U.PORTO

MESTRADO EM CIÊNCIAS DO MAR - RECURSOS MARINHOS

RAMO DE AQUACULTURA E PESCAS

Short-term swimming behaviour and metabolic performance of blue sharks under environmental gradients in the Azores

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2023

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INSTITUTO DE CIÊNCIAS BIOMÉDICAS ABEL SALAZAR

M.ICBAS 2023

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Dissertation in Aquaculture/Fisheries of the master's degree in Marine Sciences - Marine Resources submitted to the Institute of Biomedical Sciences of Abel Salazar of the University of Porto.

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Agradecimentos

Primeiramente ao meu orientador, Nuno Queiroz, obrigada por me dar a chance de realizar o meu grande sonho de estudar tubarões, pelas inúmeras oportunidades, confiança de sempre e pelos ensinamentos durante esses 5 anos.

Ao MOVE team e em especial, ao Ivo da Costa e Marisa Vedor. Obrigada pela troca, ajuda e aprendizados. Aos amigos que o MOVE me trouxe, Bruno Saraiva, Diogo Costa, Matthieu Bekaert, Sofía Hernández, Sophie Prendergast e Paola Gabasa. Obrigada pela força, carinho, incentivo, momentos felizes no Porto e aos bons encontros nos Açores.

Aos amigos que o Porto e os Açores me trouxeram. Obrigada por tanto. Em especial a Livia, Luna e Marcinho pelo apoio e acolhimento nessa reta final.

Aos amigos no Brasil. Obrigada por todo apoio e amor mesmo a um oceano de distância. Em especial a Carol e Bruna, pela escuta atenta e por não soltarem a minha mão.

A minha família em Portugal, Bia, André, Elaine, Ramalho, Pepe, Jojo e Teteu. Vocês são parte de mim. Grata pelos bons ventos terem nos unido nessa vida.

A minha família e irmãos. Obrigada por todo amor e suporte. Em especial a minha avó Berenice, sua fé me fez mais forte.

A Virginia Poitevin, obrigada por ser família quando mais precisei. Ao Pinta, obrigada por todo o amor e companheirismo.

Ao meu afilhado Antonio. Estar do seu lado no Brasil nessa reta final era o que eu precisava para seguir. A vida é bem melhor com você por perto.

Ao meu namorado e melhor amigo, Lucas Natal. Meu refúgio em mar revolto. Obrigada por todo amor, ajuda, e por me trazer toda a calma que por vezes faltava. Obrigada por me relembrar da minha força quando achava que já não a tinha.

A minha mãe que é o meu porto, Norte e abrigo. Obrigada por me permitir sonhar os meus sonhos de hoje, embarcar ao meu lado nas minhas aventuras, orientar a minha rota e acreditar em mim. Tudo isso é mérito seu. Sem você eu nada seria.

Declaração de honra

Declaro que a presente dissertação de Mestrado em Ciências do Mar – Recursos Marinhos com ênfase em Aquacultura e Pescas "Short-term swimming behaviour and metabolic costs of blue sharks under environmental gradients in the Azores" 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 de atribuição, e encontram-se devidamente indicadas no texto e nas referências bibliográficas, de acordo com as normas de referênciação. Tenho consciência de que a prática de plágio e auto-plágio constitui um ilícito acadêmico.

Porto, 30 de outubro de 2023.

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Resumo

As mudanças climáticas podem ter consequências dramáticas para os ecossistemas e animais marinhos, reduzindo e restringindo o habitat disponível para peixes pelágicos tropicais, como tubarões, levando ao declínio das populações. Os tubarões são uma das maiores linhagens de predadores do planeta que desempenham um papel funcional significativo na regulação de cima para baixo dos oceanos. Assim, biologgers avançados de alta resolução tornaram possível rastrear seu uso espacial e comportamento, fornecendo dados cruciais sobre as preferências de habitat de espécies ameaçadas, importantes para conservação e manejo. Os principais tópicos da ecologia do movimento marinho permanecem sem solução, apesar dos desenvolvimentos tecnológicos significativos ao longo dos anos. Por exemplo, os mecanismos fisiológicos e como as mudanças na temperatura e no oxigênio dissolvido (OD) influenciam o movimento e a distribuição dos predadores marinhos não são amplamente conhecidos. Esta proposta visa abordar essas questões associando o comportamento de natação em escala fina e os custos metabólicos com movimentos de forrageamento de tubarões azuis (*Prionace glauca*), a espécie de tubarão mais explorada globalmente pela pesca pelágica com palangre, sob parâmetros ambientais. Biologgers foram implantados em 11 tubarões azuis por períodos de até 24 e 48 horas. Os tubarões experimentaram uma profundidade média de 145.5 m, atingindo uma ampla gama de profundidades (<669,3 m) com movimentos oscilatórios. Uma temperatura média geral da água de 17,2 ºC com uma variação de 10.3–22.8 ºC. OD médio foi de 234.6 µmol/l com variação de 185.2–271.9 µmol/l. Sensores triaxiais permitiram o cálculo de formas de mergulho e energia de natação para esta espécie. Classificamos os mergulhos em cinco categorias com base no formato do perfil de mergulho bidimensional, predominando os mergulhos em forma de U e V (~70%). Os eventos de natação intensa em nossos resultados sugeriram que os tubarões azuis selecionam estratégias de natação que maximizam seu excedente de energia enquanto procuram alimentos. Os indivíduos oscilaram continuamente na coluna d'água, com a maioria exibindo comportamento de mergulho regular com preferência pela camada superficial. Dada a sua suscetibilidade à exploração pesqueira, o aumento do conhecimento dos padrões de movimento não apenas ajuda nos esforços de conservação, mas também aumenta a conscientização sobre as questões levantadas pelas ameaças das mudanças climáticas (ou seja,

