or exploiting feeding opportunities. Furthermore, maps were created for each variable analysed in order to facilitate the visualisation of potential alterations in the level phase within the OMZ. For blue sharks, one ID was selected for the map, which traces a trajectory from outside to inside the OMZ. For mako sharks, there are no IDs inside and outside the OMZ during the tracking periods, so the map was created for two different IDs, one inside the OMZ and one outside.

4.2.3.1 Proportion of time in level

To analyse the proportion of time spent in the Level phases, a linear mixed effects model (LMM) with logit-transformed proportions was used, incorporating the presence of OMZ as a fixed effect and individual identification and day as random effects. This modelling strategy enabled control of individual behavioural differences, temporal variation and extreme proportion values close to 0 or 1.

Blue shark:

A linear mixed-effects model (LMM) was employed using logit-transformed proportions. The LMM indicated that the difference between within and outside OMZ conditions was not statistically significant (estimate = -0.246 ; SE = 0.175 ; $p = 0.16$) (full output results in Figure S27 at Supplementary figures). This pattern is reflected in the boxplot analysis (Figure 33), which shows considerable overlap between the interquartile

ranges of the “in” (red) and “out” (blue) conditions. Whilst the “in” condition exhibits a slightly higher median proportion of time spent in the level phase (approximately 0.25 versus 0.20), the substantial overlap between the central distributions supports the non-significant difference identified by the mixed-effects model.

Individual variability between sharks was greater than temporal variability between days ($ID \approx 0.50$; $Day \approx 0.25$), reflecting substantial individual differences in behavioural patterns. The boxplot corroborates this finding, showing relatively tight distributions for both conditions with few extreme values, suggesting that whilst individual sharks may have consistent behavioural preferences, the overall population-level difference between OMZ conditions is modest.

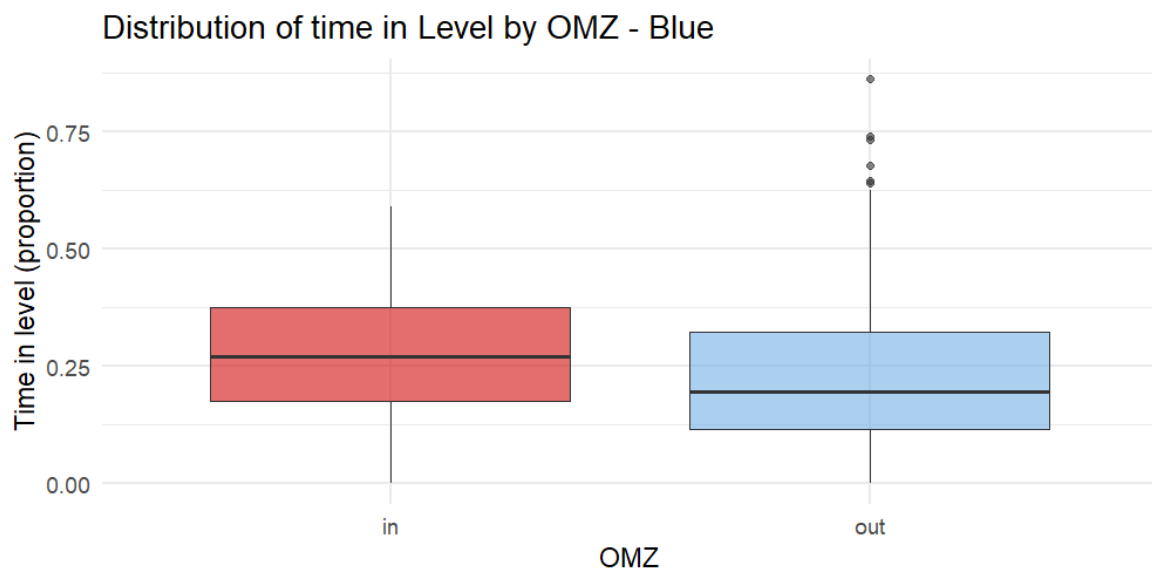


Figure 33: Boxplot illustrating the comparison of the time in the level phase in blue sharks inside (red) and outside (blue) the OMZ.

As illustrated in Figure 34, it is possible to see that the proportion of time spent at level increases when approaching the OMZ, with the proportion of time in level outside the OMZ being mostly up to 15%, whereas inside the OMZ, the blue shark analysed tends to spend 15-30% of its time at level.

Blue shark: 107085 - Proportion of Time in Level Phase

Data range: 2011-08-28 to 2011-11-29

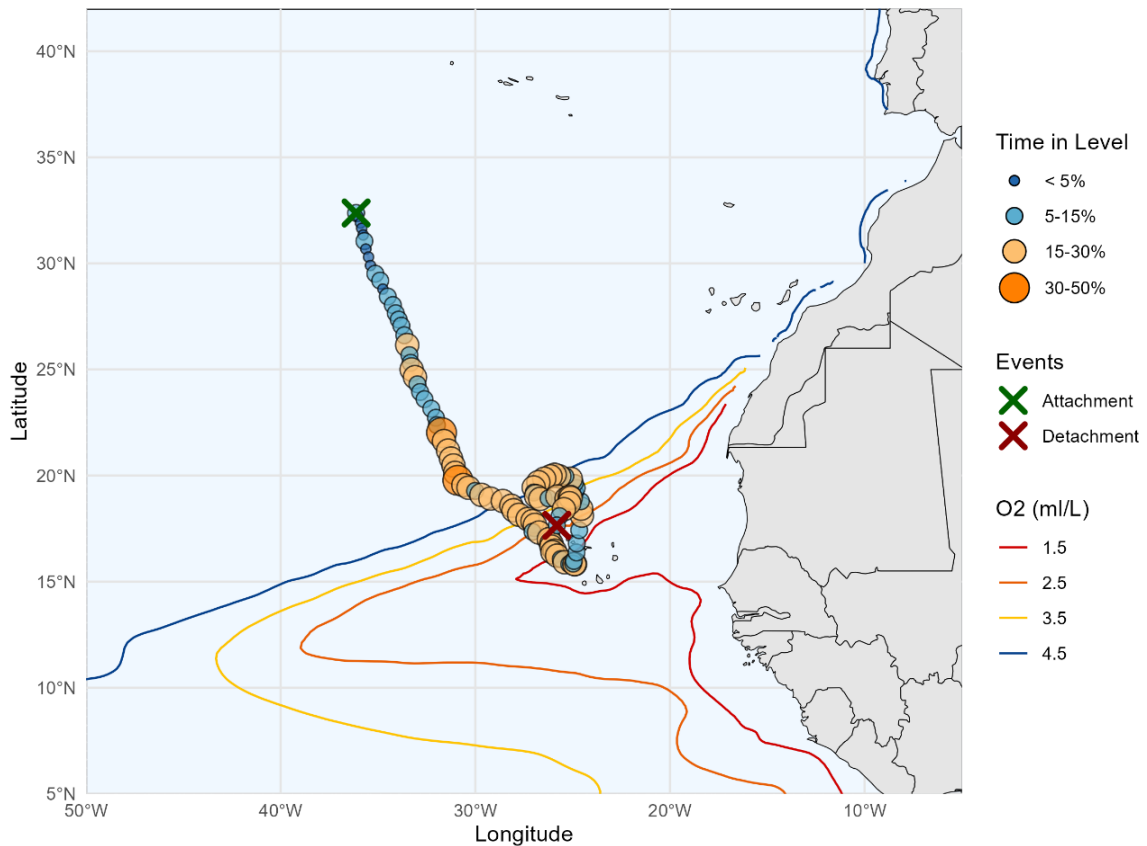


Figure 34: Map illustrating the proportion of time in the level phase along the blue shark's track, with circles increasing as time in level increases.

Mako shark:

For mako sharks, the linear mixed-effects model (LMM), the OMZ effect was not statistically significant (estimate = -0.557 , $p = 0.18$) (full output results in Figure S28 at Supplementary figures). Estimated means suggested that makos spend approximately 26% of their time in the level phase within the OMZ compared to 16% outside the OMZ. Still, the substantial variability between individuals indicates that this difference is not consistent across the population.

This pattern is clearly illustrated in the boxplot analysis (Figure 35), which reveals marked differences in the distribution characteristics between OMZ conditions. The “in” condition (red box) shows a notably higher median proportion (approximately 0.35) compared to the “out” condition (blue box, median approximately 0.25). However, the boxplot also demonstrates the considerable individual variability that may underlie the non-significant mixed-effects result. The “in” condition exhibits a broad interquartile range extending from approximately 0.25 to 0.48, while the “out” condition shows a wide range from roughly 0.15 to 0.35, with some extreme values extending above 0.6.

These findings indicate that whilst there may be a tendency for mako sharks to allocate more time in the level phase inside OMZ, this pattern is not statistically robust when accounting for individual differences. The high individual variability suggests that mako sharks exhibit diverse behavioural strategies in response to OMZ conditions, with some individuals showing marked preferences whilst others maintain relatively consistent behaviour regardless of oxygen availability.

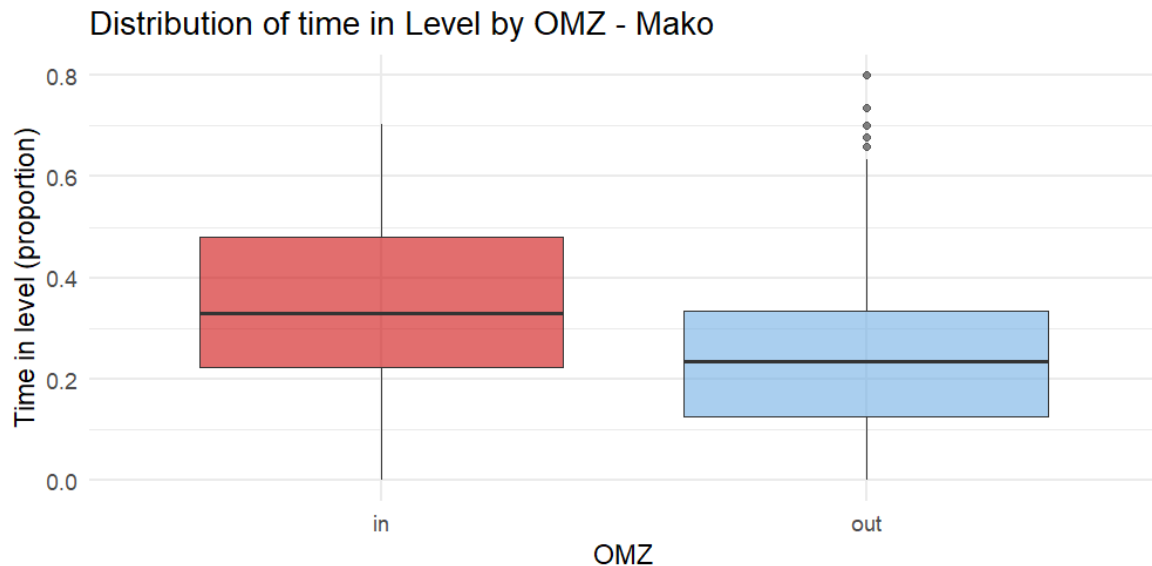


Figure 35: Boxplot illustrating the comparison of the time in the level phase in mako sharks inside (red) and outside (blue) the OMZ.

When visualising the time spent at level along the mako shark track, with one map for makos inside the OMZ (Figure 36) and another for those outside the OMZ (Figure 37), it is possible to see that there were no marked differences between the time spent at level inside and outside the OMZ. This supports the non-significant difference observed by the LMM results.

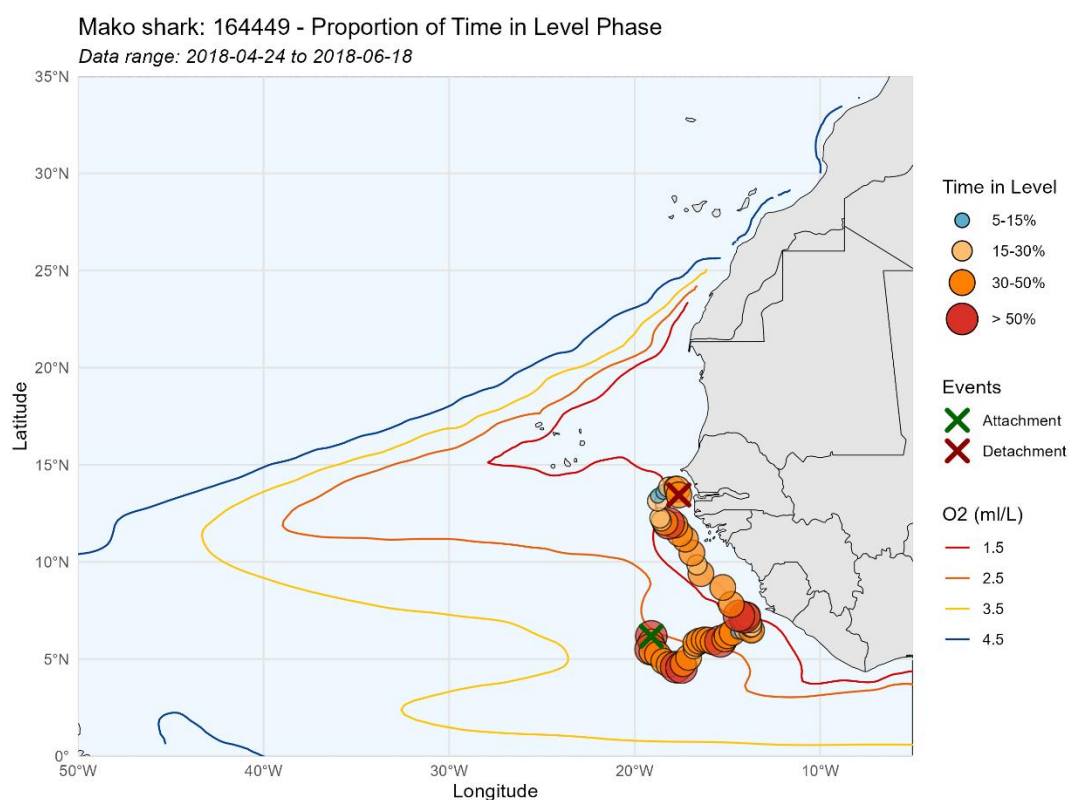


Figure 36: Map illustrating the proportion of time in the level phase along the mako shark's track inside the OMZ.

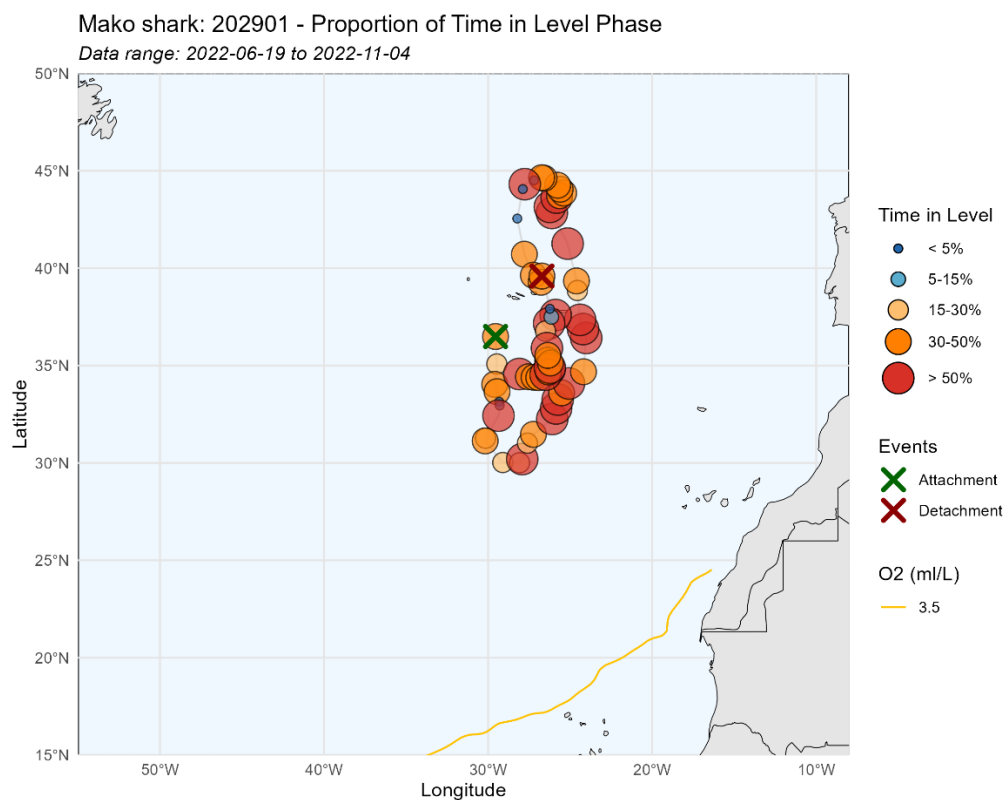


Figure 37: Map illustrating the proportion of time in the level phase along the mako shark's track outside the OMZ.

4.2.3.2 Proportion of level phases

To analyse the distribution of level phase proportions between conditions inside and outside the OMZ. The linear mixed-effects model (LMM) was fitted to the logit-transformed proportions, incorporating individual identification and day as random effects. This modelling approach controlled for both behavioural differences between individuals and daily variability.

Blue shark:

For blue sharks, the proportion of time spent in level phases varied between inside and outside the OMZ. A linear mixed-effects model fitted to logit-transformed proportions, incorporating random effects for individual ID and day, demonstrated that OMZ presence exhibited a negative influence on level phase proportions (coefficient OMZout = -0.308), indicating that sharks spend, on average, less time in level phases outside the OMZ. However, this effect was not statistically significant at the 5% threshold ($p = 0.052$), suggesting a tendency without sufficient evidence to confirm a definitive difference (full output results in Figure S29 at Supplementary figures). This marginal significance is evident in the boxplot analysis (Figure 38), which shows considerable overlap between the interquartile ranges of “in” (red) and “out” (blue) conditions, despite apparent differences in their central tendencies.

The boxplot reveals that the “in” condition exhibits a slightly higher median proportion (approximately 0.34) compared to the “out” condition (approximately 0.30). However, both conditions demonstrate similar ranges and variability, with the “in” condition showing some extreme values extending both above 0.6 and below 0.1, while the “out” condition shows a distribution with whiskers in the upper range, extending up to 0.6. The substantial overlap between the central 50% of both distributions corroborates the marginal statistical significance observed in the mixed effects analysis.

When the model considered only the random effect of individual ID, excluding day-to-day variability, the OMZ effect became statistically significant ($p = 0.037$) (full output results in Figure S30 at Supplementary figures). This result suggests that the significance of the OMZ effect is sensitive to the inclusion of daily effects, which capture temporal variations in behaviour or environmental conditions that influence the proportions of the level phase. Retaining day as a random effect is therefore crucial to avoid overestimating the OMZ influence, ensuring that observed differences reflect consistent individual variations rather than ephemeral daily fluctuations.

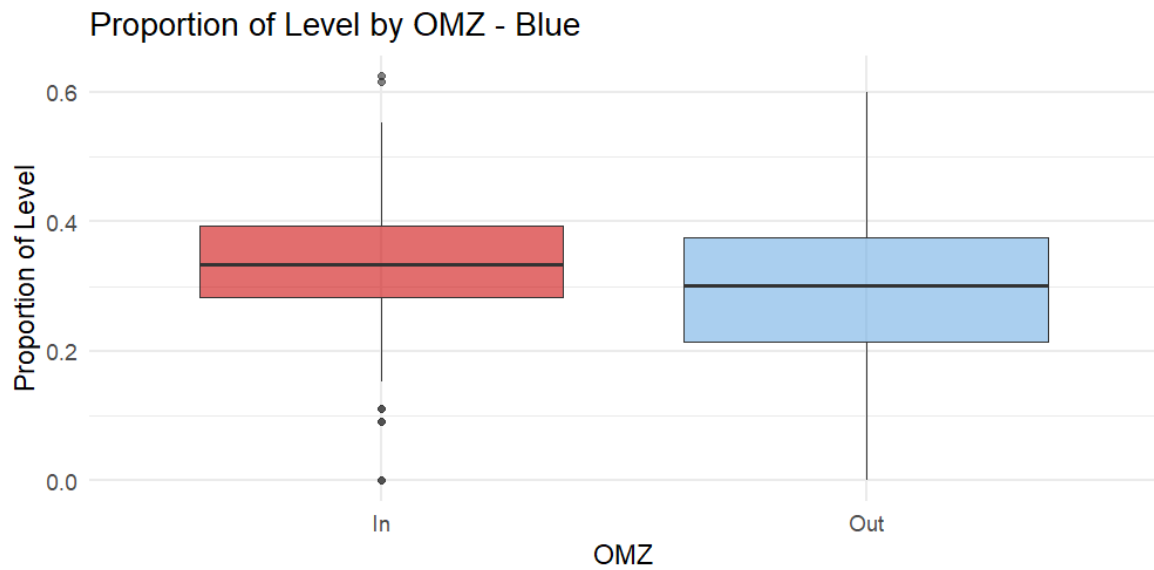


Figure 38: Boxplot illustrating the comparison of the proportion of the level phase in relation to the other phases in blue sharks inside (red) and outside (blue) the OMZ.

As illustrated in Figure 39, it is possible to see that the proportion of level increases slightly as it approaches the OMZ, with the proportion of level outside the OMZ being mostly up to 30%, whereas inside the OMZ, the blue shark analysed tends to spend 30-50% of its time at level.