aquecimento do oceano e desoxigenação) na futura sustentabilidade das populações de tubarões ameaçadas.

PALAVRAS-CHAVE: Tubarões, Predadores marinhos, Comportamento em fina escala, Gasto energético, Mudanças climáticas, Pesca.

Abstract

Ongoing climate change may have dramatic consequences for ecosystems and marine animals, reducing and constricting available habitat for tropical pelagic fishes such as sharks, leading to population declines. Sharks are one of the lineages of predators on the planet that play a significant functional role in the top-down regulation of the oceans. Thus, advanced high-resolution biologgers made possible to track their spatial-use and behaviour, providing crucial data on threatened species habitat preferences, important for conservation and management. Major topics in marine movement ecology remain unresolved despite significant technological developments over the years. For example, physiological mechanisms and how changes in temperature and oxygen influence the movement and distribution of marine predators are not widely known. This proposal aims to address these questions by associating fine-scale swimming behaviour and metabolic costs with foraging movements of blue sharks (*Prionace glauca*), the most exploited shark species globally by pelagic longline fisheries, under environmental parameters. Biologging tags were deployed on 11 blue sharks for periods of up to 24 and 48 hours. Sharks experienced a mean depth of 145.5 m, reaching a wide range of depths (<669.3 m) with up and down movements. An overall mean water temperature of 17.2 ºC with a range of 10.3–22.8 ºC. The mean DO was 234.6 µmol/l with a range of 185.2–271.9 µmol/l. Tri-axial sensors enabled the calculation of dive shapes and swimming energetics for this species. We classified the dives into five major categories based on the shape of the two-dimensional dive profile, with U- and V-shaped dives predominating (~70%). The burst swimming events in our results suggested blue sharks select swimming strategies that maximize their energy surplus while foraging. The individuals oscillated continually through the water column, with most of them exhibiting regular diving behaviour with a preference for the surface layer. Given sharks' susceptibility to fishing exploitation, increased knowledge of movement patterns not only helps conservation efforts but also enhances awareness of the issues raised by climate change threats (i.e., ocean warming and deoxygenation) in the future sustainability of threatened shark populations.

KEYWORDS: Sharks, Marine predators, Fine-scale behaviour, Energy expenditure, Climate change, Fisheries.

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List of Abbreviations

ARGOS - Advanced Research and Global Observation Satellite

DO - Dissolved Oxygen

DSL - Deep Scattering Layer

DVM - Diel Vertical Migration

GPS - Global Positioning System

ICCAT - International Commission for the Conservation of Atlantic Tunas

IUCN - International Union for Conservation of Nature

MPAs - Marine Protected Areas

NOAA - National Oceanic and Atmospheric Administration

ODBA – Overall Dynamic Acceleration

OMZ - Oxygen Minimum Zone

PLA - Polylactic Acid

PTT - Platform Transmitter Terminal

PSAT - Pop-up Satellite Archival Tags

SSL – Sound Scattering Layer

SST – Sea Surface Temperature

TBF – Tailbeat Frequency

Introduction

Sharks: an overview

As apex predators, sharks can play a key role in the functioning of marine ecosystems, contributing significantly to the top-down control of the ocean (Sims and Quayle 1998; Cortés, 2000; Myers et al. 2007; Ferretti et al., 2010; Sims, 2010; Dulvy et al., 2014). According to their evolutionary history, the Chondrichthyans have existed for at least 420 million years and are among the oldest and most ecologically complex vertebrate groups (Compagno, 1990). Regarding sharks, they are one of the most diverse lineages of predators on the planet, coping with a wide range of selective pressures while occupying a wide range of marine niches and habitats (Compagno, 1990). In addition to providing higher trophic-level indicators of ocean ecosystem condition, they are crucial living resources for human communities across the world in terms of cultural, economic, health, biodiversity, and conservation (Sims and Quayle 1998; Myers et al., 2007; Sims, 2010). However, sharks have relatively low resilience to overexploitation, being inherently susceptible to human threats (e.g., overfishing) and climate change, due to their slow growth rates, late sexual maturity, and low fecundity (Dulvy et al., 2014; Queiroz et al., 2016; Sims, 2010).

Over the last 50 years, global elasmobranch populations have declined substantially (Baum et al., 2003; Burgess et al., 2005; Myers et al., 2007; Dulvy et al., 2014; Williamson et al., 2019). The International Union for Conservation of Nature (IUCN) Red List of Threatened Species includes several pelagic sharks (Sims, 2010; Dulvy et al., 2021). In the first worldwide assessment, it was predicted that 25% of sharks were threatened with extinction classified as critically endangered, endangered, or vulnerable (Dulvy et al., 2021). Global shark catches reached an estimated peak of 63-273 million individuals per year in the early 2000s, including reported and unreported landings, discards, and shark finning (Worm et al., 2013), before declining as a result of overfishing (Dulvy et al., 2014; Dulvy et al., 2021). These "boom-and-bust catch patterns" and the expanding global shark fin trade were the drivers for the first significant status warnings (Brander, 1981; Manire and Gruber, 1990; Dulvy et al., 2021). Although sharks are now highly threatened due to fishing pressure, little is known about how they may respond to climate change (Osgood et al., 2021). Given this scenario, there is a significant population reduction worldwide with some species

now having just a fraction of their historical biomass (Baum et al., 2003; Sims, 2010).

Blue shark (*Prionace glauca*)

The blue shark, *Prionace glauca* (Linnaeus, 1758), belongs to the Carcharhinidae family and it is the ocean's widest ranging shark (Compagno, 1984; Queiroz et al., 2005), inhabiting oceanic and circumglobal seas both in temperate and tropical waters from about 60ºN to 50ºS latitude (Stevens, 1990; Queiroz et al., 2005; Nakano & Stevens, 2008) from the surface down to over 1600 m depth (Vandeperre et al., 2014; Queiroz et al., 2017; Queiroz et al., 2019). It is an easily distinguishable shark with a characteristic indigo blue dorsal coloring, metallic blue flanks and very long pectoral fins, as well as a slim large body (>300 m TL) and white undersides (Nakano and Stevens, 2008). In comparison to other pelagic sharks, *P. glauca* has a very productive life history strategy that includes rapid growth rate and a large number of smaller offspring (Cortés, 2000; Frisk et al., 2001; Aires-da-Silva and Gallucci, 2007; Nakano and Stevens, 2008; Vandeperre et al., 2014). At the age of 5-6 years, males and females reaches sexual maturity at roughly 183 cm FL and 180-185 cm FL, respectively (Pratt, 1979; Castro and Mejuto, 1995; Nakano and Stevens, 2008; Vandeperre et al., 2014). The females are placental viviparous with typical litter sizes of 37 pups (Pratt, 1979; Castro and Mejuto, 1995; Nakano and Seki, 2003), may give birth to up to 82 pups (Nakano and Stevens, 2008). Because of its high fecundity rates, the blue shark is thought to be more resilient to exploitation than other shark species but, despite repeated assurances to the contrary, Hutchings et al. (2012) proved that fecundity is not a strong predictor of extinction and other studies that looked into this assumption questioned the idea that blue shark populations could withstand high harvest rates (West et al., 2004; Aires-da-Silva and Gallucci, 2007; Vandeperre et al., 2016).

A recent research (Harding et al., 2021) confronted the concept that endothermic fish with efficient heat exchangers in muscles, such as tunas and lamnid sharks, had larger thermal niches than ectotherms (Carey and Gibson 1987, Watanabe et al., 2021). This is well represented by blue sharks that, despite their ectothermic physiology, they have a wide thermal tolerance such as water temperatures ranging from 4˚C to 30˚C (Howey et al., 2017), but prefers a much narrower temperature range (Kohler et al., 2002; Queiroz et al., 2005) –

especially in the adult stage (Vandeperre et al., 2016) –, as well as having extended vertical niches, providing a great model for studying foraging-thermoregulation relations (Queiroz et al., 2005; Watanabe et al., 2021). Moreover, they dive to significant depths with the maximum recorded of 1706m (Vandeperre et al., 2014; Queiroz et al., 2017; Queiroz et al., 2019). Blue sharks are an oceanic, ram-feeding macropredator on a wide variety of prey, including bony fishes, cephalopods, and crustaceans (Markaida and Sosa-Nishizaki, 2010; Watanabe et al., 2021).