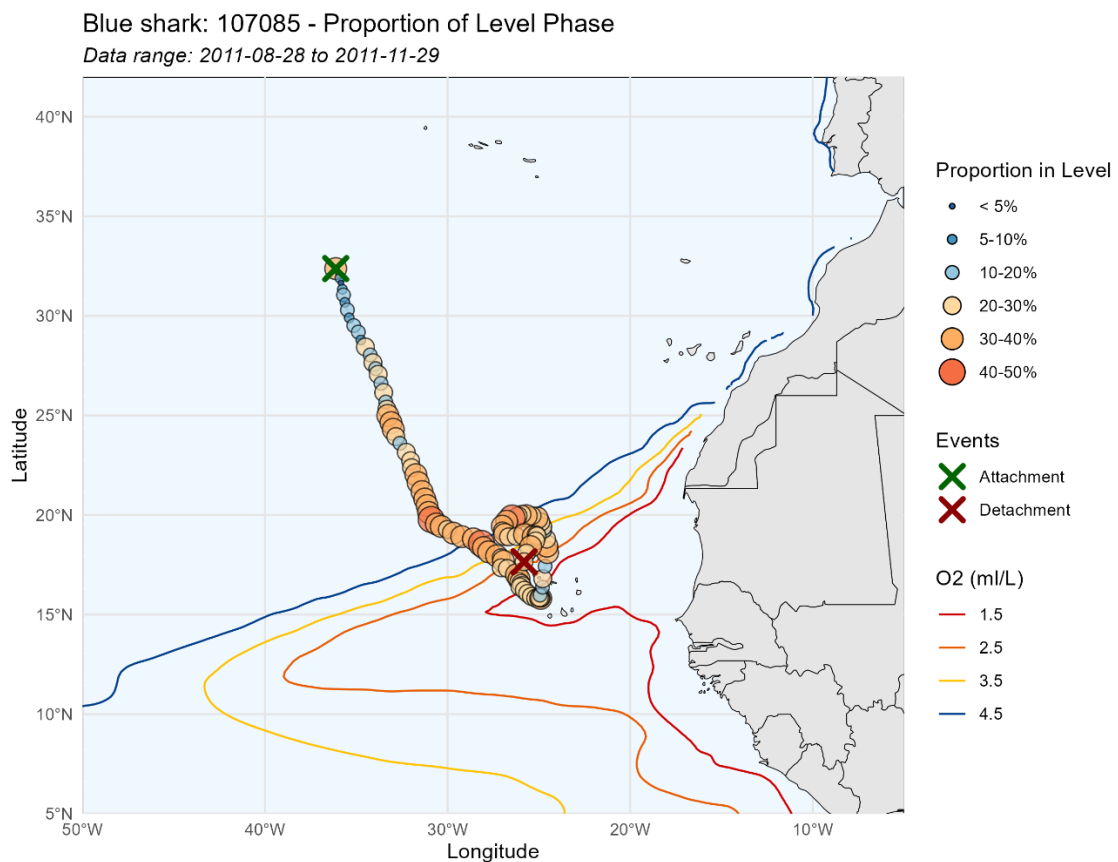


Figure 39: Map illustrating the proportion of level phases along the blue shark's track, with circles increasing as the proportion of level phases increases.

Mako shark:

For mako sharks, a linear mixed-effects model indicated a non-statistical difference between the proportion of level phases between conditions inside and outside the OMZ ($p = 0.402$).

The model intercept, representing the average proportion of the level phase within the OMZ adjusted for individual variability, was estimated at -0.948 (logit scale), corresponding to approximately 28% of dive phases being level phases. This value was statistically significant ($p = 0.004$), indicating that the average proportion of level phases within the OMZ was significantly different from 50% in the probability scale (full output results in Figure S31 at Supplementary figures).

This pattern is illustrated in the boxplot analysis (Figure 40), which demonstrates the substantial individual variability underlying the non-significant mixed-effects result. The “in” condition (red box) shows a median proportion of approximately 0.39, whilst the “out” condition (blue box) exhibits a lower median of around 0.32. However, both conditions display considerable overlap in their interquartile ranges, with the “in” condition extending from roughly 0.30 to 0.48 and the “out” condition ranging from approximately 0.25 to 0.40.

The boxplot reveals the high individual variability that prevents statistical significance in the mixed-effects analysis. The “out” condition particularly demonstrates this variability, with some extreme values extending above 0.6, indicating that certain individuals spend substantially more time in level phases outside the OMZ than the population median suggests. Conversely, the “in” condition shows fewer extreme values but maintains a broader interquartile range.

The inclusion of day as a random effect in the model contributed minimal additional variability, suggesting that day-to-day variation is negligible for this metric in mako sharks. This finding contrasts with other behavioural measures and indicates that level phase allocation in makos remains relatively consistent across temporal scales, with individual differences representing the primary source of variation.

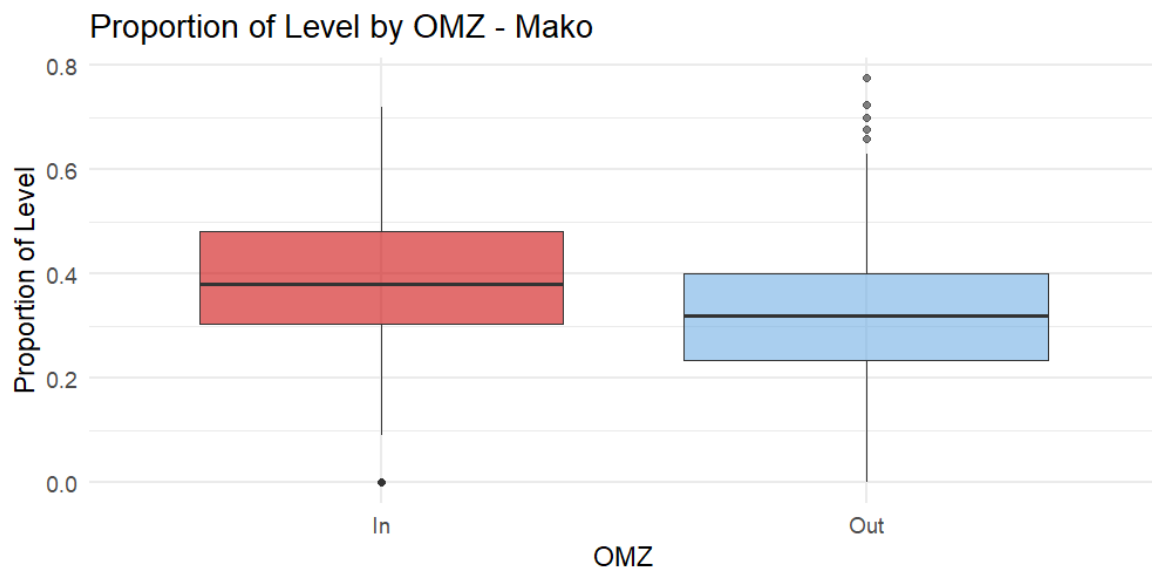


Figure 40: Boxplot illustrating the comparison of the proportion of the level phase in relation to the other phases in mako sharks inside (red) and outside (blue) the OMZ.

When visualising the proportion of level along the mako shark track, with one map for mako inside the OMZ (Figure 41) and another for those outside the OMZ (Figure 42), it can be observed that within the OMZ, the shark spends 40 to more than 50% of its dive in the level phase. Meanwhile, sharks outside the OMZ show a more distributed level proportion, with days spent <5% to more than 50% of their dive in the level phase. This can result in subtle differences, which explains the insignificant result of the LMM. However, it also demonstrates a trend towards more level phases within the OMZ.

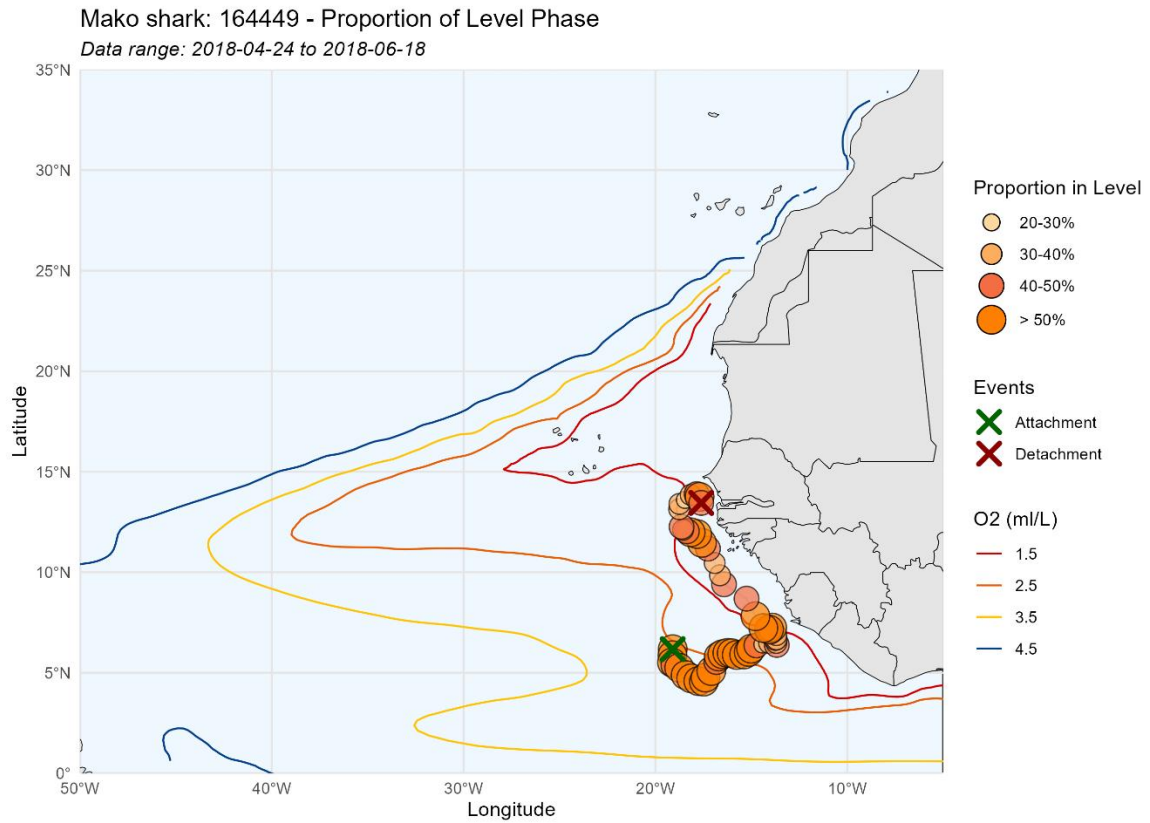


Figure 41: Map illustrating the proportion of the level phase along the mako shark's track inside the OMZ.

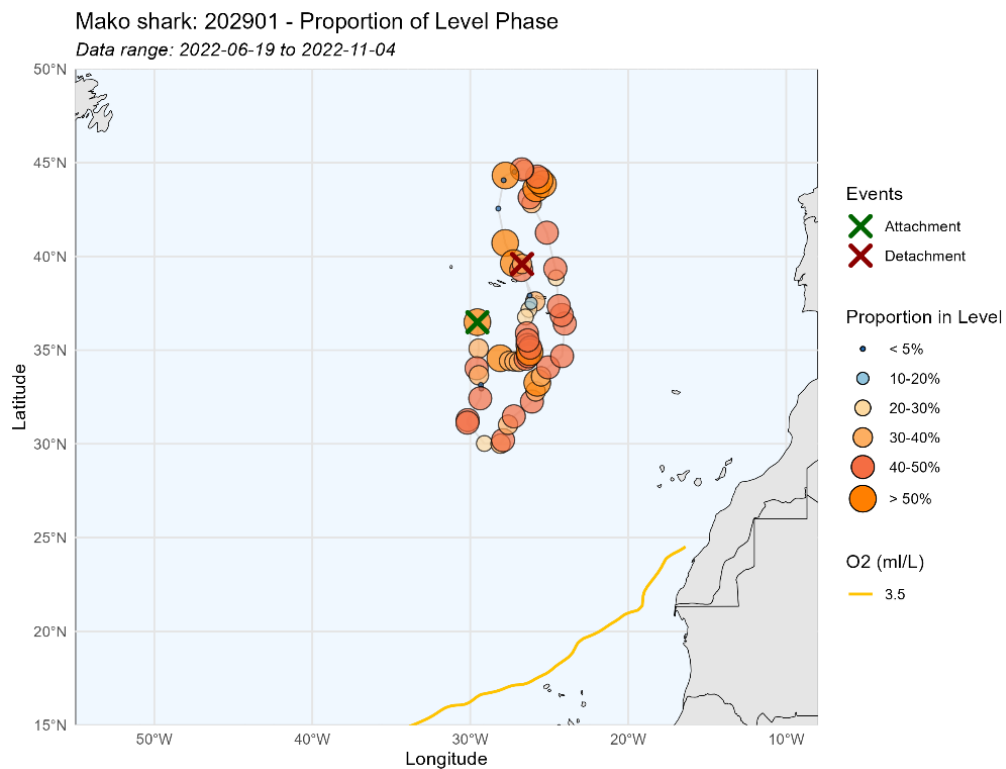


Figure 42: Map illustrating the proportion of the level phase along the mako shark's track outside the OMZ.

4.2.3.3 Depth of level phases

To analyse differences in mean depth between periods inside and outside the OMZ, a mixed linear model with random effects for the individual and, when necessary, for the day was fitted, enabling the separation of intra- and inter-individual variability and variability between days.

Blue shark:

Blue sharks exhibited significant differences in mean level phase depths between areas inside and outside the OMZ.

Linear mixed-effects modelling, controlling for variability between individuals (ID), confirmed that level phases outside the OMZ occurred at significantly greater depths (+ 68 m) than those within the OMZ ($p < 0.001$) (full output results in Figure S32 at Supplementary figures). Day was not included as a random effect, as it contributed negligibly to explaining depth variability and caused singularity issues in the model fitting process.

This pronounced depth difference is evident in the boxplot analysis (Figure 43), which demonstrates vertical separation between the two OMZ conditions with minimal overlap. The “in” condition (red box) shows level phases concentrated in shallow waters, with a median depth of approximately 120 m and an interquartile range extending from roughly 100 to 180 m. In contrast, the “out” condition (blue box) exhibits deeper level phases, with a median depth of approximately 230 m and an interquartile range spanning from about 170 to 300 m.

The boxplot reveals the consistency of this depth partitioning, with the upper quartile of the “in” condition barely overlapping with the lower quartile of the “out” condition. This clear separation reinforces the statistical significance of the observed difference and demonstrates that blue sharks maintain different depth preferences for level phases depending on OMZ conditions. The “out” condition also exhibits greater variability, as demonstrated by extreme values extending to depths greater than 500 metres, while the “in” condition remains more confined, with extreme values not exceeding 450 metres.

The visual representation underscores the biological significance of this behavioural response, showing that blue sharks consistently exploit shallower depths within OMZ waters.

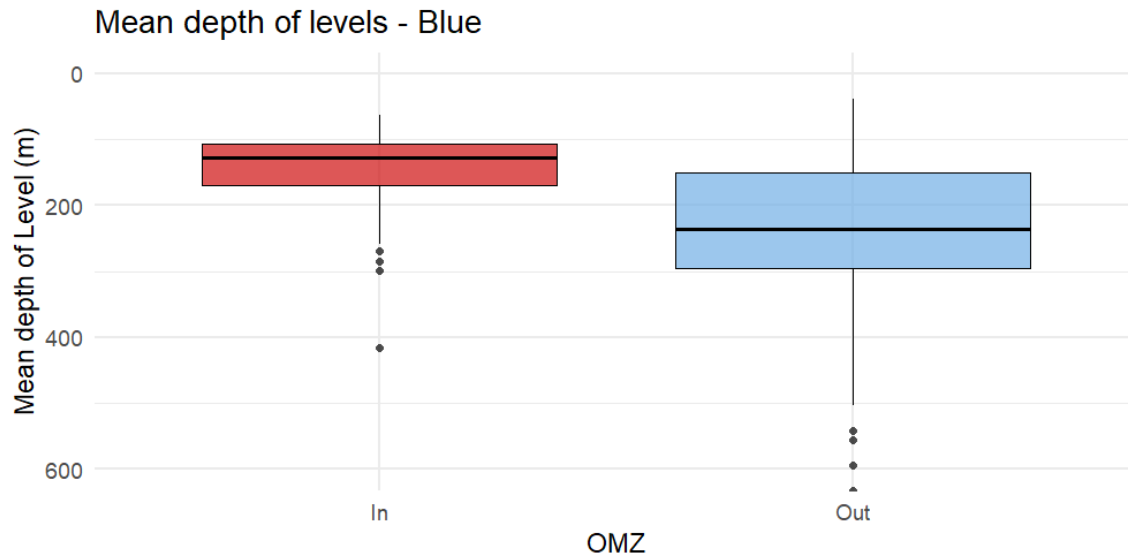


Figure 43: Boxplot illustrating the comparison of the mean depth of levels in blue sharks inside (red) and outside (blue) the OMZ.

These differences in mean depth levels inside and outside the OMZ can also be visualised by looking at the map (Figure 44). The map shows that, when the shark enters the OMZ, its depth levels are mostly restricted to less than 200 metres. Outside the OMZ, however, its depth levels are consistently greater than 250 metres. The visual representation underscores the biological significance of this behavioural response, showing that blue sharks consistently exploit shallower depths within OMZ waters.

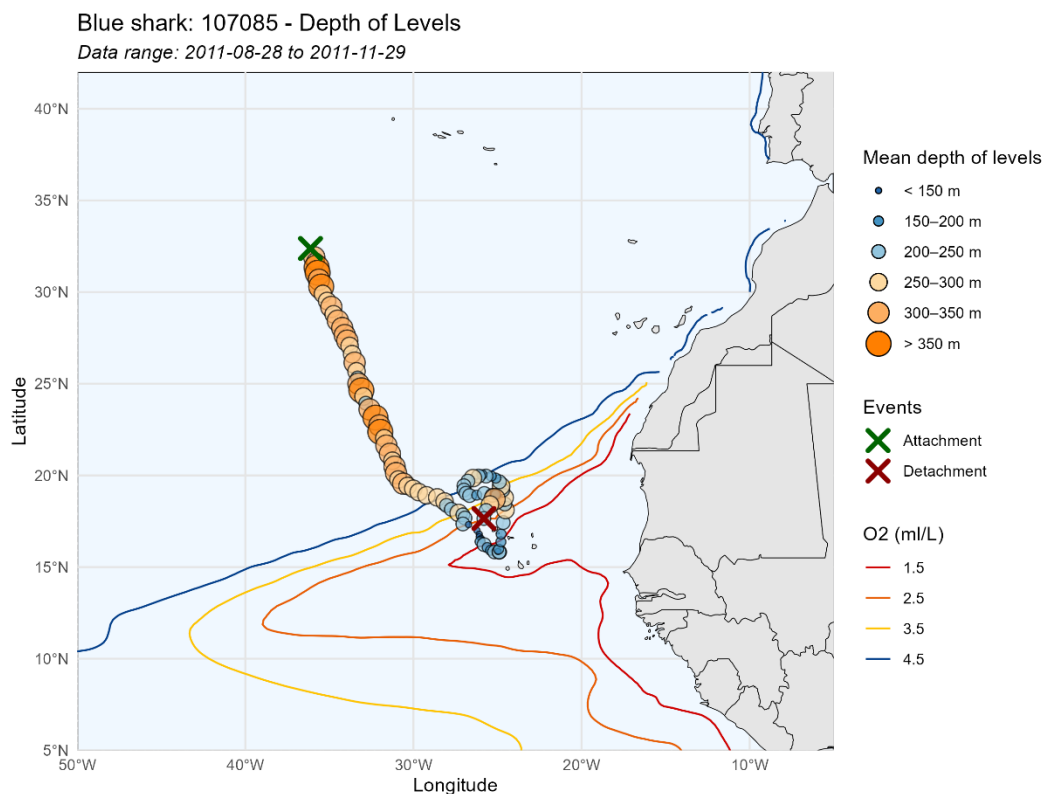


Figure 44: Map illustrating the mean depth of level along the blue shark's track, with circle sizes decreasing as the depth of level is shallower.

Mako shark:

Mean depth of level phases in mako sharks demonstrated significant differences between periods inside and outside the Oxygen Minimum Zone (OMZ).

To account for the hierarchical structure of the data, linear mixed-effects models were fitted, incorporating random effects for individual and day. In the most comprehensive model, which included both random effects, mean depth within the OMZ was estimated at approximately 101 m, whilst outside the OMZ individuals occurred at significantly greater depths, averaging 47 m deeper (coefficient = 47.32 ± 20.95 SE, $p = 0.049$). Variability between days (standard deviation = 37.4 m) and between individuals (30.6 m) contributed to the model structure (full output results in Figure S33 at Supplementary figures).

This depth difference is illustrated in the boxplot analysis (Figure 45), which shows a pattern of deeper level phases outside the OMZ despite considerable overlap between conditions. The “in” condition (red box) exhibits level phases concentrated at shallower depths, with a median of approximately 100 m and an interquartile range extending from roughly 80 to 120 m. The “out” condition (blue box) demonstrates deeper level phases with a median depth of approximately 145 m and an interquartile range spanning from about 90 to 200 m. Notably, the box plot also shows an overlap between the interquartile ranges of both conditions, reflecting the modest effect (difference of 47 m) captured by the mixed-effects model.