P.glauca is extremely migratory and capable of crossing several national boundaries and travelling long distances, including east-west and north-south trans-oceanic migrations (Kohler et al., 2002; Queiroz et al., 2012; Vandeperre et al., 2014, Verissimo et al., 2017). The blue shark is classified by the International Union for the Conservation of Nature (IUCN) Red List as Near Threatened globally, having a few catch restrictions all around the world (Vedor et al., 2021a). Moreover, it is the most exploited shark species globally by pelagic longline fisheries (Camhi et al., 2008; Queiroz et al., 2005; Oliver et al., 2015; Queiroz et al., 2016; Queiroz et al., 2019; Vedor et al., 2021a) and in the North Atlantic, constitutes up to 80% of the catches from Spain and Portugal traditionally directed at swordfish (Neves-dos-Santos et al., 2002; Mejuto et al., 2009; Vandeperre et al., 2016).

Climate change

Previous studies indicate ongoing climate change such as sea temperature warming and changing circulation associated with the hypoxia-inducing biological activity may reduce and constrict available habitat for tropical pelagic fishes (Fig. 1; Baum et al, 2003; Keeling et al., 2010; Queiroz et al., 2012; Gilly et al., 2013; Watson, 2016; Schmidtko et al., 2017; Breitburg et al., 2018; Levin, 2018; Laffoley and Baxter, 2019; Stramma and Schmidtko, 2019; Vedor et al., 2021). Due to anthropogenic greenhouse gases accumulation, the ocean is absorbing over 90% of the heat contained in our atmosphere, resulting in a predicted worldwide sea-surface temperature (SST) of up to ~5ºC by the end of the 21st century (IPCC, 2015; Birkmanis et al., 2020). These changes have a significant impact on the metabolism of marine ectotherms, once temperature regulates their distribution and fitness and may help to identify their optimal thermal niche (Payne et al., 2016a; Payne et al., 2018). In other words, their body temperature

simultaneously increases toward their upper thermal limits (Birkmanis et al., 2020). Except for lamnid mackerel sharks, most sharks are ectothermic and may be influenced by climate change (Bernal et al., 2012; Rosa et al., 2014, 2017; Syndeman et al., 2015; Pinsky et al., 2019; Birkmanis et al., 2020) with higher temperatures increasing their metabolism and oxygen consumption (Pistevos et al., 2015; Lawson et al., 2019; Birkmanis et al., 2020). Despite this, remains uncertain of how increasing temperatures will impact ectotherms sharks (Payne et al., 2016a). As the ocean temperature continues to rise due to climate change and warmer waters hold less soluble gas, it will lose yet more oxygen due to the direct effect of temperature on gas solubility (Laffoley and Baxter, 2019; Sims, 2019). As a result, once sharks are obligate water-breathers with comparatively high absolute oxygen demands, the ectotherms will present increased metabolic rates and will be less able to endure the effects of even moderate hypoxia associated with ocean deoxygenation (Payne et al., 2015; Sims, 2019).

Permanent oxygen minimum zones (OMZ) are globally distributed and are defined as areas where dissolved oxygen (DO) levels are 20–90 μmol O2 kg -1 (<0.47–2.11 ml O2 L-1) located in the depth range ~200–800 m (Gilly et al., 2013; Sims, 2019; Vedor et al, 2021). DO is critical for sustaining most marine animal life and it plays a key role in structuring marine ecosystems and controls the spatial and temporal distribution of all organisms (Gilly et al., 2013). Even though most species are expected to avoid hypoxic areas (Stramma et al., 2008), previous research has shown that top predators such as sharks, billfish, and tunas use surface waters within OMZs on a regular basis (Prince and Goodyear, 2006; Jorgensen et al., 2009; Nasby-Lucas et al., 2009; Stramma et al., 2012). This is explained by the aggregation of large numbers of sluggish mesopelagic prey in near-surface waters, which leads to more predator-prey interaction and, as a result, increased foraging opportunities for top pelagic predators (Koslow et al., 2011; Stewart et al., 2013). Thus, persistent hypoxia in warmer coastal waters is expected to cause shifts elasmobranch distributions as their available habitats will be compressed, aggregating them even more in surface waters increasing their vulnerability to overfishing (Gilly et al., 2013; Prince and Goodyear, 2006; Chan et al., 2008; Prince et al., 2010; Stramma et al., 2012; Deutsch et al., 2015; Sims, 2019).