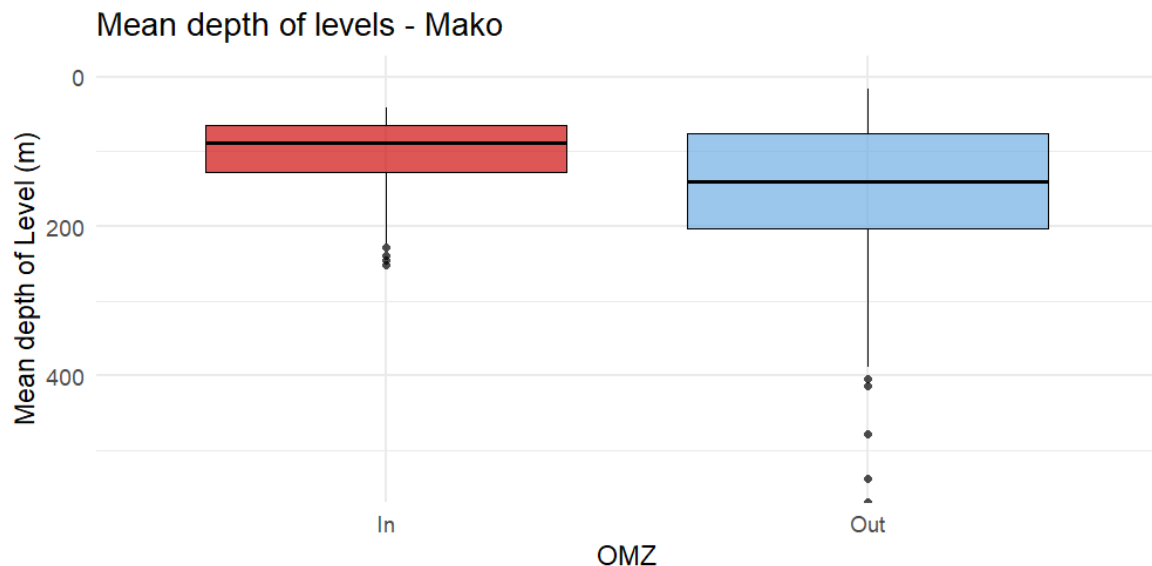


Figure 45: Boxplot illustrating the comparison of the mean depth of levels in mako sharks inside (red) and outside (blue) the OMZ.

When the mean depth of the level along the mako shark's trajectory is observed, with one map for sharks within the OMZ (Figure 46) and another for sharks outside the OMZ (Figure 47), it can be seen that, within the OMZ, the average depth of the shark is mostly less than 150 metres, while outside the OMZ the shark also exhibits depths below 150

metres, but there are occasional dives where the depth is greater than 250 metres. The similar distribution patterns and substantial overlap between oxygen conditions indicate that mako sharks maintain relatively consistent depth preferences for level phases regardless of OMZ conditions, with only adjustments to deeper waters when outside OMZ constraints.

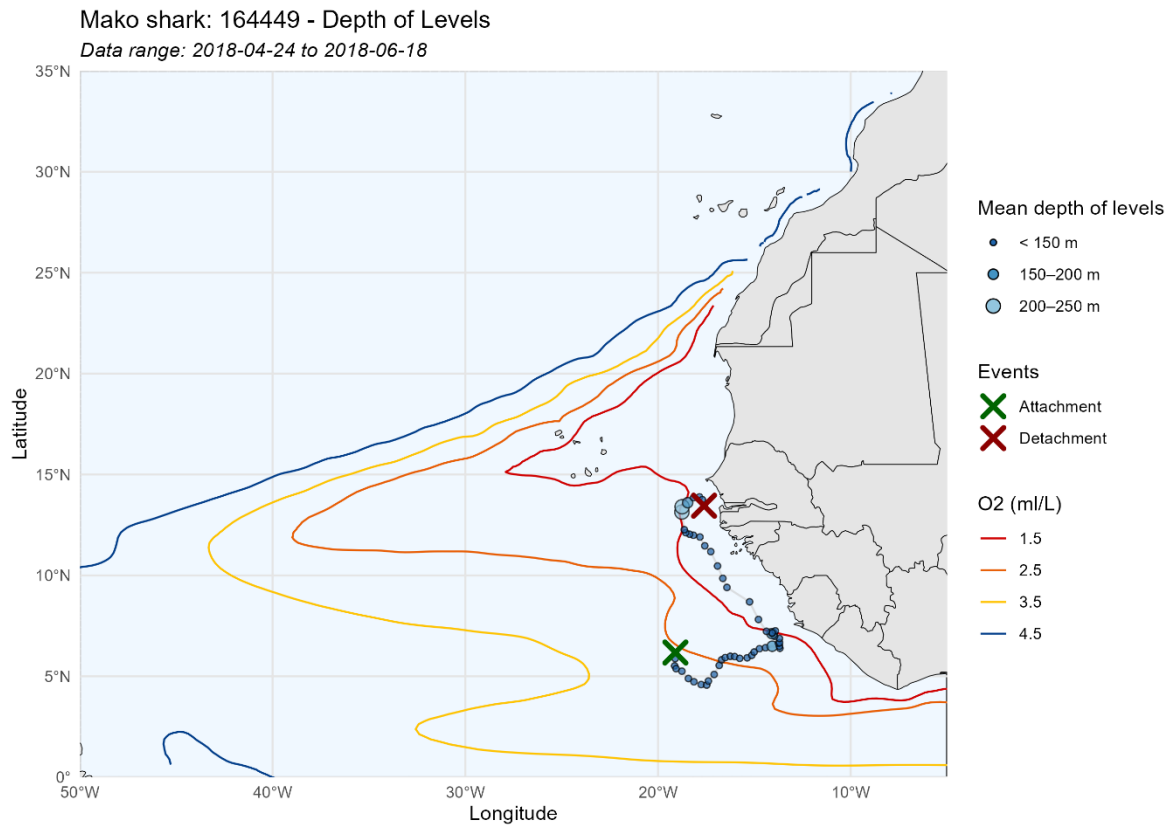


Figure 46: Map illustrating the mean depth of the level phase along the mako shark's track inside the OMZ.

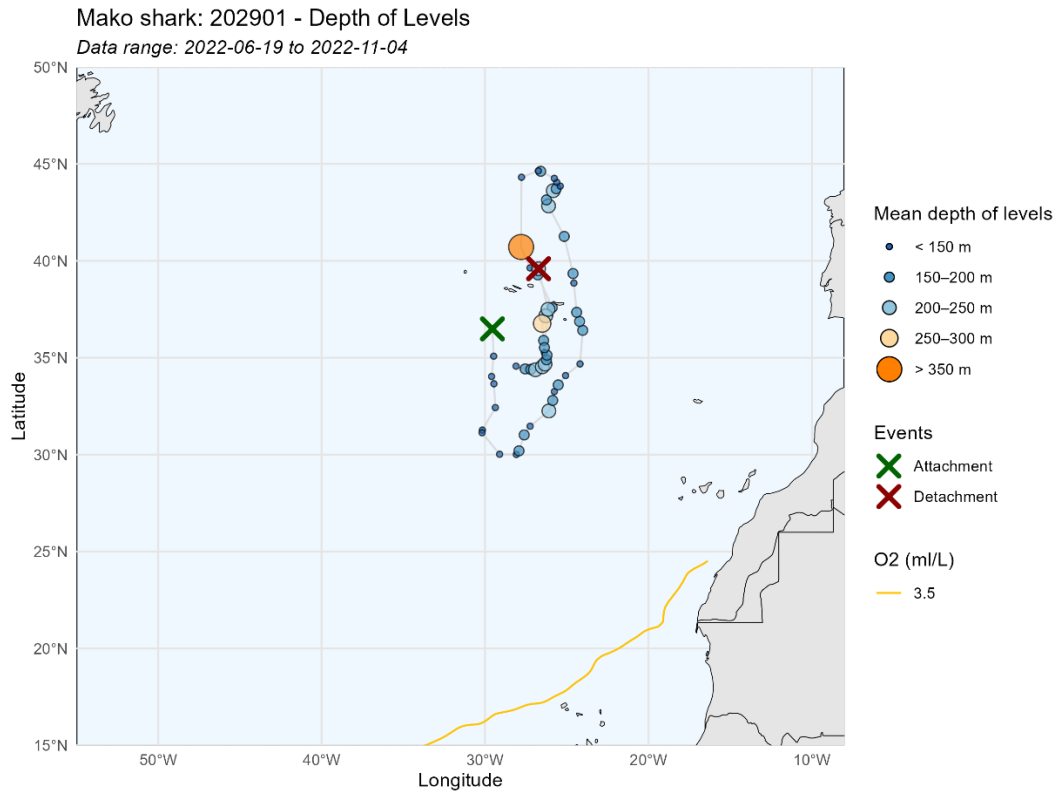


Figure 47: Map illustrating the mean depth of the level phase along the mako shark's track outside the OMZ.

4.2.3.4 Depth difference between consecutive level phases

To assess differences in the depth of consecutive level phases between periods inside and outside the OMZ, a linear mixed-effects models were fitted to account for the hierarchical structure of the data, including random effects for individual and day.

Blue shark:

Analysis of the difference in depth variation between consecutive level phases revealed significant differences between periods inside and outside the OMZ. A linear mixed-effects model was fitted, incorporating random effects for individual ID and day. The results confirmed the observed pattern: within the OMZ, the mean difference in vertical displacement between consecutive levels was low and constrained (3.6 ± 5.9 m), whilst outside the OMZ, displacements were significantly greater, averaging 21.3 ± 4.0 m. The difference between conditions was statistically significant ($p = 0.0018$) (full output results in Figure S34 and S35 at Supplementary figures).

This pronounced difference is illustrated in the comparative boxplot analyses (Figures 48 and 49). The first figure, focusing on the upper layers of the water column, clearly demonstrates the core distributional differences between conditions. Within the OMZ (red box), depth differences between consecutive levels remain consistently small, with a median near 3 m and an interquartile range extending from approximately 0 to 7 m. Outside

the OMZ (blue box), the distribution shifts dramatically, showing a median of approximately 6 m and a much broader interquartile range extending from roughly 2 to 15 m.

The second figure, including all data points, reveals the full extent of vertical variability in consecutive depth of levels phases and emphasises the constraining effect of OMZ conditions. Whilst both conditions show extreme values, the “out” condition exhibits far more extensive vertical excursions, with numerous extreme values extending beyond 100 m and some reaching over 400 m. The “in” condition shows fewer and less extreme values, with most extreme values remaining below 100 m. This pattern suggests that the presence of the OMZ reduces the magnitude of vertical displacement and limits the maximum extent of vertical excursions.

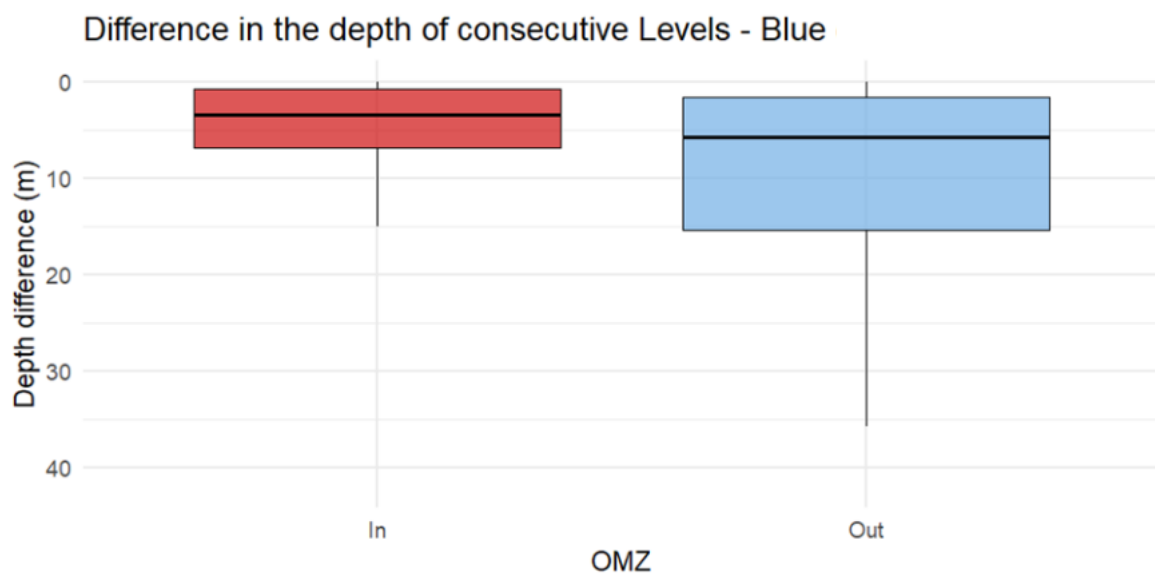


Figure 48: Boxplot illustrating the comparison of the difference in the depth of consecutive levels in blue sharks inside (red) and outside (blue) the OMZ, focusing on the upper layers of the water column.

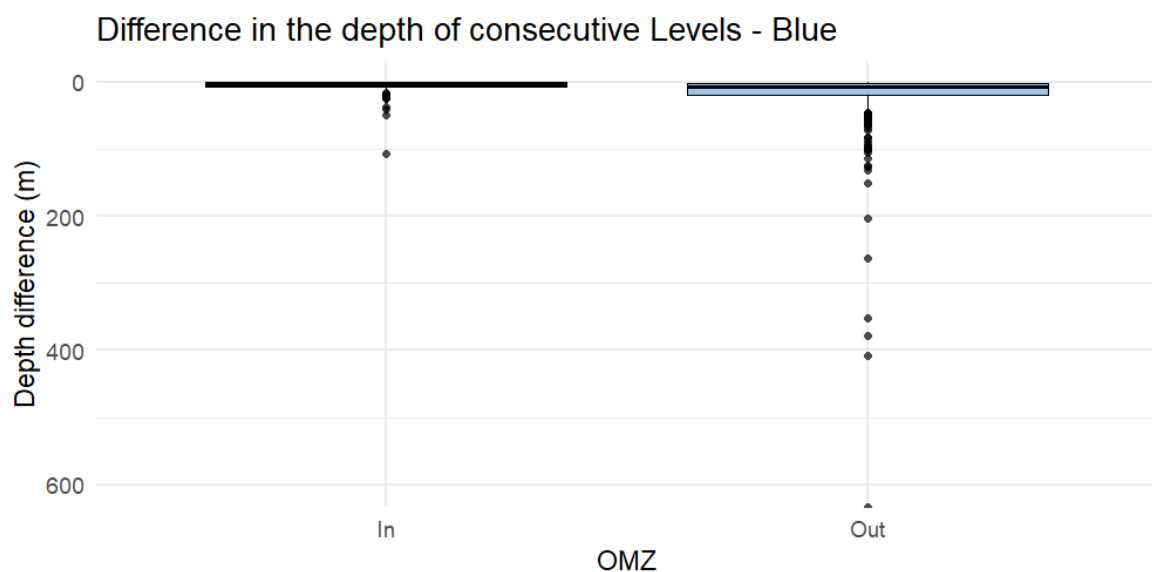


Figure 49: Boxplot illustrating the comparison of the difference in the depth of consecutive levels in blue sharks inside (red) and outside (blue) the OMZ.

These differences in depth between consecutive levels inside and outside the OMZ are also visible on the map (Figure 50). The map illustrates a reduction in the depth difference between consecutive levels as they approach the OMZ, with the difference within the OMZ being less than 10 metres. Conversely, outside the OMZ, despite the presence of low differences between levels (< 10 m), there are discrepancies of more than 30 metres between consecutive levels, a phenomenon not observed within the OMZ.

These findings demonstrate that blue sharks exhibit a significantly greater range of vertical movement outside the OMZ, suggesting a more dynamic use of the water column when they are not subject to hypoxic conditions. Visual evidence strongly supports this interpretation, showing that OMZ conditions restrict the depth of consecutive levels, potentially compressing the vertical habitat of blue sharks and/or their prey.

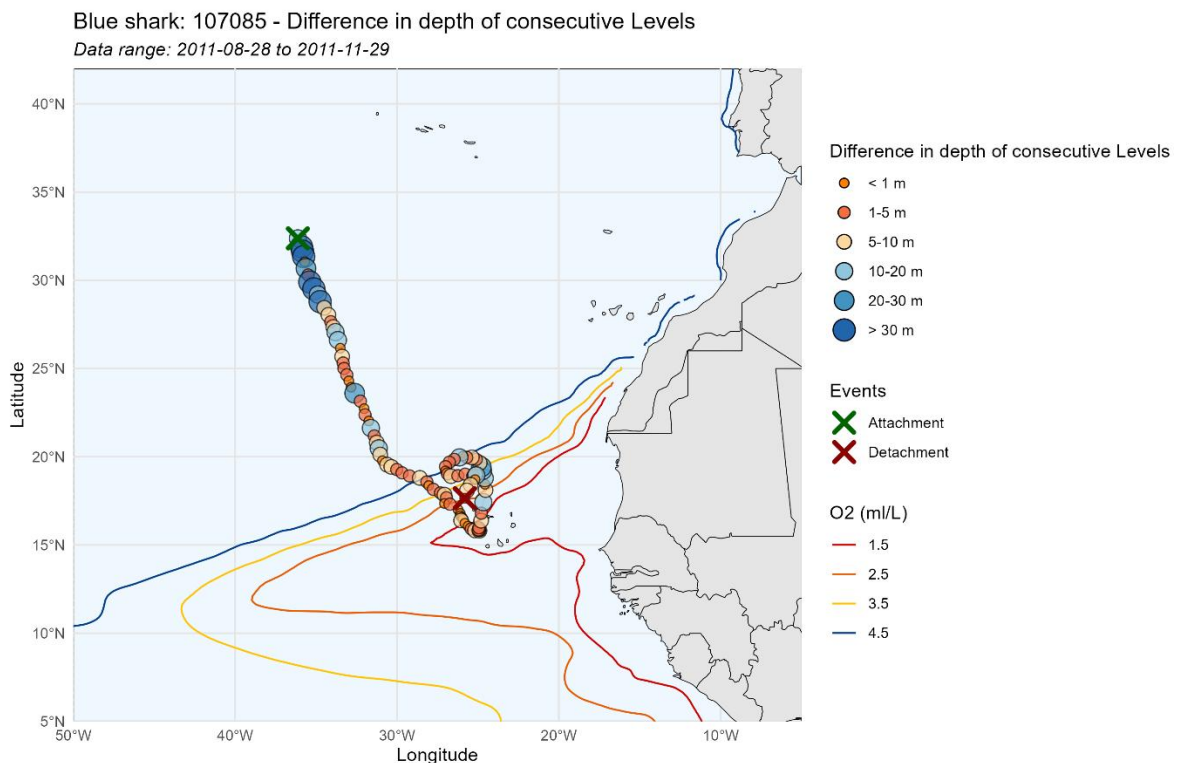


Figure 50: Map illustrating the difference in depth of consecutive levels along the blue shark's track, with circle sizes decreasing as the depth of the level is shallower.

Mako shark:

In mako sharks, analysis of the difference in depth variation between consecutive levels revealed significant differences as a function of the presence of the OMZ. A linear mixed model was fitted with random effects for individual and day. The model confirmed the identified pattern: within the OMZ, the mean magnitude of variations was reduced (8.5 ± 8.3 m), whilst outside the OMZ, vertical displacements were on average more extensive (29.9 ± 4.7 m). The difference between conditions was statistically significant, estimated at approximately 21.4 m ($p = 0.027$) (full output results in Figure S36 and 37 at Supplementary

figures). These results suggest that mako sharks exhibit more restricted vertical movement inside the OMZ but utilise the water column more dynamically and with greater amplitude outside this zone.

The boxplot analysis illustrates this behavioural pattern (Figures 51 and 52). When focusing on the upper layers of the water column (Figure 51), the difference in depth variation between consecutive levels shows mako sharks maintaining relatively small vertical movements within the OMZ (red boxes) with a median of approximately 1 m, compared to substantially larger movements outside the OMZ (blue boxes) with a median of approximately 11 m. The complete dataset, including extreme values (Figure 52), reveals the full extent of this difference, with sharks outside the OMZ occasionally exhibiting extreme value displacements exceeding 200 m, whilst movements within the OMZ remain consistently constrained to smaller depths.

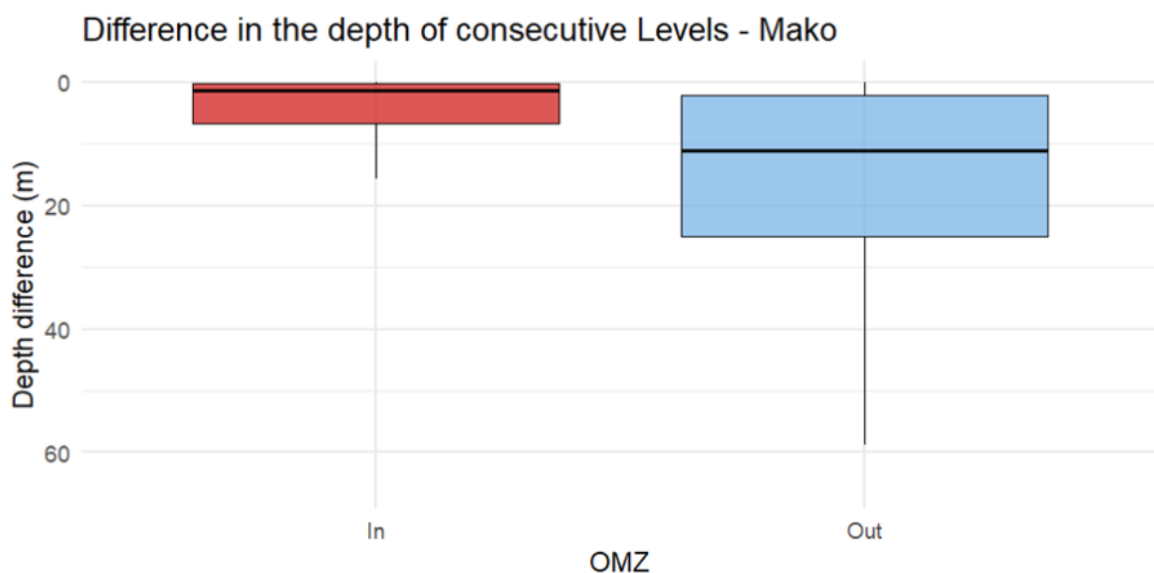


Figure 51: Boxplot illustrating the comparison of the difference in the depth of consecutive levels in mako sharks inside (red) and outside (blue) the OMZ, focusing on the upper layers of the water column.

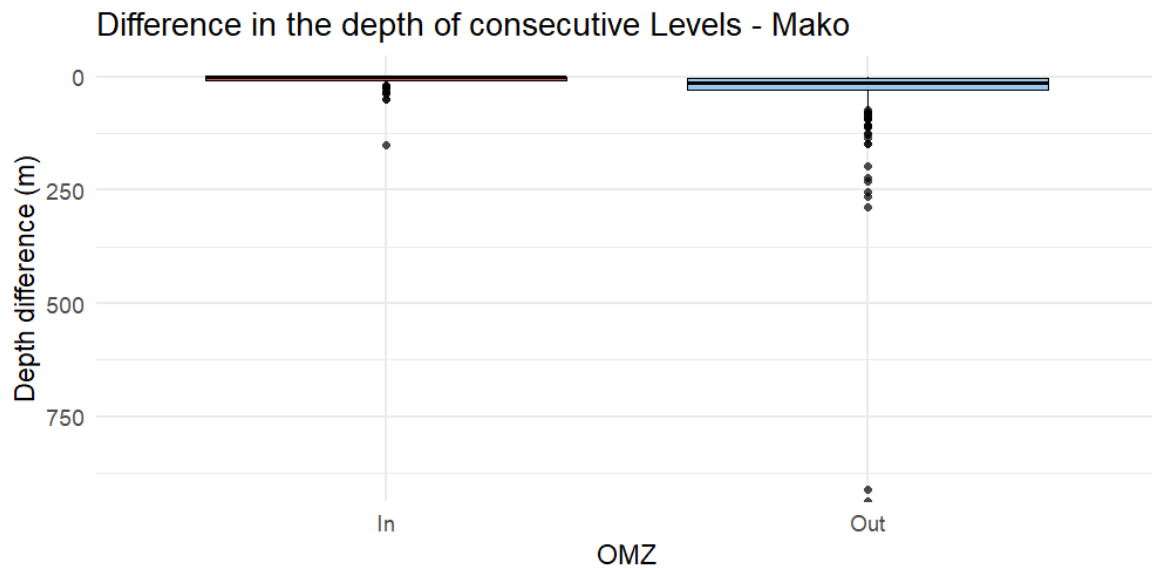


Figure 52: Boxplot illustrating the comparison of the difference in the depth of consecutive levels in mako sharks inside (red) and outside (blue) the OMZ.

When observing the difference in mean depth of consecutive levels along the mako shark's trajectory, with one map for sharks within the OMZ (Figure 53) and another for sharks outside the OMZ (Figure 54). Within the OMZ, the depth difference between shark levels is predominantly less than 1 metre, while outside the OMZ, the shark demonstrates a greater variation in depth between consecutive levels, with some differences exceeding 30 metres. This pattern demonstrates that mako sharks adopt different vertical movement strategies in response to the presence of the OMZ, with shorter depth changes in low-oxygen waters and potentially more dynamic foraging movements in well-oxygenated areas, possibly due to vertical compression of habitat due to the OMZ.

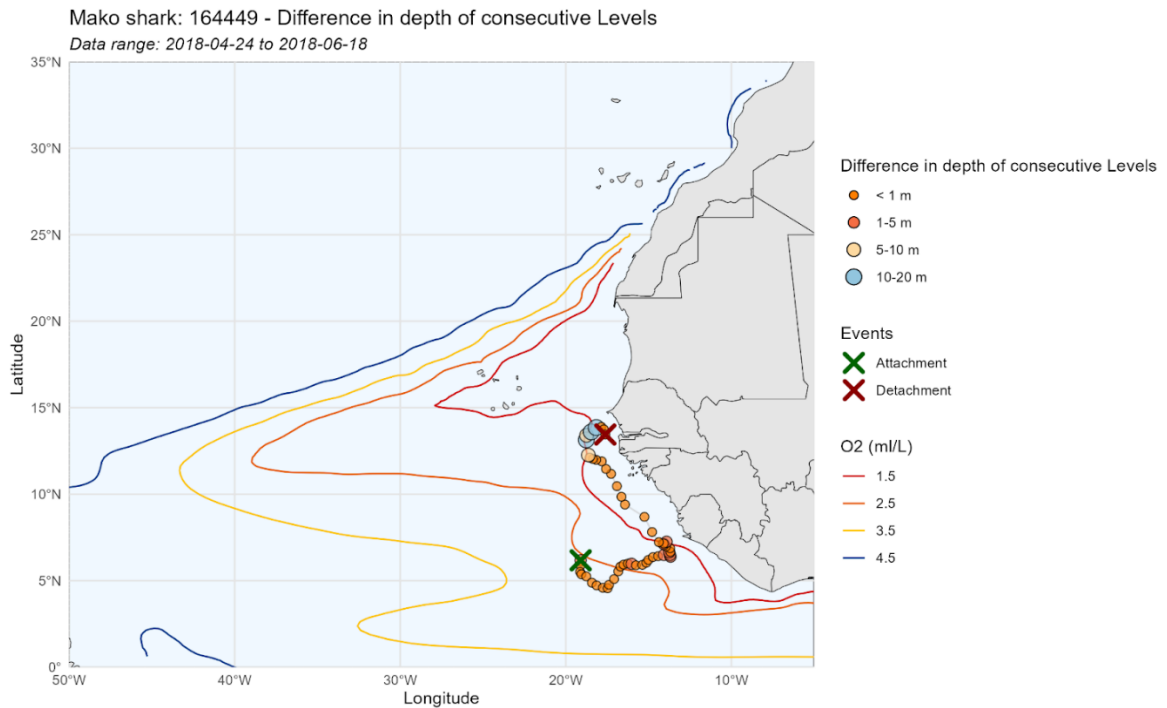


Figure 53: Map illustrating the mean difference in depth of consecutive levels along the mako shark's track inside the OMZ.

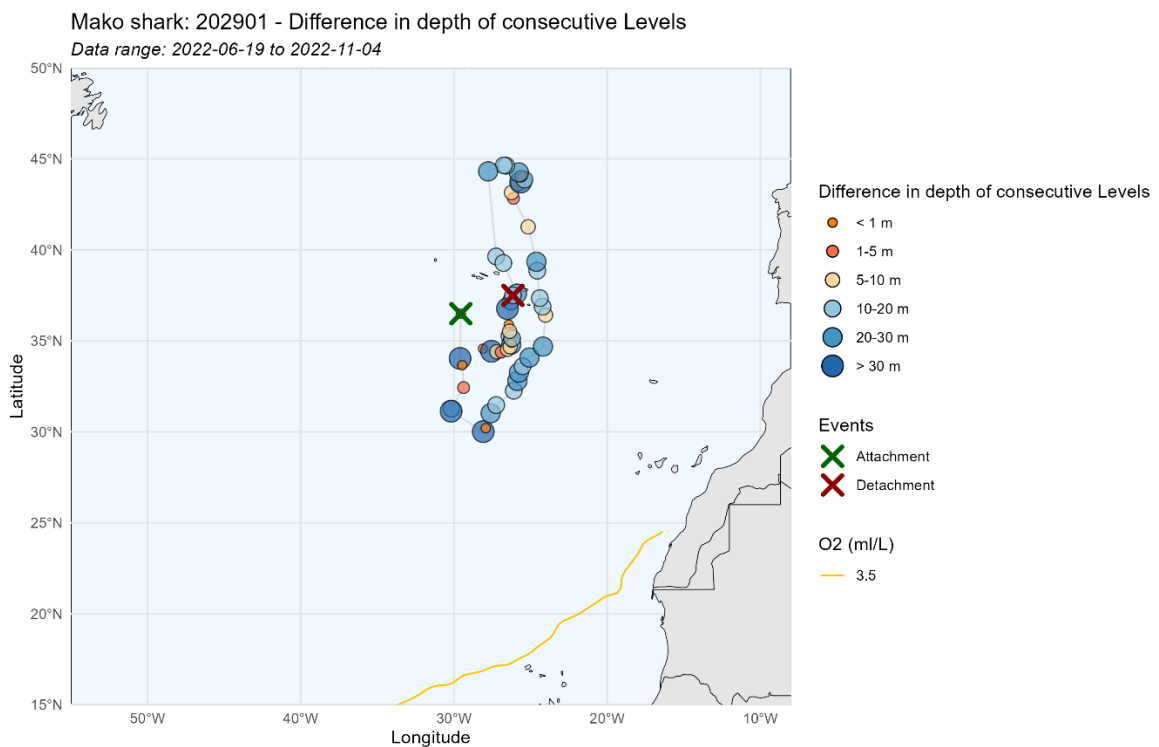


Figure 54: Map illustrating the mean difference in depth of consecutive levels along the mako shark's track outside the OMZ.

5. Discussion

The present study investigated the effects of hypoxia on the vertical movement patterns of blue sharks (*Prionace glauca*) and mako sharks (*Isurus oxyrinchus*), with a particular focus on the structure and characteristics of their diving phases. Through detailed analyses of diving metrics in relation to oxygen conditions, this research offers novel insights into how these pelagic predators respond to environmental constraints in the ocean.

Vertical habitat compression in response to oxygen minimum zones

The analysis of overall vertical movement patterns reveals that OMZs impose fundamental constraints on habitat usage in both species, resulting in pronounced vertical habitat compression. Both blue sharks and mako sharks exhibited substantial reductions in maximum daily depths when encountering hypoxic conditions. Blue sharks showed a decrease of approximately 174 m in their deepest dives inside the OMZ, whilst mako sharks demonstrated a comparable restriction of around 140 metres. These findings align with Le Croizier et al. (2022), who observed a reduction in foraging depth of 200 metres in blue sharks within the world's largest and shallowest OMZ in the northeastern Pacific compared to normoxic waters in the northeastern Atlantic.

A particularly striking observation was the complete absence of mako shark dives at depths below 600 metres in hypoxic conditions. This absolute physiological barrier likely reflects their higher metabolic rates and greater oxygen requirements compared to ectothermic sharks, as they must actively maintain body temperature through regional endothermy and ram-ventilation (Bernal et al., 2012; Sepulveda et al., 2007).

This vertical compression of habitat represents more than a simple behavioural adjustment; it fundamentally alters the ecosystem available to these top predators. The uniformity of these constraints across individuals suggests that oxygen availability acts as a primary environmental limiter, restricting access to deeper layers of prey and potentially isolating predators in vertically stratified food webs (Netburn & Anthony Koslow, 2015).

Species-specific depth usage patterns

Beyond maximum depths, the vertical redistribution of these predators manifests in distinct changes to their depth utilisation patterns. Blue sharks exhibited significant alterations primarily in the upper and intermediate water column (0-150 m), with deeper layers showing reduced influence relative to oxygen availability. In normoxic conditions, blue sharks demonstrated patterns consistent with Stevens et al. (2010), spending an average of 48% of their time in the first 50 metres. However, under hypoxic stress, sharks concentrated their activity at shallower depths, a pattern supported by Vedor et al. (2021),

who demonstrate a limited usage of deep waters (> 600 m) by blue sharks within the OMZ, with depths exceeding 250 metres being utilised more frequently.

Mako sharks demonstrated more selective adjustments, with pronounced changes occurring in specific depth strata (50-100 m and 200-250 m), spending greater proportions of time at these depths within the OMZ. Despite their physiological advantages, Abascal et al. (2011) found that mako sharks spend most of their time in DO concentrations above 3.0 ml/l O₂. However, they are occasionally able to withstand extremely low oxygen concentrations, below 0.5 ml/l in the Southeastern Pacific Ocean region.

Thermal habitat adjustments

The coupling of oxygen and temperature constraints reveals the multidimensional nature of OMZ impacts on predator behaviour. Leeuwis et al. (2021) suggested that thermal tolerance in some fish species may be directly linked to oxygen availability, with exposure to hypoxia limiting physiological responses to warming.

Blue sharks demonstrated significant thermal habitat adjustments within intermediate temperature ranges (11-23°C), showing clear preferences for warmer waters (>15°C) outside OMZs, whilst spending more time in cooler waters (11-17°C) within hypoxic zones. This thermal retreat likely represents an adaptive strategy to reduce metabolic oxygen demand under hypoxic stress, influenced by the pronounced thermocline occurring at 50-150 metres within the OMZ in the Eastern Tropical Atlantic region (Vedor et al., 2021).

Mako sharks exhibited thermal responses within narrower temperature ranges (15-17°C and 21-23°C), with their broader thermal tolerance (9-27°C) reflecting the advantages of physiological endothermy. Tokunaga et al. (2025) classified mako sharks as "controllability maximisers", demonstrating their ability to alter heat exchange rates by more than tenfold, thereby increasing foraging efficiency during surface-diving cycles in thermally stratified waters. However, even these metabolically sophisticated predators showed selective avoidance of specific hypoxic temperature combinations, indicating that OMZs create complex habitat constraints where thermally optimal zones may become physiologically inaccessible.

Contrasting diving strategies and behavioural adaptations

Analysis of daily diving patterns revealed fundamentally contrasting adaptive strategies between the two species. Blue sharks exhibited significantly higher dive frequencies in OMZ waters. This increased diving activity under hypoxic conditions may reflect intensified foraging strategies, as the presence of hypoxic water may enhance foraging opportunities, particularly near OMZ boundaries, where prey may aggregate (Craig et al., 2010; Gilly et al., 2013; W. C. Long & Seitz, 2008).

Conversely, mako sharks exhibited significantly reduced dive frequencies in OMZ waters compared to normoxic conditions. This reduction in vertical activity aligns with their high metabolic demands as endothermic predators, suggesting that physiological constraints impose stronger limitations under hypoxic stress (Sepulveda et al., 2007; Waller et al., 2023). The decreased diving frequency likely represents an energy conservation strategy, where reduced activity helps maintain physiological homeostasis in oxygen-limited environments.

Dive characteristics and depth selection behaviour

Mean dive depth analysis revealed clear depth selection behaviour in response to oxygen availability, though with distinct species-specific characteristics. Blue sharks exhibited significantly shallower distributions in OMZ waters (centred around 90 m) compared to their broader and deeper vertical distribution outside the OMZ (extending to 300-350 m), demonstrating vertical habitat compression (Logan et al., 2023; Stramma et al., 2012).

Mako sharks showed similar patterns but with notable differences in depth range and amplitude. Within OMZ waters, they demonstrated shallower diving with a median depth of approximately 80 m and a narrow interquartile range, consistent with active avoidance of hypoxic conditions, due to their elevated oxygen requirements (Bernal et al., 2012; Sepulveda et al., 2007). Outside OMZs, makos expanded their vertical range considerably (median ~120 m, frequent excursions to 300-400 m), reflecting a higher propensity for deep-diving behaviour potentially linked to elevated metabolic demands and hunting strategies.

Temporal dynamics

Dive duration patterns revealed different time allocation strategies under oxygen-limited conditions. Blue sharks maintained relatively stable dive durations regardless of oxygen conditions when individual variation was controlled, suggesting that factors other than oxygen availability, such as size, diurnal cycles, or energy constraints, primarily shape dive duration in this species (Coffey et al., 2020; Druon et al., 2022; Vedor et al., 2021).

Mako sharks showed evidence of longer dive durations within OMZ waters, though this effect was not consistently robust across analytical approaches. The trend towards extended dives in hypoxic environments may reflect behavioural strategies designed to minimise energetic costs or optimise foraging efficiency. The presence of extreme values (dives exceeding 20 hours in OMZ conditions) highlights remarkable individual variability, suggesting markedly different strategies when confronted with hypoxic stress.

Dive phase analysis

Detailed analysis of dive phase characteristics provides crucial insight into how oxygen constraints influence the temporal and spatial dynamics of diving behaviour. Blue sharks exhibited robust and uniform effects, consistently displaying shallower mean depths during all diving phases in OMZ waters. The persistence of this ~55 m reduction in mean depth, even after accounting for repeated measures and daily variability, demonstrates that oxygen availability acts as a primary determinant of vertical habitat use across all behavioural contexts (Prince et al., 2010; Prince & Goodyear, 2006; Stramma et al., 2012; Vedor, Queiroz, et al., 2021).

Mako sharks exhibited more nuanced, phase-dependent responses to OMZ conditions. Although differences in mean depth were significant during all phases, the effect diminished substantially during descent phases, when depth distributions between OMZ conditions converged. This pattern indicates greater flexibility in vertical habitat use, with behaviour adjusted according to dive cycle stage. The reduced OMZ effect during descent phases may reflect recovery or transition periods where physiological demands temporarily override oxygen constraints.

Step phase duration analysis revealed contrasting species responses, with blue sharks showing uniform temporal compression across all phases within OMZs (nearly 100 seconds reduction per phase), whilst mako sharks maintained consistent phase durations regardless of oxygen availability. This divergence suggests that blue sharks adjust both spatial and temporal dimensions of their diving behaviour under hypoxic stress, potentially limiting exposure time to minimise physiological costs.

Vertical speed analysis during ascent and descent phases revealed clear evidence of locomotory constraints under hypoxic conditions. Blue sharks demonstrated pronounced reductions in swimming speeds within OMZs (approximately 0.038 m/s reduction across both phases), with constrained speed distributions and reduced variability compared to normoxic conditions. Mako sharks showed more modest speed reductions, with weaker statistical effects that may reflect their elevated aerobic capacity and regional endothermy conferring greater resilience to hypoxic conditions. These reductions in the speed phases may reflect a strategy to conserve energy in hypoxic conditions in both species.

Level phase dynamics

Regarding level phases, both species showed slight tendencies toward increased time allocation and higher proportions of level phases within OMZ waters. This approach aligns with previous studies that have used various terminologies and strategies to analyse “Levels” as a foraging activity. Queiroz et al. (2017) employed “U-shaped dives” to classify exploratory dives with prolonged bottom phases at relatively constant depths, whilst other

studies used bottom phases as proxies for foraging behaviour in marine predators (Heerah et al., 2014; Schreer et al., 2001).

Level phase depth analysis revealed pronounced vertical habitat compression, particularly in blue sharks, which consistently occupied shallower depths during level phases within OMZs. Mako sharks demonstrated more modest depth adjustments during level phases, with substantial overlap between OMZ conditions and greater individual variability, though differences of approximately 47 m between conditions indicate a clear trend toward shallower foraging within the OMZ. This spatial restriction is consistent with the idea of vertical compression of habitat and demonstrates changes in the foraging patterns of sharks. This finding suggests vertical compression of food webs (Koslow et al., 2011), which consequently results in a reduction of foraging depth within the OMZ (Le Croizier et al., 2022).

The analysis of depth differences between consecutive level phases revealed markedly constrained vertical exploration within OMZs for both species, with blue sharks showing more pronounced restrictions. This compression of vertical movement amplitude suggests that OMZs restrict not only absolute depth range availability but also dynamic use of vertical space. The OMZ alters predator-prey dynamics by compressing prey species into upper layers, increasing foraging opportunities for pelagic predators within the OMZ (Gilly et al., 2013; W. C. Long & Seitz, 2008).

Furthermore, the restricted difference in depth between consecutive levels inside the OMZ is consistent with the analysis of mean level depth within the OMZ. The low variation in depths inside the OMZ compared to outside it shows that the depth reached is consistently restricted in both species.

Physiological basis for species-specific responses

The divergent responses between blue sharks and mako sharks reflect fundamental differences in their physiological architecture and environmental tolerances. Studies have demonstrated that blue sharks reduce dive depths within OMZs when dissolved oxygen concentrations reach 3.5 ml/l O₂, whilst mako sharks reduce dive depths at concentrations of 3.0 ml/l O₂ (Waller et al., 2024). Furthermore, mako sharks exhibit superior oxygen transport capacity in their blood, evidenced by high haematocrit and haemoglobin concentrations compared to ectothermic sharks, supporting their elevated metabolic capacities (Morrison et al., 2023). This affinity of haemoglobin for oxygen in mako sharks remains stable with increasing temperature, in contrast to the blue shark, whose affinity decreases with increasing temperature (Bernal et al., 2018). This suite of physiological adaptations may explain why mako sharks demonstrate less pronounced responses to

OMZs compared to blue sharks, which showed greater differences across most analysed metrics.

Ecological implications and management considerations

These behavioural modifications carry profound ecological implications that extend beyond individual predators to ecosystem-level processes. Habitat compression concentrates predators in reduced vertical space, potentially intensifying interspecific competition whilst simultaneously increasing vulnerability to surface fisheries (Prince & Goodyear, 2006). Vedor et al. (2021) confirmed that greater blue shark catches occur in conditions of lower DO in the water, demonstrating that the presence of OMZ increases the risk of shark catches in surface fishing such as longline fishing.

The substantial inter-individual variation observed across all behavioural metrics highlights the importance of considering individual-level heterogeneity to predict the real impacts of environmental changes on pelagic predators. Studies showed high variability among individuals in vertical movements, with influences of body size, seasonal factors, and sex (Druon et al., 2022; Nasby-Lucas et al., 2019).