Overfishing

Pelagic shark populations are declining below sustainable levels of a worldwide scale due to overfishing, representing an average of 52% of all the reported shark capture, from either shark-targeting fisheries or bycatch (Worm et al., 2013; Queiroz et al., 2019). Sharks are landed all over the world for their meat, fins, gill plates, and liver oil (Clarke et al., 2006; McClenachan et al., 2016) and there is a lack of international catch quotas, resulting in some species now at a fraction of their historical biomass (Baum et al., 2003; Block et al., 2005; Queiroz et al., 2012). Studies suggests that sharks spend much of the time in areas where pelagic longlining activities are often highest making them more susceptible to overexploitation that may threaten their sustainability, where recovery may be difficult or not be possible even if fishing pressure is removed (Queiroz et al., 2019; Vedor et al., 2021). Queiroz et al. (2019) evaluated how much longline fishing vessels overlapped with hotspots and reported an average of 24% worldwide. As a result, most high-seas fishing activities are nowadays focused on ecologically significant shark hotspots across the world. Some important commercially species such as the blue shark may have limited habitat use in the future due to the industrial longline fishing effort, since, with on average 76% of their space use is overlapping with longlines every month (Queiroz et al., 2019). Likewise, the blue shark represents ~90% of all reported pelagic shark catches in the Atlantic (Oliver et al., 2015), and its fins are the most frequently traded in international markets (Fields et al., 2018). Furthermore, reporting of catches remains poor and there is a lack of international catch quotas, resulting in uncertainties regarding the current state of blue shark stocks, mask their true population trajectories (Baum et al., 2003; Block et al., 2005; Queiroz et al., 2012; Campana, 2016; Vedor et al., 2021).

Shark movements

The sustainable management of shark populations demands a thorough understanding of their spatial ecology (Sims, 2010). Broader-scale patterns in distribution and population structure result from the outcome of different biotic and abiotic variables in response to environmental fluctuations (Sims and Quayle, 1998; Sims, 2010). Animals move to locate resource paths such as food, compatible mates and timing of courtship, nursery and spawning areas, hazardous conditions (i.e., avoiding predation) while minimizing movement and

energy expenditures (Queiroz et al., 2012; Prince et al., 2010; Abascal et al., 2011; Meese and Lowe, 2020), which consist of a trade-off between benefits and costs (Fahrig, 2007; Hussey et al., 2015). Mobile animals exhibit a range of movement patterns (i.e., search strategies) that establish populations and ecosystems, sustain ecological function, and ultimately decide global aquatic production once these daily movements provide bottom-up effects through the transport nutrients into reef ecosystems from pelagic environments and dynamic energy through different ecosystems (Hussey et al., 2015; Williamson et al., 2019). Knowing the importance of large marine predators in structuring trophic flow and nutrient cycling in oceanic environments demands an understanding of their fine-scale swimming behaviours in response to heterogeneous conditions with unequally distributed resources.

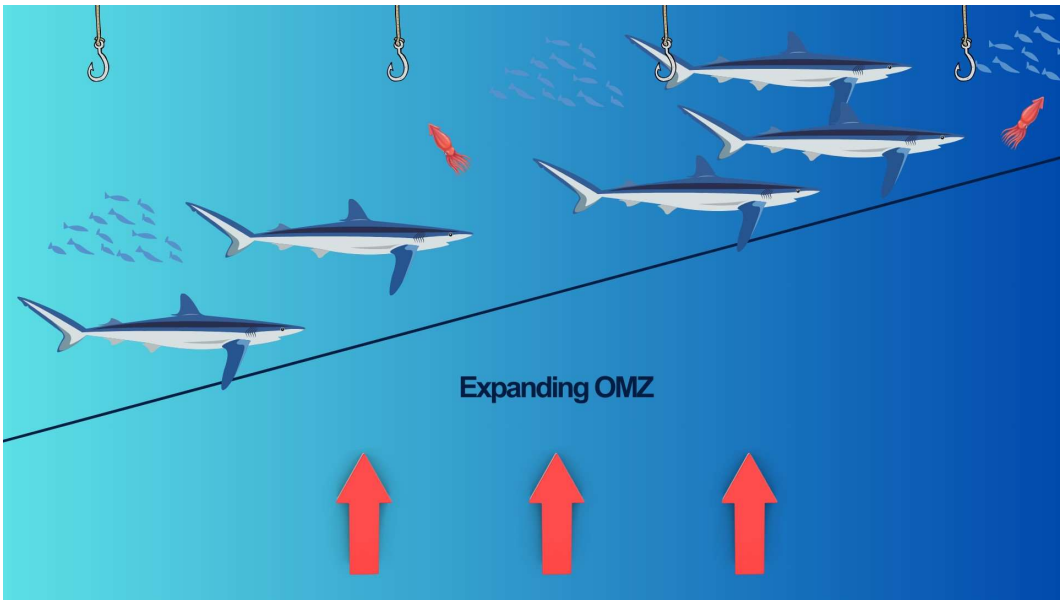


Figure 1. Expanding oxygen minimum zones (OMZ). Scenario of how OMZ will potentially affect pelagic sharks compressing their habitat, being even more vulnerable to overfishing (adapted from Sims, 2019).

Successful conservation and management at multiple spatial scales of shark populations needs understanding how and why they move, migrate and aggregate in addition to detailed knowledge of their breeding and feeding habitat (Bonfil, 1997; Simpfendorfer et al., 2010; Speed et al., 2010; Jacoby et al., 2012; Knip et al., 2012; Williamson et al., 2019). One of the key factors that regulates the vertical habitat selection by sharks is the diel vertical migration (DVM) of

zooplankton (Sims et al., 2005). DVMs frequently occur across different species in the pelagic environment representing a trade-off between the functions of food gathering and avoiding predation, from zooplankton moving up into surface layers at night to avoid visual predators to apex predators pursuing migrating prey to optimize foraging chances, principally brought on by variations in light intensity over the day (Hays, 2003; Sims et al., 2005; Andrews et al., 2009; Weng et al., 2009; Queiroz et al., 2012; Coffey et al., 2017; Hafker et al., 2017; Vedor et al., 2021b; Watanabe et al., 2021). Thus, shifts in depth distributions occur at dawn and dusk where fish are distributed deeper during the day and shallower at night. Since sharks display a range of differences in feeding strategies (Frazetta, 1994; Motta and Wilga, 2001), recent studies have shown that some pelagic fish, including sharks, exhibit highly conserved movement patterns that are thought primarily to represent searching and foraging behaviors (Sims et al., 2008; Humphries et al., 2010; Queiroz et al., 2017). Likewise, two-dimensional dive profiles have been shown to provide valuable information on the behavior of diving animals (Bost et al., 2007; Queiroz et al., 2017), with movement patterns appearing to be theoretically optimal for the likely prey abundances encountered in the particular habitats (Humphries et al., 2010, 2016). Environmental conditions and foraging behaviour have been linked to shark movements and habitat decisions (Sims and Quayle, 1998; Sims, 2003; Nasby-Lucas et al., 2009; Queiroz et al., 2012; Williamson et al., 2019) strongly connected to prey distribution and availability (Sims, 2003). Foraging is critical in ecology because it impacts energy acquisition and, ultimately, animal fitness (Stephens and Krebs, 1986; Begon et al., 2006). Monitoring foraging is challenging, especially in marine habitats where direct observations are infrequent (Watanabe and Takahashi, 2013).

The study of marine animal movements remains an important issue due to the difficulties of making observations on hidden, highly migratory species in the ocean. In addition to improving conservation efforts by identifying predator hotspots in the ocean (Worm et al., 2003) and enabling the best possible design of MPAs, increased information on movement patterns also improves awareness of the dangers presented by challenges including industrial fishing, habitat compression, pollution, and climate change (Chin et al., 2010; Espinoza et al., 2014; Schlaff et al., 2014; Williamson 2019).

Environmental drivers

Understanding the habitat use and foraging ecology of marine megafauna is important for predicting why and where individuals or populations move and migrate, and it is mainly concerned with how the physical environment impacts mobility (Speed et al., 2010; Hays et al., 2016; Jacoby and Freeman, 2016). The drivers of vertical movement patterns of marine megafauna may be both physical (e.g., temperature, light level, DO) and biological variables (e.g., primary production), influencing how animals may move, coupled with the eco-physiological characteristics of each species and their interactions (Longhurst, 1967; Giske et al., 1990; Watanabe et al., 2021). These environmental drivers set the maximum limits for vertical distributions.

The influence of the physical environment on regional blue shark habitat preferences have been widely explored in the Atlantic (Queiroz et al., 2005; Campana et al., 2011; Queiroz, et al., 2012; Vandeperre et al., 2014a; Howey et al., 2017). Blue sharks showed a strong preference for certain SST ranges for several reasons. Previous studies found that blue sharks prefer waters temperature above ~15°C in the Northeast Atlantic (Nakano, 1994; Vandeperre et al., 2016; Howey et al., 2017) and off Australia (Stevens et al., 2010). Age and sex have a role in determining blue shark distribution in relation to water temperature (Nakano and Seki, 2003). Immature females in the North Atlantic occupied colder temperatures than both adult and immature males (Vandeperre et al., 2014a; Howey et al., 2017). Yet, other studies have claimed that cooler temperatures may delay growth rates for immature females (Carlson et al., 2004). Blue sharks often migrate north throughout the summer as surface waters at higher latitudes warm (Queiroz et al., 2010), as evidenced by known migrations into productive regions of the northern Gulf Stream and North Atlantic Current (Queiroz et al., 2019; Vedor et al., 2021b). Likewise, large juvenile females in the North Atlantic are known to migrate seasonally until they reach maturity, moving towards northern waters during the warmer summer months (Vandeperre et al., 2014a; Vandeperre et al., 2016). Fishing records have shown that pregnant female sharks are hypothesized to select warmer waters to reduce gestation and development time of embryos (Jirik and Lowe, 2012; Carvalho et al., 2015). In contrast, adult female blue sharks prefer relatively cold waters outside of the ovulation-fertilization-parturition stages (Pratt, 1979). Changes in the thermal profile of the water column as well as the distribution and timing of peak production have also been