Study limitations and future path

It is important to acknowledge that defining the Eastern Tropical Atlantic OMZ as regions with concentrations of 3.5 ml/l O₂, using modelled data at 100 m depth, assumes that sharks present in these areas experienced hypoxic stress whilst above the OMZ. This approach constitutes a study limitation, as precise determination of dissolved oxygen levels to which each individual was exposed was not possible. Furthermore, factors such as size, sex, age, and individual physiological requirements may influence how oxygen deficiency affects each shark. Future studies could overcome this limitation by employing tags equipped with dissolved oxygen sensors (Coffey & Holland, 2015; da Costa et al., 2024), thereby enabling a direct correlation between environmental conditions and the biological needs of each shark.

Climate change implications and conservation perspectives

As climate change drives global expansion and intensification of OMZs (Keeling et al., 2010; Stramma et al., 2008a; Zhou et al., 2022), the behavioural constraints documented in this study become increasingly important for understanding deoxygenation effects on these crucial pelagic predator species. The comprehensive analysis reveals that OMZs impose multifaceted constraints on pelagic shark behaviour, operating across spatial, temporal, and physiological dimensions. The consistent patterns of vertical habitat compression, combined with species-specific adjustments in diving frequency, temporal

allocation, and locomotory performance, demonstrate that oxygen availability serves as a fundamental environmental filter structuring predator behaviour in the open ocean.

Understanding these species-specific responses and underlying individual variation is crucial for developing effective management strategies for marine ecosystems facing unprecedented environmental change. Blue sharks, as ectothermic predators, exhibit more pronounced behavioural adjustments across multiple dimensions, potentially reflecting greater physiological constraints under hypoxic stress. Mako sharks, supported by regional endothermy and high aerobic capacity, demonstrate greater resilience to oxygen limitations but show restricted water column usage, possibly due to their elevated oxygen requirements.

6. Conclusion

This study provides comprehensive evidence that ocean deoxygenation, manifested through oxygen minimum zones (OMZs), significantly constrains the vertical movement patterns and diving behaviour of two ecologically important pelagic shark species: *Prionace glauca* (blue shark) and *Isurus oxyrinchus* (mako shark). Through detailed analysis of satellite archival tag data, spanning multiple years and geographic regions, this research addresses fundamental questions about how hypoxic conditions alter predator behaviour and habitat use in the open ocean.

6.1 Key findings and hypothesis validation

The primary hypothesis that low oxygen conditions affect the behaviour of these large pelagic predators has been conclusively supported. Both species demonstrated significant alterations in their vertical habitat use when encountering OMZ conditions, with consistent patterns of vertical habitat compression observed across multiple behavioural metrics.

Regarding the first research question: "Does hypoxia alter the vertical behaviour of blue and mako sharks?" - the evidence is unequivocal. Both species exhibited marked reductions in maximum daily depths within OMZs, with blue sharks showing approximately 174 m shallower dives and mako sharks demonstrating 140 m restrictions compared to normoxic conditions. The complete absence of dives below 600 m for mako sharks in hypoxic conditions represents a particularly striking finding, suggesting absolute physiological barriers imposed by oxygen limitation.

For the second research question: "Can the frequency, duration, and depth of dive phases be affected by hypoxia?" - the results reveal species-specific responses that reflect underlying physiological differences. Blue sharks increased their diving frequency inside OMZs (when individual variation was controlled), potentially indicating intensified foraging

behaviour near oxygen boundaries. Conversely, mako sharks reduced diving frequency in hypoxic waters, suggesting energy conservation strategies aligned with their higher metabolic demands as endothermic predators.

The detailed dive phase analysis revealed that OMZs impose multifaceted constraints operating across spatial, temporal, and physiological dimensions. Blue sharks consistently exhibited shallower depths across all dive phases (~55 m reduction) and reduced swimming speeds (~0.038 m/s decrease) within OMZs. The uniformity of these effects demonstrates that oxygen availability acts as a fundamental environmental filter structuring predator behaviour.

6.2 Species-specific responses and physiological implications

The contrasting responses between blue sharks and mako sharks highlight the critical importance of physiological architecture in determining species vulnerability to environmental change. Blue sharks, as ectothermic predators, exhibited more pronounced and consistent behavioural adjustments across multiple dimensions, reflecting greater physiological constraints under hypoxic stress. These included compressed temporal allocation (98-second reduction in phase durations), restricted thermal habitat use, and consistent vertical habitat compression.

Mako sharks demonstrated more nuanced, phase-dependent responses that likely reflect their enhanced physiological capabilities. Their regional endothermy and superior oxygen transport capacity (higher haematocrit and haemoglobin concentrations) appear to confer greater resilience to hypoxic conditions. However, their higher metabolic demands and oxygen requirements still resulted in notable behavioural modifications, including reduced diving frequency and depth restrictions.

The coupling of oxygen and temperature constraints revealed the multidimensional nature of OMZ impacts. Blue sharks demonstrated clear thermal habitat adjustments, preferring warmer waters outside OMZs while retreating to cooler temperatures within hypoxic zones. Mako sharks exhibited thermal responses with broader temperature ranges, reflecting their higher thermal tolerance enabled by endothermic capabilities.

6.3 Ecological and Conservation Implications

These behavioural modifications carry profound ecological implications that extend beyond individual predators to ecosystem-level processes. The vertical compression of habitat concentrates predators in reduced vertical space, potentially intensifying interspecific competition while simultaneously increasing vulnerability to surface fisheries. This finding has direct conservation relevance, as it suggests that expanding OMZs may increase bycatch rates and fishing mortality for these already vulnerable species.

The substantial inter-individual variation observed across all behavioural metrics emphasises that population-level responses to environmental change cannot be predicted without considering individual-level heterogeneity. This variability may serve as a critical mechanism enabling some individuals to cope with spatially and temporally variable oxygen conditions, highlighting the importance of maintaining genetic diversity within populations.

The demonstrated habitat compression and altered movement patterns suggest that OMZ expansion could fundamentally restructure pelagic food webs. Compressed vertical habitats may lead to altered predator-prey dynamics.

6.4 Limitations and Future Directions

This study's approach of defining OMZ boundaries using modelled oxygen concentrations at 100 m depth represents a limitation, as it does not provide direct measures of oxygen exposure for individual sharks. Future research should prioritise the deployment of tags equipped with dissolved oxygen sensors to enable direct correlation between environmental conditions and behavioural responses.

Additionally, factors such as body size, sex, age, and individual physiological condition likely influence how oxygen deficiency affects each shark, warranting investigation in future studies. The high degree of inter-individual variation observed suggests that understanding population-level responses will require larger sample sizes and longer-term monitoring programs. Future research directions should include: Direct measurement of oxygen exposure using DO-equipped tags(da Costa et al., 2024); investigation of sex- and size-specific responses to hypoxia and long-term monitoring to assess adaptation potential.

6.5 Global Change Context and Management Implications

As climate change drives the continued expansion and intensification of OMZs globally, the behavioural constraints documented in this study become increasingly relevant for predicting ecosystem responses to environmental change.

These findings have direct implications for fisheries management and marine conservation planning. Understanding how OMZ expansion alters predator distribution and vulnerability is crucial for developing adaptive management strategies that can effectively protect these species under changing ocean conditions.

The research contributes directly to UN Sustainable Development Goals 13 (Climate Action) and 14 (Life Below Water) by providing scientific evidence of climate change impacts on marine ecosystems and informing conservation strategies for ocean health.

6.6 Final Considerations

This study demonstrates that ocean deoxygenation represents a significant and underappreciated threat to pelagic shark populations. The consistent patterns of

behavioural constraint across species, combined with evidence of physiological limitations, suggest that expanding OMZs could fundamentally alter the ecology of open ocean ecosystems.

The integration of satellite telemetry data with oceanographic modelling has proven effective for detecting environmental influences on predator behaviour at ocean basin scales. As OMZ expansion continues under climate change scenarios, this approach provides a valuable framework for monitoring ecosystem responses and informing adaptive management strategies.

Ultimately, this research underscores the urgent need for comprehensive climate action to mitigate ocean deoxygenation, while simultaneously highlighting the importance of species-specific management approaches that account for differential vulnerabilities to environmental change. The behavioural plasticity demonstrated by both species provides some hope for adaptation, but the magnitude of projected environmental changes suggests that conservation success will depend on both effective emission reductions and adaptive management strategies informed by a detailed understanding of species-environment interactions.

The findings of this study contribute essential knowledge for predicting and managing the impacts of global ocean change on pelagic predator communities, providing a foundation for evidence-based conservation in an era of unprecedented environmental transformation.

7. References

- Abascal, F. J., Quintans, M., Ramos-Cartelle, A., & Mejuto, J. (2011). Movements and environmental preferences of the shortfin mako, *Isurus oxyrinchus*, in the southeastern Pacific Ocean. *Marine Biology*, 158(5), 1175–1184. <https://doi.org/10.1007/s00227-011-1639-1>
- Bernal, D., Carlson, J. K., Goldman, K. J., & Lowe, G. (2012). Energetics, Metabolism, and Endothermy in Sharks and Rays. In *Biology of Sharks and Their Relatives: Second Edition* (pp. 57–95). CRC Press. <https://doi.org/10.1201/b11867-10>
- Bernal, D., Reid, J. P., Roessig, J. M., Matsumoto, S., Sepulveda, C. A., Cech, J. J., & Graham, J. B. (2018). Temperature effects on the blood oxygen affinity in sharks. *Fish Physiology and Biochemistry*, 44(3), 949–967. <https://doi.org/10.1007/s10695-018-0484-2>
- Bertrand, A., Ballón, M., & Chaigneau, A. (2010). Acoustic observation of living organisms reveals the upper limit of the oxygen minimum zone. *PLoS ONE*, 5(4). <https://doi.org/10.1371/journal.pone.0010330>
- Bornatowski, H., Angelini, R., Coll, M., Barreto, R. R. P., & Amorim, A. F. (2018). Ecological role and historical trends of large pelagic predators in a subtropical marine ecosystem of the South Atlantic. *Reviews in Fish Biology and Fisheries*, 28(1), 241–259. <https://doi.org/10.1007/s11160-017-9492-z>
- Brandt, P., Hormann, V., Körtzinger, A., Visbeck, M., Krahmann, G., Stramma, L., Lumpkin, R., & Schmid, C. (2010). Changes in the ventilation of the oxygen minimum zone of the tropical North Atlantic. *Journal of Physical Oceanography*, 40(8), 1784–1801. <https://doi.org/10.1175/2010JPO4301.1>
- Braun, C. D., Kaplan, M. B., Horodysky, A. Z., & Llopiz, J. K. (2015). Satellite telemetry reveals physical processes driving billfish behavior. In *Animal Biotelemetry* (Vol. 3, Issue 1). BioMed Central Ltd. <https://doi.org/10.1186/s40317-014-0020-9>
- Breitbart, D., Levin, L. A., Oschlies, A., Grégoire, M., Chavez, F. P., Conley, D. J., Garçon, V., Gilbert, D., Gutiérrez, D., Isensee, K., Jacinto, G. S., Limburg, K. E., Montes, I., Naqvi, S. W. A., Pitcher, G. C., Rabalais, N. N., Roman, M. R., Rose, K. A., Seibel, B. A., ... Zhang, J. (2018). Declining oxygen in the global ocean and coastal waters. In *Science* (Vol. 359, Issue 6371). American Association for the Advancement of Science. <https://doi.org/10.1126/science.aam7240>
- Camhi, M., A. Musick, J., Fowler, S., & Brautigam, A. (1998). *Sharks and Their Relatives-Ecology and Conservation*. IUCN. <https://www.researchgate.net/publication/248535331>
- Camhi, Merry., Pikitch, E. K. ., & Babcock, E. A. . (2008). *Sharks of the open ocean : biology, fisheries and conservation*. Blackwell Science.
- Campana, S. E., Dorey, A., Fowler, M., Joyce, W., Wang, Z., Wright, D., & Yashayaev, I. (2011). Migration pathways, behavioural thermoregulation and overwintering grounds of blue sharks in the Northwest Atlantic. *PLoS ONE*, 6(2). <https://doi.org/10.1371/journal.pone.0016854>
- Campana, S. E., Marks, L., & Joyce, W. (2005). The biology and fishery of shortfin mako sharks (*Isurus oxyrinchus*) in Atlantic Canadian waters. *Fisheries Research*, 73(3), 341–352. <https://doi.org/10.1016/j.fishres.2005.01.009>
- Cardeñosa, D., Shea, S. K., Zhang, H., Fischer, G. A., Simpfendorfer, C. A., & Chapman, D. D. (2022). Two thirds of species in a global shark fin trade hub

- are threatened with extinction: Conservation potential of international trade regulations for coastal sharks. *Conservation Letters*, 15(5).
<https://doi.org/10.1111/conl.12910>
- Chan, F., Barth, J. A., Lubchenco, J., Kirincich, A., Weeks, H., Peterson, W. T., & Menge, B. A. (2008). Emergence of anoxia in the California current large marine ecosystem. In *Science* (Vol. 319, Issue 5865, p. 920).
<https://doi.org/10.1126/science.1149016>
- Chan, F., Sokolova, I., & Vopel, K. (2025). Ocean hypoxia: The science of climate change in the sea. In *Scientific Reports* (Vol. 15, Issue 1). Nature Research.
<https://doi.org/10.1038/s41598-025-86706-4>
- Chu, P. C., & Fan, C. (2017). Exponential leap-forward gradient scheme for determining the isothermal layer depth from profile data. *Journal of Oceanography*, 73(4), 503–526. <https://doi.org/10.1007/s10872-017-0418-0>
- Clarke, S. C., McAllister, M. K., Milner-Gulland, E. J., Kirkwood, G. P., Michielsens, C. G. J., Agnew, D. J., Pikitch, E. K., Nakano, H., & Shivji, M. S. (2006). Global estimates of shark catches using trade records from commercial markets. *Ecology Letters*, 9(10), 1115–1126.
<https://doi.org/10.1111/j.1461-0248.2006.00968.x>
- Clarke, S., Sato, M., Small, C., Sullivan, B., Inoue, Y., & Ochi, D. (2014). *Bycatch in Longline Fisheries for Tuna and Tuna-like Species: a Global Review of Status and Mitigation Measures* (1st ed.). FAO.
<https://openknowledge.fao.org/handle/20.500.14283/i4017e>
- Coelho, R., Fernandez-Carvalho, J., Lino, P. G., & Santos, M. N. (2012). An overview of the hooking mortality of elasmobranchs caught in a swordfish pelagic longline fishery in the Atlantic Ocean. In *Aquatic Living Resources* (Vol. 25, Issue 4, pp. 311–319). <https://doi.org/10.1051/alr/2012030>
- Coffey, D. M., & Holland, K. N. (2015). First autonomous recording of in situ dissolved oxygen from free-ranging fish. *Animal Biotelemetry*, 3(1).
<https://doi.org/10.1186/s40317-015-0088-x>
- Coffey, D. M., Royer, M. A., Meyer, C. G., & Holland, K. N. (2020). Diel patterns in swimming behavior of a vertically migrating deepwater shark, the bluntnose sixgill (*Hexanchus griseus*). *PLoS ONE*, 15(1).
<https://doi.org/10.1371/journal.pone.0228253>
- Collette, B. B., Carpenter, K. E., Polidoro, B. A., Juan-Jordá, M. J., Boustany, A., Die, D. J., Elfes, C., Fox, W., Graves, J., Harrison, L. R., McManus, R., Mente-Vera, C. V., Nelson, R., Restrepo, V., Schratwieser, J., Sun, C. L., Amorim, A., Brick Peres, M., Canales, C., ... Yáñez, E. (2011). High value and long life - Double jeopardy for tunas and billfishes. In *Science* (Vol. 333, Issue 6040, pp. 291–292). <https://doi.org/10.1126/science.1208730>
- Compagno, L. J. V. . (2001). *Sharks of the world : an annotated and illustrated catalogue of shark species known to date*. FAO.
- Cornejo, R., & Koppelman, R. (2006). Distribution patterns of mesopelagic fishes with special reference to *Vinciguerria lucetia* Garman 1899 (Phosichthyidae: Pisces) in the Humboldt Current Region off Peru. *Marine Biology*, 149(6), 1519–1537. <https://doi.org/10.1007/s00227-006-0319-z>
- Cortés, E. (1999). Standardized diet compositions and trophic levels of sharks. In *ICES Journal of Marine Science* (Vol. 56). <http://www.idealibrary.comon>
- Craig, J. K., Gillikin, P. C., Magelnicki, M. A., & May, L. N. (2010). Habitat use of cownose rays (*Rhinoptera bonasus*) in a highly productive, hypoxic

- continental shelf ecosystem. *Fisheries Oceanography*, 19(4), 301–317.
<https://doi.org/10.1111/j.1365-2419.2010.00545.x>
- da Costa, I., Sims, D. W., Loureiro, B., Waller, M. J., Womersley, F. C., Loveridge, A., Humphries, N. E., Southall, E. J., Vedor, M., Mucientes, G., Prendergast, S., Fontes, J., Afonso, P., Macena, B. C. L., Watanabe, Y. Y., & Queiroz, N. (2024). Measuring deoxygenation effects on marine predators: A new animal-attached archival tag recording in situ dissolved oxygen, temperature, fine-scale movements and behaviour. *Methods in Ecology and Evolution*, 15(8), 1360–1379. <https://doi.org/10.1111/2041-210X.14360>
- Da Silva, T. E. F., Lessa, R., & Santana, F. (2021). Current knowledge on biology, fishing and conservation of the blue shark (*Prionace glauca*). *Neotropical Biology and Conservation*, 16(1), 71–88.
<https://doi.org/10.3897/neotropical.16.58691>
- Dent, F., & Clarke, S. (2015). *State of the global market for shark products*.
<https://www.researchgate.net/publication/303265323>
- Diaz, R. J., & Rosenberg, R. (2008). Spreading dead zones and consequences for marine ecosystems. In *Science* (Vol. 321, Issue 5891, pp. 926–929).
<https://doi.org/10.1126/science.1156401>
- Díez, G., Soto, M., & Blanco, J. M. (2015). Biological characterization of the skin of shortfin mako shark *Isurus oxyrinchus* and preliminary study of the hydrodynamic behaviour through computational fluid dynamics. *Journal of Fish Biology*, 87(1), 123–137. <https://doi.org/10.1111/jfb.12705>
- Druon, J. N., Campana, S., Vandeperre, F., Hazin, F. H. V., Bowlby, H., Coelho, R., Queiroz, N., Serena, F., Abascal, F., Damalas, D., Musyl, M., Lopez, J., Block, B., Afonso, P., Dewar, H., Sabarros, P. S., Finucci, B., Zanzi, A., Bach, P., ... Travassos, P. (2022). Global-Scale Environmental Niche and Habitat of Blue Shark (*Prionace glauca*) by Size and Sex: A Pivotal Step to Improving Stock Management. *Frontiers in Marine Science*, 9.
<https://doi.org/10.3389/fmars.2022.828412>
- Dulvy, N. K., Fowler, S. L., Musick, J. A., Cavanagh, R. D., Kyne, P. M., Harrison, L. R., Carlson, J. K., Davidson, L. N. K., Fordham, S. V., Francis, M. P., Pollock, C. M., Simpfendorfer, C. A., Burgess, G. H., Carpenter, K. E., Compagno, L. J. V., Ebert, D. A., Gibson, C., Heupel, M. R., Livingstone, S. R., ... White, W. T. (2014). Extinction risk and conservation of the world's sharks and rays. *ELife*, 2014(3). <https://doi.org/10.7554/elife.00590>
- Ekau, W., Auel, H., Portner, H. O., & Gilbert, D. (2010). Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). *Biogeosciences*, 7(5), 1669–1699.
<https://doi.org/10.5194/bg-7-1669-2010>
- Ferretti, F., Worm, B., Britten, G. L., Heithaus, M. R., & Lotze, H. K. (2010). Patterns and ecosystem consequences of shark declines in the ocean. In *Ecology Letters* (Vol. 13, Issue 8, pp. 1055–1071).
<https://doi.org/10.1111/j.1461-0248.2010.01489.x>
- Fields, A. T., Fischer, G. A., Shea, S. K. H., Zhang, H., Abercrombie, D. L., Feldheim, K. A., Babcock, E. A., & Chapman, D. D. (2018). Species composition of the international shark fin trade assessed through a retail-market survey in Hong Kong. *Conservation Biology*, 32(2), 376–389.
<https://doi.org/10.1111/cobi.13043>
- Francis, M. P., Shivji, M. S., Duffy, C. A. J., Rogers, P. J., Byrne, M. E., Wetherbee, B. M., Tindale, S. C., Lyon, W. S., & Meyers, M. M. (2019).