associated with variations in diel vertical behaviour (Vedor et al., 2021b). For instance, blue and salmon sharks have been seen to have increased surface occupancy in highly productive frontal zones characterized by low surface temperatures and strong water column stratification (Queiroz et al., 2012; Coffey et al., 2017). Sims et al. (2006) results shown that catsharks improve their energy efficiency by reducing daytime activity in deep, cold waters and foraging at night in shallow, warmer waters.

Recent research revealed that, in addition to significant horizontal movements, tracked blue sharks exhibited high residency in specific areas, which were largely correlated with mesoscale oceanic features such as thermal fronts and upwelling regions (Vedor et al., 2021b). When exploring areas with high primary productivity (i.e., frontal systems or prominent topographic features), some elasmobranch species have been seen to change their foraging strategies and creating large aggregations (Sims and Quayle, 1998; Sims et al., 2000; Worm, Lotze and Myers, 2003; Weng et al., 2008; Humphries et al., 2010; Venegas et al., 2011; Queiroz et al., 2012; Miller et al., 2015; Williamson et al., 2019). Individuals tracked in the West Atlantic displayed extended periods in frontal regions of high primary productivity and forage accumulation, where megafauna is known to gather (Campana et al., 2011; Scales et al., 2014; Braun et al., 2019b; Vedor et al., 2021b). Frontal areas are large-scale horizontal gradients often associated with mesoscale eddies and coastal currents (Denny and Dawd, 2022). Fronts are usually defined by a narrow layer being a boundary between two distinct water masses or different vertical structures (Belkin, 2002; Belkin and Cornillon, 2007; Belkin, 2009) providing gradients in temperature, salinity, and oxygen analogous to those of the thermocline, although these horizontal gradients are typically much less steep than those in the thermocline (Le Fevre, 1986; Olson et al., 1994; Wolanski and Hamner, 1998; Genin, 2004; Queiroz et al., 2012). Hence, they influence the behaviour, movement, and distribution of marine predators (Shaffer et al., 2006; Zainuddin et al., 2006; Queiroz et al., 2012) suggesting they may orientate themselves to high productivity frontal zones to find food, remaining there for extended periods of time, which eventually contributes to their spatial aggregation creating a hotspot of marine life from phytoplankton to apex predators (Sims and Quayle, 1998). Thermocline is a distinct layer, where temperature drops rapidly with increasing depth. It acts as a barrier that limits prey and may explain variations in dives and top predator

distribution. Such as fronts, it may play a key function in shaping vertical habitat use patterns for marine animals. Thermocline offers significant spatial variation available to vertically migratory species throughout most of the ocean, frequently as a concomitant to their diel vertical migration (DVM; Danny and Dawd, 2022). It has been linked to the vertical migration of Pacific bluefin tuna, with individuals remaining in shallower depths and performing dives across it to maximize the chance of encountering prey (Kitagawa et al., 2007).

Considering that fluctuations of water properties impact oxygen solubility (Xing et al., 2014), significant temperature variations across persistent thermal frontal systems are expected to be reflected in substantial variations in DO concentrations as well. Increased SST results in lower oxygen solubility, higher stratification of the water column, and higher rates of oxygen consumption due to increased metabolic rates. Thus, as mentioned before, ocean deoxygenation is severely impacted by global warming (Keeling et al., 2010; Schmidtko et al., 2017; Breitburg et al., 2018; Levin, 2018). There is a type of DO front linked to hypoxic areas. OMZs are expected to continue expanding its ranges both horizontally and vertically, emphasizing the importance of understanding how sharks with different metabolic strategies and high commercial interest interact with these ongoing growing areas in a changing ocean. Vedor et al. (2019a) predicted that blue shark habitat will become more constricted above OMZs in the future given to increasing ocean deoxygenation and being more prone to overfishing. They modelled DO data from oceanographic data sets that were matched with locations along the paths of tracked pelagic sharks (Sims, 2019), which may therefore differ from actual DO concentrations in the habitats selected by sharks (Vedor et al., 2019a). This has also been a limitation in most previous shark studies. Hence, the use of data-logging tags capable of measuring direct DO are required to better understand how low DO levels in the environment may impede pelagic shark movement (Coffey and Holland, 2015). Coffey et al. (2020) demonstrated using DO sensor tags that bluntnose sixgill sharks (*Hexanchus griseus)* off Hawaii, Pacific Ocean, can tolerate very low DO concentrations (~0.8 ml O2 l−1 at 5˚C) during their normal vertical movement during dives to nearly 700 m depth. In that way, these types of sensors will allow new studies on the physiological responses of ram-ventilating pelagic sharks to low DO in the wild (Sims, 2019).