- Oceanic nomad or coastal resident? Behavioural switching in the shortfin mako shark (*Isurus oxyrinchus*). *Marine Biology*, 166(1).
<https://doi.org/10.1007/s00227-018-3453-5>
- Garcia-Soto, C., Cheng, L., Caesar, L., Schmidtko, S., Jewett, E. B., Cheripka, A., Rigor, I., Caballero, A., Chiba, S., Báez, J. C., Zielinski, T., & Abraham, J. P. (2021). An Overview of Ocean Climate Change Indicators: Sea Surface Temperature, Ocean Heat Content, Ocean pH, Dissolved Oxygen Concentration, Arctic Sea Ice Extent, Thickness and Volume, Sea Level and Strength of the AMOC (Atlantic Meridional Overturning Circulation). In *Frontiers in Marine Science* (Vol. 8). Frontiers Media S.A.
<https://doi.org/10.3389/fmars.2021.642372>
- Gilly, W. F., Michael Beman, J., Litvin, S. Y., & Robison, B. H. (2013). Oceanographic and biological effects of shoaling of the oxygen minimum zone. *Annual Review of Marine Science*, 5, 393–420.
<https://doi.org/10.1146/annurev-marine-120710-100849>
- Gruber, N. (2011). Warming up, turning sour, losing breath: Ocean biogeochemistry under global change. In *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* (Vol. 369, Issue 1943, pp. 1980–1996). <https://doi.org/10.1098/rsta.2011.0003>
- Heerah, K., Hindell, M., Guinet, C., & Charrassin, J. B. (2014). A new method to quantify within dive foraging behaviour in marine predators. *PLoS ONE*, 9(6).
<https://doi.org/10.1371/journal.pone.0099329>
- Heithaus, M. R., Frid, A., Wirsing, A. J., & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. In *Trends in Ecology and Evolution* (Vol. 23, Issue 4, pp. 202–210). Elsevier Ltd.
<https://doi.org/10.1016/j.tree.2008.01.003>
- Hoving, H. J. T., Neitzel, P., Hauss, H., Christiansen, S., Kiko, R., Robison, B. H., Silva, P., & Körtzinger, A. (2020). In situ observations show vertical community structure of pelagic fauna in the eastern tropical North Atlantic off Cape Verde. *Scientific Reports*, 10(1). <https://doi.org/10.1038/s41598-020-78255-9>
- Humphries, N. E., Queiroz, N., Dyer, J. R. M., Pade, N. G., Musyl, M. K., Schaefer, K. M., Fuller, D. W., Brunnschweiler, J. M., Doyle, T. K., Houghton, J. D. R., Hays, G. C., Jones, C. S., Noble, L. R., Wearmouth, V. J., Southall, E. J., & Sims, D. W. (2010). Environmental context explains Lévy and Brownian movement patterns of marine predators. *Nature*, 465(7301), 1066–1069.
<https://doi.org/10.1038/nature09116>
- Intergovernmental Panel on Climate Change (IPCC). (2013). *Technical Summary. In: Climate Change 2013: The Physical Science Basis*.
- Intergovernmental Panel on Climate Change (IPCC). (2021). Technical Summary. In *Climate Change 2021 – The Physical Science Basis* (pp. 35–144). Cambridge University Press. <https://doi.org/10.1017/9781009157896.002>
- Karstensen, J., Stramma, L., & Visbeck, M. (2008). Oxygen minimum zones in the eastern tropical Atlantic and Pacific oceans. *Progress in Oceanography*, 77(4), 331–350. <https://doi.org/10.1016/j.pocean.2007.05.009>
- Keeling, R. F., Körtzinger, A., & Gruber, N. (2010). Ocean deoxygenation in a warming world. *Annual Review of Marine Science*, 2(1), 199–229.
<https://doi.org/10.1146/annurev.marine.010908.163855>
- Klöcker, C. A., Bjelland, O., Ferter, K., Arostegui, M. C., Braun, C. D., da Costa, I., Cidade, T., Queiroz, N., Sims, D. W., & Junge, C. (2025). Basking sharks of

- the Arctic Circle: year-long, high-resolution tracking data reveal wide thermal range and prey-driven vertical movements across habitats. *Animal Biotelemetry*, 13(1). <https://doi.org/10.1186/s40317-025-00407-3>
- Koslow, J. A., Goericke, R., Lara-Lopez, A., & Watson, W. (2011). Impact of declining intermediate-water oxygen on deepwater fishes in the California Current. *Marine Ecology Progress Series*, 436, 207–218. <https://doi.org/10.3354/meps09270>
- Le Croizier, G., Sonke, J. E., Lorrain, A., Serre, S., Besnard, L., Schaal, G., Amezcua-Martinez, F., & Point, D. (2022). Mercury stable isotopes suggest reduced foraging depth in oxygen minimum zones for blue sharks. *Marine Pollution Bulletin*, 181. <https://doi.org/10.1016/j.marpolbul.2022.113892>
- Leeuwis, R. H. J., Zanuzzo, F. S., Peroni, E. F. C., & Gamperl, A. K. (2021). Research on sablefish (*Anoplopoma fimbria*) suggests that limited capacity to increase heart function leaves hypoxic fish susceptible to heat waves. *Proceedings of the Royal Society B: Biological Sciences*, 288(1946). <https://doi.org/10.1098/rspb.2020.2340>
- Limburg, K. E., Breitburg, D., Swaney, D. P., & Jacinto, G. (2020). Ocean Deoxygenation: A Primer. In *One Earth* (Vol. 2, Issue 1, pp. 24–29). Cell Press. <https://doi.org/10.1016/j.oneear.2020.01.001>
- Logan, R. K., Vaudo, J. J., Wetherbee, B. M., & Shivji, M. S. (2023). Seasonally mediated niche partitioning in a vertically compressed pelagic predator guild. *Proceedings of the Royal Society B: Biological Sciences*, 290(2012). <https://doi.org/10.1098/rspb.2023.2291>
- Long, M. C., Deutsch, C., & Ito, T. (2016). Finding forced trends in oceanic oxygen. *Global Biogeochemical Cycles*, 30(2), 381–397. <https://doi.org/10.1002/2015GB005310>
- Long, W. C., & Seitz, R. D. (2008). Trophic interactions under stress: Hypoxia enhances foraging in an estuarine food web. *Marine Ecology Progress Series*, 362, 59–68. <https://doi.org/10.3354/meps07395>
- Lucifora, L. O., García, V. B., Menni, R. C., & Worm, B. (2012). Spatial patterns in the diversity of sharks, rays, and chimaeras (Chondrichthyes) in the Southwest Atlantic. *Biodiversity and Conservation*, 21(2), 407–419. <https://doi.org/10.1007/s10531-011-0189-7>
- Luyten, J. R., Pedlosky, J., & Stommel, H. (1983). The Ventilated Thermocline. *Journal of Physical Oceanography*, 13, 293–309. [https://doi.org/10.1175/1520-0485\(1983\)013<0292:TVT>2.0.CO;2](https://doi.org/10.1175/1520-0485(1983)013<0292:TVT>2.0.CO;2)
- Ma, J., Song, J., Li, X., Wang, Q., Zhong, G., Yuan, H., Li, N., & Duan, L. (2021). The OMZ and Its Influence on POC in the Tropical Western Pacific Ocean: Based on the Survey in March 2018. *Frontiers in Earth Science*, 9. <https://doi.org/10.3389/feart.2021.632229>
- Maia, A., Queiroz, N., Correia, J. P., & Cabral, H. (2006). Food habits of the shortfin mako, *Isurus oxyrinchus*, off the southwest coast of Portugal. *Environmental Biology of Fishes*, 77(2), 157–167. <https://doi.org/10.1007/s10641-006-9067-7>
- Markaida, U., & 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. In *Journal of the Marine Biological Association of the United Kingdom* (Vol. 90, Issue 5, pp. 977–994). <https://doi.org/10.1017/S0025315409991597>

- Mas, F., Cortés, E., Coelho, R., Defeo, O., Miller, P., Carlson, J., Gulak, S., & Domingo, A. (2024). Blue shark (*Prionace glauca*) movements, habitat use, and vertical overlap with longline fishing gears in the southwestern Atlantic Ocean. *Marine Biology*, 171(5). <https://doi.org/10.1007/s00227-024-04421-6>
- Mejuto, J., Fernández-Costa, J., García-Cortés, B., & Ramos-Cardelle, A. (2017). Updated standardized catch rates of shortfin mako (*Isurus oxyrinchus*) caught by the Spanish surface longline fishery targeting swordfish in the Atlantic Ocean during the period 1990-2015. *Collective Volume of Scientific Papers ICCAT*, 74(4), 1730–1745.
- Morato, T., Hoyle, S. D., Allain, V., & Nicol, S. J. (2010). Seamounts are hotspots of pelagic biodiversity in the open ocean. *Proceedings of the National Academy of Sciences of the United States of America*, 107(21), 9707–9711. <https://doi.org/10.1073/pnas.0910290107>
- Morrison, P. R., Bernal, D., Sepulveda, C. A., & Brauner, C. J. (2023). The effect of temperature on haemoglobin-oxygen binding affinity in regionally endothermic and ectothermic sharks. *Journal of Experimental Biology*, 226(2). <https://doi.org/10.1242/jeb.244979>
- Mucientes, G., Queiroz, N., Humphries, N., & Sims, D. (2012). *Movements and diving behaviour of mako shark in North Atlantic*.
- Myers, R. A., & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature*, 423, 280–283. <https://doi.org/10.1038/nature01610>
- Nasby-Lucas, N., Dewar, H., Sosa-Nishizaki, O., Wilson, C., Hyde, J. R., Vetter, R. D., Wraith, J., Block, B. A., Kinney, M. J., Sippel, T., Holts, D. B., & Kohin, S. (2019). Movements of electronically tagged shortfin mako sharks (*Isurus oxyrinchus*) in the eastern North Pacific Ocean. *Animal Biotelemetry*, 7(1). <https://doi.org/10.1186/s40317-019-0174-6>
- Navia, A. F., Cruz-Escalona, V. H., Giraldo, A., & Barausse, A. (2016). The structure of a marine tropical food web, and its implications for ecosystem-based fisheries management. *Ecological Modelling*, 328, 23–33. <https://doi.org/10.1016/j.ecolmodel.2016.02.009>
- Netburn, A. N., & Anthony Koslow, J. (2015). Dissolved oxygen as a constraint on daytime deep scattering layer depth in the southern California current ecosystem. *Deep-Sea Research Part I: Oceanographic Research Papers*, 104, 149–158. <https://doi.org/10.1016/j.dsr.2015.06.006>
- Oliver, S., Braccini, M., Newman, S. J., & Harvey, E. S. (2015). Global patterns in the bycatch of sharks and rays. *Marine Policy*, 54, 86–97. <https://doi.org/10.1016/j.marpol.2014.12.017>
- Oosthuizen, W. C., Schoombie, S., Chimienti, M., Pistorius, P. A., & Lowther, A. D. (2025). Dive wiggles as a proxy of prey consumption in krill-feeding penguins. *Journal of Experimental Marine Biology and Ecology*, 590. <https://doi.org/10.1016/j.jembe.2025.152115>
- Porcher, I. F., & Darvell, B. W. (2022). Shark Fishing vs. Conservation: Analysis and Synthesis. In *Sustainability (Switzerland)* (Vol. 14, Issue 15). MDPI. <https://doi.org/10.3390/su14159548>
- Prince, E. D., & Goodyear, C. P. (2006). Hypoxia-based habitat compression of tropical pelagic fishes. *Fisheries Oceanography*, 15(6), 451–464. <https://doi.org/10.1111/j.1365-2419.2005.00393.x>
- Prince, E. D., Luo, J., Phillip Goodyear, C., Hoolihan, J. P., Snodgrass, D., Orbesen, E. S., Serafy, J. E., Ortiz, M., & Schirripa, M. J. (2010). Ocean scale hypoxia-based habitat compression of Atlantic istiophorid billfishes. *Fisheries*

- Oceanography*, 19(6), 448–462. <https://doi.org/10.1111/j.1365-2419.2010.00556.x>
- Queiroz, N., Humphries, N. E., Couto, A., Vedor, M., da Costa, I., Sequeira, A. M. M., Mucientes, G., Santos, A. M., Abascal, F. J., Abercrombie, D. L., Abrantes, K., Acuña-Marrero, D., Afonso, A. S., Afonso, P., Anders, D., Araujo, G., Arauz, R., Bach, P., Barnett, A., ... Sims, D. W. (2019). Global spatial risk assessment of sharks under the footprint of fisheries. *Nature*, 572(7770), 461–466. <https://doi.org/10.1038/s41586-019-1444-4>
- Queiroz, N., Humphries, N. E., Mucientes, G., Hammerschlag, N., Lima, F. P., Scales, K. L., Miller, P. I., Sousa, L. L., Seabra, R., & Sims, D. W. (2016). Ocean-wide tracking of pelagic sharks reveals extent of overlap with longline fishing hotspots. *Proceedings of the National Academy of Sciences of the United States of America*, 113(6), 1582–1587. <https://doi.org/10.1073/pnas.1510090113>
- Queiroz, N., Humphries, N. E., Noble, L. R., Santos, A. M., & Sims, D. W. (2010). Short-term movements and diving behaviour of satellite-tracked blue sharks *Prionace glauca* in the northeastern Atlantic Ocean. *Marine Ecology Progress Series*, 406, 265–279. <https://doi.org/10.3354/meps08500>
- Queiroz, N., Humphries, N. E., Noble, L. R., Santos, A. M., & Sims, D. W. (2012). Spatial dynamics and expanded vertical niche of blue sharks in oceanographic fronts reveal habitat targets for conservation. *PLoS ONE*, 7(2). <https://doi.org/10.1371/journal.pone.0032374>
- Queiroz, N., Vila-Pouca, C., Couto, A., Southall, E. J., Mucientes, G., Humphries, N. E., & Sims, D. W. (2017). Convergent foraging tactics of marine predators with different feeding strategies across heterogeneous ocean environments. *Frontiers in Marine Science*, 4(AUG). <https://doi.org/10.3389/fmars.2017.00239>
- Rigby, C. L., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M. P., Herman, K., Jabado, R. W., Liu, K. M., Marshall, A., Pacoureau, N., Romanov, E., Sherley, R. B., & Winker, H. (2019). *Prionace glauca*. The IUCN Red List of Threatened Species 2019. In *IUCN Red List of Threatened Species*. <https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T39381A2915850.en>
- Rigby, C. L., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M. P., Jabado, R. W., Liu, K. M., Marshall, A., Pacoureau, N., Romanov, E., Sherley, R. B., & Winker, H. (2018). *Isurus oxyrinchus*: Rigby, C.L., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M.P., Jabado, R.W., Liu, K.M., Marshall, A., Pacoureau, N., Romanov, E., Sherley, R.B. & Winker, H. In *IUCN Red List of Threatened Species*. <https://doi.org/10.2305/IUCN.UK.2019-1.RLTS.T39341A2903170.en>
- Rogers, P. J., Huveneers, C., Page, B., Goldsworthy, S. D., Coyne, M., Lowther, A. D., Mitchell, J. G., & Seuront, L. (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), 205–218. <https://doi.org/10.1111/fog.12103>
- Santos, C. C., Domingo, A., Carlson, J., Natanson, L. J., Travassos, P., Macías, D., Cortés, E., Miller, P., Hazin, F., Mas, F., Ortiz de Urbina, J., Lino, P. G., & Coelho, R. (2021). Movements, Habitat Use, and Diving Behavior of Shortfin Mako in the Atlantic Ocean. *Frontiers in Marine Science*, 8. <https://doi.org/10.3389/fmars.2021.686343>

- Schmidtko, S., Stramma, L., & Visbeck, M. (2017). Decline in global oceanic oxygen content during the past five decades. *Nature*, 542(7641), 335–339. <https://doi.org/10.1038/nature21399>
- Schreer, J. F., Kovacs, K. M., & O'Hara Hines, R. J. (2001). Comparative diving patterns of pinnipeds and seabirds. *Ecological Monographs*, 71(1), 137–162. [https://doi.org/10.1890/0012-9615\(2001\)071\[0137:CDPOPA\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2001)071[0137:CDPOPA]2.0.CO;2)
- Sepulveda, C. A., Graham, J. B., & Bernal, D. (2007). Aerobic metabolic rates of swimming juvenile mako sharks, *Isurus oxyrinchus*. *Marine Biology*, 152(5), 1087–1094. <https://doi.org/10.1007/s00227-007-0757-2>
- Stevens, J. D., Bradford, R. W., & West, G. J. (2010). Satellite tagging of blue sharks (*Prionace glauca*) and other pelagic sharks off eastern Australia: Depth behaviour, temperature experience and movements. *Marine Biology*, 157(3), 575–591. <https://doi.org/10.1007/s00227-009-1343-6>
- Stramma, L., Brandt, P., Schafstall, J., Schott, F., Fischer, J., & Körtzinger, A. (2008). Oxygen minimum zone in the North Atlantic south and east of the Cape Verde Islands. *Journal of Geophysical Research: Oceans*, 113(4). <https://doi.org/10.1029/2007JC004369>
- Stramma, L., C. Johnson, G., Firing, E., & Sunke, S. (2010). *Eastern Pacific oxygen minimum zones Supply paths and multidecadal changes*. <https://doi.org/10.1029/2009JC005976>
- Stramma, L., C. Johnson, G., Sprintall, J., & Mohrholz, V. (2008). Expanding Oxygen-Minimum Zones in the Tropical Oceans. *Science*. <https://doi.org/10.1126/science.1153847>
- Stramma, L., Prince, E. D., Schmidtko, S., Luo, J., Hoolihan, J. P., Visbeck, M., Wallace, D. W. R., Brandt, P., & Körtzinger, A. (2012). Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nature Climate Change*, 2(1), 33–37. <https://doi.org/10.1038/nclimate1304>
- Tokunaga, S., Chiang, W. C., Nakamura, I., Matsumoto, R., & Watanabe, Y. Y. (2025). Enhanced thermoregulation abilities of shortfin mako sharks as the key adaptive significance of regional endothermy in fishes. *Journal of Animal Ecology*. <https://doi.org/10.1111/1365-2656.70116>
- Vaudo, J. J., Byrne, M. E., Wetherbee, B. M., Harvey, G. M., & Shivji, M. S. (2017). Long-term satellite tracking reveals region-specific movements of a large pelagic predator, the shortfin mako shark, in the western North Atlantic Ocean. *Journal of Applied Ecology*, 54(6), 1765–1775. <https://doi.org/10.1111/1365-2664.12852>
- Vaudo, J. J., Wetherbee, B. M., Wood, A. D., Weng, K., Howey-Jordan, L. A., Harvey, G. M., & Shivji, M. S. (2016). Vertical movements of shortfin mako sharks *Isurus oxyrinchus* in the western North Atlantic Ocean are strongly influenced by temperature. *Marine Ecology Progress Series*, 547, 163–175. <https://doi.org/10.3354/meps11646>
- Vedor, M., Mucientes, G., Hernández-Chan, S., Rosa, R., Humphries, N., Sims, D. W., & Queiroz, N. (2021). Oceanic Diel Vertical Movement Patterns of Blue Sharks Vary With Water Temperature and Productivity to Change Vulnerability to Fishing. *Frontiers in Marine Science*, 8. <https://doi.org/10.3389/fmars.2021.688076>
- Vedor, M., Queiroz, N., Mucientes, G., Couto, A., da Costa, I., Dos Santos, A., Vandeperre, F., Fontes, J., Afonso, P., Rosa, R., Humphries, N. E., & Sims, D. W. (2021). Climate-driven deoxygenation elevates fishing vulnerability for

- the ocean's widest ranging shark. *ELife*, 10, 1–29.
<https://doi.org/10.7554/eLife.62508>
- Vetter, R., Kohin, S., Preti, A., McClatchie, S., & Dewar, H. (2008). Predatory interactions and niche overlap between mako shark, *Isurus oxyrinchus*, and jumbo squid, *Dosidicus gigas*, in the California Current. *CalCOFI Reports*, 49. <https://www.researchgate.net/publication/236117652>
- Waller, M. J., Humphries, N. E., Womersley, F. C., Loveridge, A., Jeffries, A. L., Watanabe, Y., Payne, N., Semmens, J., Queiroz, N., Southall, E. J., & Sims, D. W. (2024). The vulnerability of sharks, skates, and rays to ocean deoxygenation: Physiological mechanisms, behavioral responses, and ecological impacts. In *Journal of Fish Biology* (Vol. 105, Issue 2, pp. 482–511). John Wiley and Sons Inc. <https://doi.org/10.1111/jfb.15830>
- Waller, M. J., Queiroz, N., da Costa, I., Cidade, T., Loureiro, B., Womersley, F. C., Fontes, J., Afonso, P., Macena, B. C. L., Loveridge, A., Humphries, N. E., Southall, E. J., & Sims, D. W. (2023). Direct measurement of cruising and burst swimming speeds of the shortfin mako shark (*Isurus oxyrinchus*) with estimates of field metabolic rate. *Journal of Fish Biology*, 103(5), 864–883. <https://doi.org/10.1111/jfb.15475>
- Watanabe, Y. Y., Nakamura, I., & Chiang, W. C. (2021). Behavioural thermoregulation linked to foraging in blue sharks. *Marine Biology*, 168(11). <https://doi.org/10.1007/s00227-021-03971-3>
- Whitney, F. A., Freeland, H. J., & Robert, M. (2007). Persistently declining oxygen levels in the interior waters of the eastern subarctic Pacific. *Progress in Oceanography*, 75(2), 179–199. <https://doi.org/10.1016/j.pocean.2007.08.007>
- Worm, B., Davis, B., Kettmer, L., Ward-Paige, C. A., Chapman, D., Heithaus, M. R., Kessel, S. T., & Gruber, S. H. (2013). Global catches, exploitation rates, and rebuilding options for sharks. *Marine Policy*, 40(1), 194–204. <https://doi.org/10.1016/j.marpol.2012.12.034>
- Worm, B., Lotze, H. K., & Myers, R. A. (2003). *Predator diversity hotspots in the blue ocean*. www.pnas.org
- Wright, J. J., Konwar, K. M., & Hallam, S. J. (2012). Microbial ecology of expanding oxygen minimum zones. In *Nature Reviews Microbiology* (Vol. 10, Issue 6, pp. 381–394). <https://doi.org/10.1038/nrmicro2778>
- Zhou, Y., Gong, H., & Zhou, F. (2022). Responses of Horizontally Expanding Oceanic Oxygen Minimum Zones to Climate Change Based on Observations. *Geophysical Research Letters*, 49(6). <https://doi.org/10.1029/2022GL097724>

8. Supplementary material

8.1 Summary tables

Table S1: Information on data collection for all blue sharks. Includes shark ID, date of tag attachment, and detachment. Sharks with (*) are archival: tags were physically recovered, providing high-resolution data recorded at 1-second intervals.

All Mako sharks	ID	Start date	End date
1	mk_dws86408*	26/06/2010	20/10/2010
2	mk_dws164446	24/01/2017	25/03/2017
3	mk_dws164447	23/04/2018	24/06/2018
4	mk_dws164448	23/04/2018	06/06/2018
5	mk_dws164449*	24/04/2018	26/06/2018
6	mk_dws164450	24/04/2018	18/05/2018
7	mk_dws181757	15/06/2022	12/11/2022
8	mk_dws202893	16/06/2022	12/11/2022
9	mk_dws202895	25/06/2021	24/10/2021
10	mk_dws202901	15/06/2022	04/11/2022
11	mk_dws202902	15/06/2022	26/08/2022
12	mk_fa79813	29/12/2010	20/06/2011
13	mk_fa79802	07/12/2010	03/01/2011
14	mk_fa79796	13/12/2010	08/03/2011
15	mk_fa79794	11/12/2010	22/12/2010
16	mk_fa54552	07/12/2010	19/12/2011
17	mk_dws148786	27/01/2017	28/03/2017
18	mk_dws107092	03/09/2011	01/01/2012
19	mk_dws107090	22/08/2011	20/12/2011
20	mk_dws107089	21/08/2011	19/12/2011
21	mk_dws96031	05/07/2010	02/11/2010
22	mk_dws96030	04/07/2010	01/11/2010
23	mk_dws86407	03/07/2010	01/10/2010
24	mk_dws86402	24/04/2009	23/06/2009
25	mk_dws86401	30/06/2010	28/09/2010
26	mk_dws86400	23/04/2009	23/05/2009
27	mk_dws86399	25/06/2010	24/08/2010

Table S2: Information on data collection for all mako sharks. Includes shark ID, date of tag attachment, and detachment. Sharks with (*) are archival: tags were physically recovered, providing high-resolution data recorded at 1-second intervals.

All Blue sharks	ID	Start date	End date
1	bl_nq107085*	28/08/2011	29/11/2011
2	bl_nq164441	24/01/2017	23/04/2017
3	bl_nq164442	27/01/2017	25/04/2017
4	bl_nq164443	25/01/2017	25/05/2017
5	bl_nq164444	28/01/2017	28/05/2017
6	bl_nq181758	17/06/2022	13/08/2022
7	bl_nq202904	13/06/2022	27/09/2022
8	bl_nq85693*	26/08/2011	11/11/2011
9	bl_nq96036*	26/06/2010	08/07/2010
10	bl_pa98174*	18/10/2009	27/01/2010
11	bl_nq85136	21/08/2011	19/11/2011
12	bl_nq85140	22/08/2011	20/12/2011
13	bl_nq85697	26/08/2011	24/12/2011
14	bl_nq86396	27/06/2010	22/08/2010
15	bl_nq86395	26/06/2010	23/09/2010
16	bl_nq91026	21/08/2011	19/11/2011
17	bl_nq91658	26/08/2011	24/12/2011
18	bl_nq96034	29/06/2010	27/10/2010
19	bl_nq96035	30/06/2010	27/07/2010
20	bl_nq96037	25/06/2010	02/07/2010
21	bl_nq96039	25/06/2010	22/12/2010
22	bl_nq107084	27/08/2011	25/12/2011
23	bl_nq148781	21/01/2017	22/03/2017
24	bl_nq148783	23/01/2017	12/03/2017
25	bl_nq148784	24/01/2017	25/03/2017
26	bl_pa91068	26/02/2009	25/05/2009

Table S3: Information on blue shark data collection used in Dive Analysis. Includes shark ID, date of tag attachment, detachment, number of days spent inside and outside the OMZ, and total number of days with data. Sharks with (*) are archival: tags were physically recovered, providing high-resolution data recorded at 1-second intervals.

Dive Analysis						
Shark	ID	Start date	End date	Days inside OMZ	Days outside OMZ	Total days with data
1	bl_nq107085*	28/08/2011	29/11/2011	29	65	94
2	bl_nq164441	24/01/2017	23/04/2017	5	34	39
3	bl_nq164442	27/01/2017	25/04/2017	70	0	70
4	bl_nq164443	25/01/2017	25/05/2017	25	80	105
5	bl_nq164444	28/01/2017	28/05/2017	13	95	108
6	bl_nq181758	17/06/2022	13/08/2022	0	5	5
7	bl_nq202904	13/06/2022	27/09/2022	0	68	68
8	bl_nq85693*	26/08/2011	11/11/2011	0	78	78
9	bl_nq96036*	26/06/2010	08/07/2010	0	13	13
10	bl_pa98174*	18/10/2009	27/01/2010	0	102	102

Table S4: Information on mako shark data collection used in Dive Analysis. Includes shark ID, date of tag attachment, detachment, number of days spent inside and outside the OMZ, and total number of days with data. Sharks with (*) are archival: tags were physically recovered, providing high-resolution data recorded at 1-second intervals.

Dive Analysis						
Shark	ID	Start date	End date	Days inside OMZ	Days outside OMZ	Total days with data
1	mk_dws86408*	26/06/2010	20/10/2010	0	112	112
2	mk_dws164446	24/01/2017	25/03/2017	33	0	33
3	mk_dws164447	23/04/2018	24/06/2018	7	0	7
4	mk_dws164448	23/04/2018	06/06/2018	39	0	39
5	mk_dws164449*	24/04/2018	26/06/2018	53	0	53
6	mk_dws164450	24/04/2018	18/05/2018	23	0	23
7	mk_dws181757	15/06/2022	12/11/2022	0	85	85
8	mk_dws202893	16/06/2022	12/11/2022	0	116	116
9	mk_dws202895	25/06/2021	24/10/2021	0	102	102
10	mk_dws202901	15/06/2022	04/11/2022	0	60	60
11	mk_dws202902	15/06/2022	26/08/2022	0	5	5

8.2 Supplementary figures

8.2.1 Maximum daily depth

Blue:

Table S5: Full output of the linear mixed model for maximum daily depth in blue sharks.

```
Modelo misto (lmer):  
Linear mixed model fit by maximum likelihood . t-tests use Satterthwaite's method ['lmerModLmerTest']  
Formula: MaxDepth ~ OxygenLevel + (1 | ID)  
Data: blue_combined_raw  
  
      AIC      BIC    logLik deviance df.resid  
19695.8 19716.8 -9843.9 19687.8    1390  
  
Scaled residuals:  
      Min       1Q   Median       3Q      Max  
-1.8386 -0.5701 -0.1773  0.2635  4.6144  
  
Random effects:  
Groups   Name             Variance Std.Dev.  
ID       (Intercept)    9398      96.94  
Residual              77017     277.52  
Number of obs: 1394, groups: ID, 26  
  
Fixed effects:  
              Estimate Std. Error    df t value Pr(>|t|)  
(Intercept)    433.81      21.83  28.47  19.868 < 2e-16 ***  
OxygenLevellow -174.40      30.16 1001.26 -5.782 9.85e-09 ***  
---  
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1  
  
Correlation of Fixed Effects:  
      (Intr)  
OxygenLvllw -0.166
```

Mako:

Table S6: Full output of the linear mixed model for maximum daily depth in mako sharks.

```
Modelo misto (lmer):  
Linear mixed model fit by maximum likelihood . t-tests use Satterthwaite's method ['lmerModLmerTest']  
Formula: MaxDepth ~ OxygenLevel + (1 | ID)  
Data: blue_combined_raw  
  
      AIC      BIC    logLik deviance df.resid  
19695.8 19716.8 -9843.9 19687.8    1390  
  
Scaled residuals:  
      Min       1Q   Median       3Q      Max  
-1.8386 -0.5701 -0.1773  0.2635  4.6144  
  
Random effects:  
Groups   Name             Variance Std.Dev.  
ID       (Intercept)    9398      96.94  
Residual              77017     277.52  
Number of obs: 1394, groups: ID, 26  
  
Fixed effects:  
              Estimate Std. Error    df t value Pr(>|t|)  
(Intercept)    433.81      21.83  28.47  19.868 < 2e-16 ***  
OxygenLevellow -174.40      30.16 1001.26 -5.782 9.85e-09 ***  
---  
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1  
  
Correlation of Fixed Effects:  
      (Intr)  
OxygenLvllw -0.166
```

8.2.2 Time-at-depth

Blue:

Table S7: Full output of the Wilcoxon rank-sum test for time-at-depth in blue sharks.

```
> wilcox_results
      Depth_bin w_stat      p_value
W      50-100 3188.5 1.653298e-10
W1     100-150 1961.5 2.957720e-03
W2     150-200 1080.5 8.213947e-01
W3     200-250  465.5 5.256369e-01
W4       0-50 1434.5 4.589143e-02
W5     250-300  131.5 1.000000e+00
W6     300-350   63.5 7.805788e-01
1       <NA>      NA      NA
W7     350-400   25.5 1.705977e-01
11     400-450      NA      NA
12     450-500      NA      NA
13     550-600      NA      NA
14       >600      NA      NA
15     500-550      NA      NA
```

Mako:

Table S8: Full output of the Wilcoxon rank-sum test for time-at-depth in blue sharks.

```
> wilcox_results
      Depth_bin w_stat      p_value
W       0-50 2104.0 0.2080860231
W1     50-100 3216.5 0.0009186884
W2     100-150 1543.5 0.6099687625
1       <NA>      NA      NA
W3     150-200 1136.0 0.7643978125
W4     200-250  878.5 0.0356015857
W5     250-300  232.5 0.8788083084
W6     300-350  121.0 0.1954550648
W7     350-400   32.0 0.8700918802
W8     400-450    8.0 0.7121545377
11     500-550      NA      NA
12     450-500      NA      NA
13     550-600      NA      NA
```

8.2.3 Time-at-temperature

Blue:

Table S9: Full output of the Wilcoxon rank-sum test for time-at-temperature in blue sharks.

```
> wilcox_results_TAT
      Temp_bin w_stat      p_value
1       <NA>      NA      NA
W      [11,13) 114.5 3.000548e-02
W1     [13,15) 583.0 8.748326e-03
W2     [15,17) 947.5 3.321623e-01
W3     [17,19) 689.5 2.535888e-05
W4     [19,21) 972.0 9.356391e-02
W5     [23,25)  63.5 8.549850e-01
W6     [21,23) 428.0 5.200373e-05
11     [5,7)      NA      NA
12     [7,9)      NA      NA
W7     [9,11)  27.5 9.868539e-02
13     [25,27]      NA      NA
```

Mako:

Table S10: Full output of the Wilcoxon rank-sum test for time-at-temperature in mako sharks.

```
> wilcox_results_TAT
  Temp_bin w_stat      p_value
w  [15,17)  815.5 8.211131e-03
w1 [17,19) 1947.0 2.853720e-01
w2 [19,21) 1809.5 7.986857e-01
w3 [21,23)  650.5 4.005301e-06
w4 [23,25)  260.0 2.629837e-01
1  <NA>      NA          NA
w5 [13,15)  773.5 6.959593e-02
11 [11,13)    NA          NA
12 [9,11)    NA          NA
w6 [25,27]   33.5 3.267546e-01
```

8.2.4 Number of daily dives

Blue:

Table S11: Full output of the linear model for the number of daily dives with OMZ as a fixed effect in blue sharks.

```
Call:
lm(formula = num_dives ~ OMZ, data = dive_count)

Residuals:
    Min       1Q   Median       3Q      Max
-8.189 -5.189 -1.141  4.811 19.811

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  9.14085    0.51602  17.714  <2e-16 ***
OMZout       0.04804    0.57991   0.083   0.934
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 6.149 on 680 degrees of freedom
Multiple R-squared:  1.009e-05, Adjusted R-squared:  -0.00146
F-statistic: 0.006864 on 1 and 680 DF, p-value: 0.934
```

Table S12: Full output of the linear model for the number of daily dives with OMZ as a fixed effect and ID included to control for individual variability in blue sharks.

```
Call:
lm(formula = num_dives ~ OMZ + ID, data = dive_count)

Residuals:
    Min       1Q   Median       3Q      Max
-15.6795  -2.4997  -0.4997   2.3205  15.4020

Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept)    18.0015     0.5073  35.482 < 2e-16 ***
OMZout         -3.4638     0.4923  -7.036 4.89e-12 ***
IDbl_nq164441 -11.8536     0.7004 -16.925 < 2e-16 ***
IDbl_nq164442 -12.3015     0.6689 -18.391 < 2e-16 ***
IDbl_nq164443  -9.3339     0.5191 -17.983 < 2e-16 ***
IDbl_nq164444  -8.0380     0.5228 -15.376 < 2e-16 ***
IDbl_nq181758 -11.9378     1.6808  -7.102 3.14e-12 ***
IDbl_nq202904 -11.3319     0.6002 -18.881 < 2e-16 ***
IDbl_nq85693   2.1417     0.5789   3.700 0.000234 ***
IDbl_nq96036   -8.7685     1.0899  -8.045 3.91e-15 ***
IDbl_pa98174   -1.9397     0.5431  -3.571 0.000381 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 3.647 on 671 degrees of freedom
Multiple R-squared:  0.6528,    Adjusted R-squared:  0.6477
F-statistic: 126.2 on 10 and 671 DF,  p-value: < 2.2e-16
```

Mako:

Table S13: Full output of the linear model for the number of daily dives with OMZ as a fixed effect in mako sharks.

```
Call:
lm(formula = num_dives ~ OMZ, data = dive_count)

Residuals:
    Min       1Q   Median       3Q      Max
-3.775 -1.775 -0.775   2.225 11.225

Coefficients:
              Estimate Std. Error t value Pr(>|t|)
(Intercept)    3.7742     0.2312  16.324 < 2e-16 ***
OMZout         1.0008     0.2659   3.763 0.000183 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 2.878 on 633 degrees of freedom
Multiple R-squared:  0.02189,    Adjusted R-squared:  0.02034
F-statistic: 14.16 on 1 and 633 DF,  p-value: 0.0001832
```

Table S14: Full output of the linear model for the number of daily dives with OMZ as a fixed effect and ID included to control for individual variability in mako sharks.

```
Call:
lm(formula = num_dives ~ OMZ + ID, data = dive_count)

Residuals:
    Min       1Q   Median       3Q      Max
-5.286 -1.941 -0.550  1.513 11.233

Coefficients: (1 not defined because of singularities)
              Estimate Std. Error t value Pr(>|t|)
(Intercept)    4.0303    0.4690   8.594 < 2e-16 ***
OMZout         2.2554    0.5336   4.227 2.73e-05 ***
IDmk_dws164447 -2.6017    1.1211  -2.321 0.02062 *
IDmk_dws164448 -0.5431    0.6372  -0.852 0.39436
IDmk_dws164449 -0.1624    0.5974  -0.272 0.78586
IDmk_dws164450  0.3610    0.7318   0.493 0.62197
IDmk_dws181757 -2.3445    0.3876  -6.050 2.50e-09 ***
IDmk_dws202893 -1.5185    0.3569  -4.255 2.42e-05 ***
IDmk_dws202895 -1.0406    0.3687  -2.822 0.00492 **
IDmk_dws202901 -3.7357    0.4310  -8.667 < 2e-16 ***
IDmk_dws202902 -3.8857    1.2314  -3.155 0.00168 **
IDmk_dws86408      NA         NA      NA      NA
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 2.694 on 624 degrees of freedom
Multiple R-squared:  0.1553,    Adjusted R-squared:  0.1418
F-statistic: 11.48 on 10 and 624 DF,  p-value: < 2.2e-16
```

8.2.5 Mean dive depth

Blue:

Table S15: Full output of the Wilcoxon rank-sum test for the mean dive depth in blue sharks.

```
wilcoxon rank sum test with continuity correction

data: mean_depth_daily by OMZ
W = 17254, p-value < 2.2e-16
alternative hypothesis: true location shift is not equal to 0
```

Mako:

Table S16: Full output of the Wilcoxon rank-sum test for the mean dive depth in mako sharks.

```
wilcoxon rank sum test with continuity correction

data: mean_depth_daily by OMZ
W = 21093, p-value = 5.008e-16
alternative hypothesis: true location shift is not equal to 0
```

8.2.6 Dive duration

Blue:

Table S17: Full output of the linear model for the dive duration with OMZ as a fixed effect and ID included to control for individual variability in blue sharks.

```
Linear mixed model fit by REML ['lmerMod']
Formula: mean_dive_duration ~ OMZ + (1 | ID)
Data: mean_duration_per_day

REML criterion at convergence: 1513.6

Scaled residuals:
    Min       1Q   Median       3Q      Max
-2.3482 -0.5844 -0.1584  0.3647  9.6828

Random effects:
Groups   Name             Variance Std.Dev.
ID       (Intercept)    0.3734    0.6110
Residual                  0.5089    0.7134
Number of obs: 682, groups: ID, 10

Fixed effects:
              Estimate Std. Error t value
(Intercept)  1.45202    0.21246   6.834
OMZout       0.04494    0.09530   0.472

Correlation of Fixed Effects:
      (Intr)
OMZout -0.366
```

Mako:

Table S18: Full output of the linear model for the dive duration with OMZ as a fixed effect and ID included to control for individual variability in mako sharks.

```
Linear mixed model fit by REML ['lmerMod']
Formula: mean_dive_duration ~ OMZ + (1 | ID)
Data: mean_duration_per_day

REML criterion at convergence: 3057.6

Scaled residuals:
    Min       1Q   Median       3Q      Max
-2.4087 -0.2757 -0.0699  0.0979  7.4075

Random effects:
Groups   Name             Variance Std.Dev.
ID       (Intercept)    4.814    2.194
Residual                  7.254    2.693
Number of obs: 628, groups: ID, 11

Fixed effects:
              Estimate Std. Error t value
(Intercept)   3.629    1.018   3.566
OMZout       -1.958    1.372  -1.427

Correlation of Fixed Effects:
      (Intr)
OMZout -0.742
```

8.2.7 Mean depth per step phase

Blue:

Table S19: Full output of the linear model for the mean depth per step phase with OMZ as a fixed effect, and ID and Day included to control for individual variability along the days in blue sharks.

```
Linear mixed model fit by REML. t-tests use Satterthwaite's
method [lmerModLmerTest]
Formula: mean_depth ~ OMZ + step_phase + (1 | ID) + (1 | Day)
Data: mean_depth_per_phase

REML criterion at convergence: 22745

Scaled residuals:
    Min       1Q   Median       3Q      Max
-2.9506 -0.6074 -0.1049  0.5079  6.1635

Random effects:
Groups   Name             Variance Std.Dev.
Day      (Intercept) 1399      37.41
ID       (Intercept) 1768      42.05
Residual                 3882      62.30
Number of obs: 2012, groups: Day, 406; ID, 10

Fixed effects:
              Estimate Std. Error    df t value Pr(>|t|)
(Intercept)  148.353    14.819   11.412  10.011  5.4e-07 ***
OMZout        55.485     6.472 1533.485   8.573  < 2e-16 ***
step_phaseD -118.166     3.385 1533.444 -34.904  < 2e-16 ***
step_phaseL   13.156     3.420 1539.366   3.847  0.000124 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
              (Intr) OMZout stp_pD
OMZout       -0.359
step_phaseD  -0.115  0.000
step_phaseL  -0.114  0.003  0.496
```

Table S20: Full output of estimated marginal means for the mean depth in blue sharks, comparing OMZ conditions across step phases.

```
> emmeans(lmm, pairwise ~ OMZ | step_phase)
$emmeans
step_phase = A:
OMZ emmean SE df lower.CL upper.CL
in 148.4 14.8 12.40 116.13 180.6
out 203.8 13.9 9.62 172.73 234.9

step_phase = D:
OMZ emmean SE df lower.CL upper.CL
in 30.2 14.8 12.40 -2.04 62.4
out 85.7 13.9 9.62 54.56 116.8

step_phase = L:
OMZ emmean SE df lower.CL upper.CL
in 161.5 14.8 12.42 129.28 193.7
out 217.0 13.9 9.65 185.88 248.1

Degrees-of-freedom method: kenward-roger
Confidence level used: 0.95

$constrasts
step_phase = A:
contrast estimate SE df t.ratio p.value
in - out -55.5 6.51 1608 -8.521 <.0001

step_phase = D:
contrast estimate SE df t.ratio p.value
in - out -55.5 6.51 1608 -8.521 <.0001

step_phase = L:
contrast estimate SE df t.ratio p.value
in - out -55.5 6.51 1608 -8.521 <.0001

Degrees-of-freedom method: kenward-roger
```

Mako:

Table S21: Full output of the linear model for the mean depth per step phase with OMZ as a fixed effect, and ID and Day included to control for individual variability along the days in mako sharks.

```
> summary(lmm)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: mean_depth ~ OMZ + step_phase + (1 | ID) + (1 | Day)
Data: mean_depth_per_phase

REML criterion at convergence: 21097

Scaled residuals:
    Min       1Q   Median       3Q      Max
-3.4132 -0.5560 -0.0735  0.4628  6.7458

Random effects:
 Groups Name Variance Std.Dev.
 Day (Intercept) 2259.9 47.54
 ID (Intercept) 170.3 13.05
 Residual 4084.0 63.91
Number of obs: 1847, groups: Day, 443; ID, 11

Fixed effects:
              Estimate Std. Error      df t value Pr(>|t|)
(Intercept) 138.285      8.879    15.310 15.574 8.43e-11 ***
OMZout       39.025     10.834     9.958  3.602 0.00486 **
step_phaseD -114.325     3.600 1344.040 -31.760 < 2e-16 ***
step_phaseL -30.841      3.683 1356.849 -8.374 < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
      (Intr) OMZout stp_pD
OMZout -0.775
step_phaseD -0.203 0.000
step_phaseL -0.199 0.002 0.489
```

Table S22: Full output of estimated marginal means for the mean depth in mako sharks, comparing OMZ conditions across step phases.

```
> emmeans(lmm, pairwise ~ OMZ | step_phase)
$emmeans
step_phase = A:
  OMZ emmean   SE    df lower.CL upper.CL
in    138 8.93 21.6   119.74   156.8
out   177 6.92 10.7   162.03   192.6

step_phase = D:
  OMZ emmean   SE    df lower.CL upper.CL
in    24 8.93 21.5    5.41    42.5
out   63 6.92 10.7   47.71    78.3

step_phase = L:
  OMZ emmean   SE    df lower.CL upper.CL
in   107 8.96 21.9   88.85   126.0
out  146 6.97 11.0  131.13   161.8

Degrees-of-freedom method: kenward-roger
Confidence level used: 0.95

$constrasts
step_phase = A:
  contrast estimate    SE df t.ratio p.value
in - out      -39 10.9 14  -3.575  0.0030

step_phase = D:
  contrast estimate    SE df t.ratio p.value
in - out      -39 10.9 14  -3.575  0.0030

step_phase = L:
  contrast estimate    SE df t.ratio p.value
in - out      -39 10.9 14  -3.575  0.0030

Degrees-of-freedom method: kenward-roger
```

8.2.8 Step phase duration

Blue:

Table S23: Full output of the linear model for the step phase duration with OMZ as a fixed effect, and ID and Day included to control for individual variability along the days in blue sharks.

```
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: step_phase_duration ~ OMZ + step_phase + (1 | ID) + (1 | Day)
Data: BlueTbl_steps_wiggles

REML criterion at convergence: 439889.9

Scaled residuals:
    Min       1Q   Median       3Q      Max
-1.4549 -0.6309 -0.2434  0.3775 10.3035

Random effects:
 Groups   Name      Variance Std.Dev.
 Day      (Intercept) 5163     71.86
 ID       (Intercept) 40557    201.39
 Residual                    457689  676.53
Number of obs: 27701, groups: Day, 406; ID, 10

Fixed effects:
              Estimate Std. Error      df t value Pr(>|t|)
(Intercept)   903.370     66.331    9.867  13.619 1.01e-07 ***
OMZout         97.595     16.401  1223.373   5.951 3.48e-09 ***
step_phased   -34.902      9.774  27413.150  -3.571 0.000356 ***
step_phasel  -439.792     10.171  27689.719 -43.238 < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
              (Intr) OMZout stp_pD
OMZout       -0.199
step_phased  -0.075  0.006
step_phasel  -0.078  0.017  0.480
```

Table S24: Full output of estimated marginal means for the step phase duration in blue sharks, comparing OMZ conditions.

```
$emmeans
step_phase = A:
OMZ emmean SE df asymp.LCL asymp.UCL
in   903 66.3 Inf      773      1033
out  1001 65.1 Inf      873      1129

step_phase = D:
OMZ emmean SE df asymp.LCL asymp.UCL
in   868 66.3 Inf      738      998
out  966 65.1 Inf      838     1094

step_phase = L:
OMZ emmean SE df asymp.LCL asymp.UCL
in   464 66.3 Inf      334      594
out  561 65.1 Inf      434      689

Degrees-of-freedom method: asymptotic
Confidence level used: 0.95

$contrasts
step_phase = A:
contrast estimate SE df z.ratio p.value
in - out    -97.6 16.4 Inf  -5.951 <.0001

step_phase = D:
contrast estimate SE df z.ratio p.value
in - out    -97.6 16.4 Inf  -5.951 <.0001

step_phase = L:
contrast estimate SE df z.ratio p.value
in - out    -97.6 16.4 Inf  -5.951 <.0001

Degrees-of-freedom method: asymptotic
```

Mako:

Table S25: Full output of the linear model for the step phase duration with OMZ as a fixed effect, and ID and Day included to control for individual variability along the days in mako sharks.

```
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: step_phase_duration ~ OMZ + step_phase + (1 | ID) + (1 | Day)
Data: BlueTbl_steps_wiggles

REML criterion at convergence: 322010.7

Scaled residuals:
    Min       1Q   Median       3Q      Max
-1.8961 -0.5197 -0.2189  0.2754 10.4277

Random effects:
Groups   Name             Variance Std.Dev.
Day      (Intercept)    16313    127.7
ID       (Intercept)    14162    119.0
Residual                    448943  670.0
Number of obs: 20290, groups: Day, 443; ID, 11

Fixed effects:
              Estimate Std. Error      df t value Pr(>|t|)
(Intercept)   917.97      58.45     9.10  15.704 6.69e-08 ***
OMZout         71.29      77.22     8.35   0.923  0.382
step_phaseD   -220.01     12.20 19906.19 -18.028 < 2e-16 ***
step_phaseL   -402.11     11.50 20252.64 -34.954 < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
              (Intr) OMZout stp_pD
OMZout      -0.746
step_phaseD -0.103  0.002
step_phaseL -0.111  0.007  0.516
```

Table S26: Full output of estimated marginal means for the step phase duration in mako sharks, comparing OMZ conditions.

```
$emmeans
step_phase = A:
  OMZ emmean SE df asymp.LCL asymp.UCL
in   918 58.5 Inf      803      1033
out  989 51.4 Inf      888      1090

step_phase = D:
  OMZ emmean SE df asymp.LCL asymp.UCL
in   698 58.5 Inf      583      813
out  769 51.5 Inf      668      870

step_phase = L:
  OMZ emmean SE df asymp.LCL asymp.UCL
in   516 58.3 Inf      402      630
out  587 51.4 Inf      486      688

Degrees-of-freedom method: asymptotic
Confidence level used: 0.95

$contrasts
step_phase = A:
  contrast estimate SE df z.ratio p.value
in - out    -71.3 77.2 Inf  -0.923  0.3559

step_phase = D:
  contrast estimate SE df z.ratio p.value
in - out    -71.3 77.2 Inf  -0.923  0.3559

step_phase = L:
  contrast estimate SE df z.ratio p.value
in - out    -71.3 77.2 Inf  -0.923  0.3559

Degrees-of-freedom method: asymptotic
```

8.2.9 Vertical speed per step phases

Blue:

Table S27: Full output of the linear model for the vertical speed per step phases (Ascent and Descent) with OMZ as a fixed effect, and ID and Day included to control for individual variability along the days in blue sharks.

```
> summary(lmm_speed)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: mean_step_phase_speed ~ OMZ + step_phase + (1 | ID) + (1 | Day)
Data: speed_data

REML criterion at convergence: -3595.9

Scaled residuals:
    Min       1Q   Median       3Q      Max
-2.2120 -0.4568 -0.1165  0.2646  8.8667

Random effects:
 Groups   Name                Variance Std.Dev.
 Day      (Intercept)  0.0015102  0.03886
 ID       (Intercept)  0.0009964  0.03157
 Residual                    0.0029978  0.05475
Number of obs: 1356, groups: Day, 406; ID, 10

Fixed effects:
              Estimate Std. Error      df t value Pr(>|t|)
(Intercept)  8.433e-02  1.201e-02  1.576e+01  7.021 3.14e-06 ***
OMZout       3.776e-02  6.828e-03  1.111e+03  5.530 4.00e-08 ***
step_phaseD  1.951e-02  2.976e-03  8.365e+02  6.557 9.59e-11 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
              (Intr) OMZout
OMZout      -0.466
step_phaseD -0.124  0.000
```

Table S28: Full output of estimated marginal means for the vertical speed per step phases (Ascent and Descent) in blue sharks, comparing OMZ conditions.

```
> emm_speed$emmeans # Estimated means
step_phase = A:
  OMZ emmean    SE      df lower.CL upper.CL
in   0.0843 0.0121 15.12   0.0586   0.110
out  0.1221 0.0107  9.81   0.0981   0.146

step_phase = D:
  OMZ emmean    SE      df lower.CL upper.CL
in   0.1038 0.0121 15.11   0.0782   0.130
out  0.1416 0.0107  9.81   0.1177   0.166

Degrees-of-freedom method: kenward-roger
Confidence level used: 0.95
> emm_speed$contrasts # Differences in - out
step_phase = A:
contrast estimate      SE      df t.ratio p.value
in - out   -0.0378 0.0069 1132   -5.472  <.0001

step_phase = D:
contrast estimate      SE      df t.ratio p.value
in - out   -0.0378 0.0069 1132   -5.472  <.0001

Degrees-of-freedom method: kenward-roger
```

Mako:

Table S29: Full output of the linear model for the vertical speed per step phases (Ascent and Descent) with OMZ as a fixed effect, and ID and Day included to control for individual variability along the days in mako sharks.

```
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: mean_step_phase_speed ~ OMZ + step_phase + (1 | ID) + (1 | Day)
Data: speed_data

REML criterion at convergence: -3214.3

Scaled residuals:
    Min       1Q   Median       3Q      Max
-1.7221 -0.6094 -0.1429  0.3943  8.7394

Random effects:
Groups   Name             Variance Std.Dev.
Day      (Intercept)  0.0007915  0.02813
ID       (Intercept)  0.0008433  0.02904
Residual                    0.0037576  0.06130
Number of obs: 1262, groups: Day, 443; ID, 11

Fixed effects:
              Estimate Std. Error      df t value Pr(>|t|)
(Intercept)  7.545e-02  1.420e-02  1.021e+01   5.314  0.000318 ***
OMZout       3.875e-02  1.883e-02  9.307e+00   2.059  0.068597 .
step_phaseD  3.405e-02  3.453e-03  7.791e+02   9.863 < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
      (Intr) OMZout
OMZout      -0.743
step_phaseD -0.122  0.000
```

Table S30: Full output of estimated marginal means for the vertical speed per step phases (Ascent and Descent) in mako sharks, comparing OMZ conditions.

```
> emm_speed$emmeans # Estimated means
step_phase = A:
OMZ emmean      SE      df lower.CL upper.CL
in  0.0755 0.0142 10.27   0.0439   0.107
out 0.1142 0.0126  9.01   0.0856   0.143

step_phase = D:
OMZ emmean      SE      df lower.CL upper.CL
in  0.1095 0.0142 10.27   0.0779   0.141
out 0.1483 0.0126  9.01   0.1197   0.177

Degrees-of-freedom method: kenward-roger
Confidence level used: 0.95
> emm_speed$contrasts # Differences in - out
step_phase = A:
contrast estimate      SE      df t.ratio p.value
in - out  -0.0388 0.0189  9.37   -2.054  0.0690

step_phase = D:
contrast estimate      SE      df t.ratio p.value
in - out  -0.0388 0.0189  9.37   -2.054  0.0690

Degrees-of-freedom method: kenward-roger
```

8.2.10 Proportion of time in level

Blue:

Table S31: Full output of the linear model for the proportion of time in level with OMZ as a fixed effect, and ID and Day included to control for individual variability along the days in blue sharks.

```
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: level_prop_logit ~ OMZ + (1 | ID) + (1 | day_bin)
Data: level_daily_tbl

REML criterion at convergence: 2328.3

Scaled residuals:
    Min       1Q   Median       3Q      Max
-4.5192 -0.2175  0.1481  0.5055  2.2308

Random effects:
Groups   Name             Variance Std.Dev.
day_bin  (Intercept)  0.0601    0.2452
ID        (Intercept)  0.2539    0.5039
Residual                    1.6601    1.2884
Number of obs: 682, groups: day_bin, 406; ID, 10

Fixed effects:
              Estimate Std. Error    df t value Pr(>|t|)
(Intercept)  -1.2718     0.2215  18.5420  -5.741 1.72e-05 ***
OMZout       -0.2456     0.1705  419.7600  -1.441  0.15
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
      (Intr)
OMZout -0.620
```

Mako:

Table S32: Full output of the linear model for the proportion of time in level with OMZ as a fixed effect, and Day included to control for variability along the days in mako sharks.

```
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: level_prop_logit ~ OMZ + (1 | ID)
Data: level_daily_tbl

REML criterion at convergence: 2513.4

Scaled residuals:
    Min       1Q   Median       3Q      Max
-3.4710 -0.1411  0.2393  0.5514  1.6104

Random effects:
Groups   Name             Variance Std.Dev.
ID        (Intercept)  0.2817    0.5307
Residual                    2.9803    1.7264
Number of obs: 635, groups: ID, 11

Fixed effects:
              Estimate Std. Error    df t value Pr(>|t|)
(Intercept)  -1.0683     0.2853  10.5455  -3.744  0.00348 **
OMZout       -0.5565     0.3743   9.1215  -1.487  0.17083
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
      (Intr)
OMZout -0.762
```

8.2.11 Proportion of level phases

Blue:

Table S33: Full output of the linear model for the proportion of level phases with OMZ as a fixed effect, and ID and Day included to control for individual variability along the days in blue sharks.

```
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: prop_level_logit ~ OMZ + (1 | ID) + (1 | day_bin)
Data: step_props_daily

REML criterion at convergence: 2240.8

Scaled residuals:
    Min       1Q   Median       3Q      Max
-4.9359 -0.1222  0.1696  0.4443  1.6088

Random effects:
 Groups   Name      Variance Std.Dev.
 day_bin  (Intercept) 0.1358   0.3685
 ID       (Intercept) 0.1271   0.3566
 Residual                1.3913   1.1795
Number of obs: 682, groups: day_bin, 406; ID, 10

Fixed effects:
              Estimate Std. Error    df t value Pr(>|t|)
(Intercept)  -0.8119     0.1806  26.0441  -4.497 0.000127 ***
OMZout       -0.3076     0.1574 291.8650  -1.954 0.051657 .
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
      (Intr)
OMZout -0.700
```

Table S34: Full output of the linear model for the proportion of level phases with OMZ as a fixed effect, and ID included to control for individual variability in blue sharks.

```
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: prop_level_logit ~ OMZ + (1 | ID)
Data: step_props_daily

REML criterion at convergence: 2244

Scaled residuals:
    Min       1Q   Median       3Q      Max
-5.0558 -0.1050  0.1944  0.4484  1.3805

Random effects:
 Groups   Name      Variance Std.Dev.
 ID       (Intercept) 0.1249   0.3534
 Residual                1.5281   1.2362
Number of obs: 682, groups: ID, 10

Fixed effects:
              Estimate Std. Error    df t value Pr(>|t|)
(Intercept)  -0.7947     0.1778  25.2352  -4.47 0.000144 ***
OMZout       -0.3243     0.1551 306.4415  -2.09 0.037408 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
      (Intr)
OMZout -0.698
```

Mako:

Table S35: Full output of the linear model for the proportion of level phases with OMZ as a fixed effect, and ID and Day included to control for individual variability along the days in blue sharks.

```
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: prop_level_logit ~ OMZ + (1 | ID) + (1 | day_bin)
Data: step_props_daily

REML criterion at convergence: 2524.7

Scaled residuals:
    Min       1Q   Median       3Q      Max
-3.4054  0.0010  0.2628  0.4675  1.4683

Random effects:
 Groups   Name      Variance Std.Dev.
 day_bin  (Intercept) 0.0000   0.0000
 ID       (Intercept) 0.2056   0.4534
 Residual                    3.0445   1.7449
Number of obs: 635, groups:  day_bin, 443; ID, 11

Fixed effects:
              Estimate Std. Error    df t value Pr(>|t|)
(Intercept)  -0.9483     0.2565   9.8695  -3.698  0.00422 **
OMZOut       -0.2942     0.3331   8.1961  -0.883  0.40234
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
      (Intr)
OMZOut -0.770
optimizer (nloptwrap) convergence code: 0 (OK)
boundary (singular) fit: see help('isSingular')
```

8.2.12 Depth of level phases

Blue:

Table S36: Full output of the linear model for the depth of level phases with OMZ as a fixed effect, and Day included to control for variability along the days in blue sharks.

```
Linear mixed model fit by REML. t-tests use
Satterthwaite's method [lmerModLmerTest]
Formula: mean_depth ~ OMZ + (1 | ID)
Data: level_depth_daily

REML criterion at convergence: 7605.3

Scaled residuals:
    Min       1Q   Median       3Q      Max
-2.8385 -0.6363 -0.0574  0.5077  5.8770

Random effects:
Groups   Name              Variance Std.Dev.
ID       (Intercept)      3132      55.96
Residual                    6189      78.67
Number of obs: 656, groups: ID, 10

Fixed effects:
              Estimate Std. Error    df t value
(Intercept)   152.08      20.21  12.72  7.525
OMZout         68.13      10.58  640.78  6.438
              Pr(>|t|)
(Intercept) 4.95e-06 ***
OMZout      2.37e-10 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
      (Intr)
OMZout -0.425
```

Mako:

Table S37: Full output of the linear model for the depth of level phases with OMZ as a fixed effect, and ID and Day included to control for individual variability along the days in mako sharks.

```
Linear mixed model fit by REML. t-tests use Satterthwaite's method [lmerModLmerTest]
Formula: mean_depth ~ OMZ + (1 | ID) + (1 | day_bin)
Data: level_depth_daily

REML criterion at convergence: 6714

Scaled residuals:
    Min       1Q   Median       3Q      Max
-1.8061 -0.5446 -0.1413  0.3890  5.4155

Random effects:
Groups   Name              Variance Std.Dev.
day_bin  (Intercept)      1401.1    37.43
ID       (Intercept)      936.8     30.61
Residual                    4305.4    65.62
Number of obs: 585, groups: day_bin, 420; ID, 11

Fixed effects:
              Estimate Std. Error    df t value Pr(>|t|)
(Intercept)   101.240     15.860  10.665   6.384 5.98e-05 ***
OMZout         47.320     20.947   9.477   2.259  0.0488 *
              Pr(>|t|)
(Intercept) 5.98e-05 ***
OMZout      0.0488 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
      (Intr)
OMZout -0.757
```

8.2.13 Depth difference between consecutive level phases

Blue shark:

Table S38: Full output of the linear model for the depth difference between consecutive level phases with OMZ as a fixed effect, and ID and Day included to control for variability along the days in blue sharks.

```
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: abs_diff ~ OMZ + (1 | day_bin) + (1 | ID)
Data: levels_tbl_daily_mean

REML criterion at convergence: 6411

Scaled residuals:
    Min       1Q   Median       3Q      Max
-0.8946 -0.3187 -0.1474  0.0459 14.3352

Random effects:
Groups   Name              Variance Std.Dev.
day_bin  (Intercept)        7.795    2.792
ID       (Intercept)    104.416   10.218
Residual                    1709.392  41.345
Number of obs: 623, groups: day_bin, 388; ID, 10

Fixed effects:
              Estimate Std. Error    df t value Pr(>|t|)
(Intercept)    3.629      5.725   27.486   0.634  0.53137
OMZOut         17.652      5.327  198.631   3.314  0.00109 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
      (Intr)
OMZOut -0.743
```

Table S39: Full output of estimated marginal means for the depth difference between consecutive level phases in blue sharks, comparing OMZ conditions.

```
> emm_abs <- emmeans(lmm_abs, ~ OMZ)
> emm_abs
  OMZ emmean    SE    df lower.CL upper.CL
In   3.63  5.89 24.17  -8.53    15.8
Out  21.28  4.03  9.01  12.17    30.4

Degrees-of-freedom method: kenward-roger
Confidence level used: 0.95
> contrast(emm_abs, "revpairwise")
contrast estimate    SE    df t.ratio p.value
Out - In      17.7  5.56 179    3.175  0.0018

Degrees-of-freedom method: kenward-roger
```

Mako shark:

Table S40: Full output of the linear model for the depth difference between consecutive level phases with OMZ as a fixed effect, and ID and Day included to control for variability along the days in mako sharks.

```
> summary(lmm_abs)
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: abs_diff ~ OMZ + (1 | day_bin) + (1 | ID)
Data: levels_tbl_daily_mean

REML criterion at convergence: 5817.2

Scaled residuals:
    Min       1Q   Median       3Q      Max
-3.3664 -0.1147 -0.0492  0.0800  3.6379

Random effects:
 Groups   Name                Variance Std.Dev.
 day_bin  (Intercept)         4902.43   70.017
 ID       (Intercept)          22.96    4.792
 Residual                    409.06   20.225
Number of obs: 535, groups: day_bin, 392; ID, 11

Fixed effects:
              Estimate Std. Error      df t value Pr(>|t|)
(Intercept)    8.511      8.254 179.939   1.031  0.3038
OMZOut         21.369      9.498 116.118   2.250  0.0263 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
      (Intr)
OMZOut -0.869
```

Table S41: Full output of estimated marginal means for the depth difference between consecutive level phases in mako sharks, comparing OMZ conditions.

```
> emm_abs <- emmeans(lmm_abs, ~ OMZ)
> emm_abs
OMZ emmean SE      df lower.CL upper.CL
In   8.51 8.28 172.3   -7.83    24.9
Out  29.88 4.74  36.4   20.28    39.5

Degrees-of-freedom method: kenward-roger
Confidence level used: 0.95
> contrast(emm_abs, "revpairwise")
contrast estimate SE  df t.ratio p.value
Out - In      21.4 9.54 108   2.240  0.0271

Degrees-of-freedom method: kenward-roger
```