Understanding how marine animals respond to variation in the physical environment is crucial. When it comes to fisheries, to quantify the post-release mortality rates are difficult, as there is unknown percentages of dead sharks by the physical or physiological effects of capture stress (Molina and Cooke, 2012; Skomal, 2007; Skomal and Bernal, 2010; Whitney et al., 2019). In terms of changing temperature regimes associated with climate change and expanding oxygen minimum zones (OMZs), and since the majority of sharks are ectotherms, the water temperature regulates their physiological and behavioural processes, such as energy budgets, foraging strategies, daily activity levels and movement patterns (Payne et al., 2014; Whitney et al., 2019). Therefore, it can drive huge shifts in several species, that cannot change their space use to search for optimal temperatures (Whitney et al., 2019).

Animal tracking: an historical perspective

Using telemetry and biologging techniques enable to track of spatial dynamics and behaviour, providing important information on sharks' movement patterns and their habitat preferences with a minimum observer interference and in inaccessible monitored areas (Queiroz et al., 2012). Since sharks spend most, if not all, of their time below the sea surface, where they cannot be observed directly, satellite-linked telemetry devices are usually required to remotely monitor their wide-ranging and unpredictable movements patterns through time and space-use of the ocean areas they inhabit (Ferreira et al., 2018). Scientists have been actively researching how animals move since the first tag-recapture studies on Atlantic salmon in 1873 (Everhart, 1975). Biologging techniques have documented vertical movement patterns in pelagic sharks for several decades and despite these animals occupies a 3-D environment, most early tagging studies focused on horizontal patterns of movement (Speed et al. 2010; Thums et al. 2013).

The development of satellite transmitting tags in the 80s has since allowed accurate positioning of surface-oriented species such as sharks (Priede, 1984). It was introduced with the integration of the ARGOS (Advanced Research and Global Observation Satellite) system on NOAA (National Oceanic and Atmospheric Administration) satellites, allowing the location of an animal-attached platform transmitter terminal (PTT) anywhere on the planet as long as it remained out of the water for a sufficient amount of time (Sims, 2010). Satellite-linked

transmitters are designed to obtain near-real time tracks of horizontal movements of a range of animals such as sharks, that can be analyzed at a much higher resolution (hundreds to thousands of kilometers) (Hammerschlag et al., 2011; Ferreira et al., 2018). Unlike archival tags, satellite-linked tags are equipped with radio transmitters that communicate with polar-orbiting Argos satellites at an altitude of 850 km, with a footprint of 5000 km, and completing their orbital revolution in approximately 100 minutes and passing over the poles approximately 14 times per day (Hammerschlag et al., 2011). Satellite-linked tags are focused on species that spend time at the sea surface and it has wet–dry sensors incorporated which initiates tag transmission when above the water's surface (wet) and indicate when the tag is out of the water (dry) (Hammerschlag et al., 2011; Argos, 2016; Ferreira et al., 2018). Location accuracies are determined from all messages received during a satellite pass via Doppler shift calculations whenever a passing satellite received two or more signals from a tag (Hammerschlag et al., 2011; Argos, 2016; Ferreira et al., 2018). Argos locations indicates the level of spatial accuracy assigned on a decreasing location class (LC) scale of 3, 2, 1, 0, A, B, and Z, in the estimates of latitude and longitude (www.argos-system.org) (Hammerschlag et al., 2011; Argos, 2016; Ferreira et al., 2018). When four or more messages are received from the satellite-linked tag, only provides location classes of 3, 2, 1, and 0 (Ferreira et al., 2018). Therefore, when three messages are received provides a location class A and location class B when only one message is received (Ferreira et al., 2018). The location class Z reflects an unsuccessful effort to acquire location, but an estimative is supplied (Hammerschlag et al., 2011; Ferreira et al., 2018). Thereby, Argos system provides the following estimated errors in latitude and longitude for each location classes: LC 3: <250 m, LC 2: 250 m – 500 m, LC 1: 500 m – 1500 m and LC 0: >1500 m (Hammerschlag et al., 2011; Ferreira et al., 2018). Argos does not provide accuracy estimates for LC A and LC B (Hammerschlag et al., 2011; Argos, 2016; Ferreira et al., 2018). Once sharks spend periods of brief and infrequently durations at the surface, satellite-linked tags report location estimates with a high proportion of the less reliable location classes (LC 0, A, B), leading to average errors of location of 3.03 to 11.48 km (Hays et al., 2001; Vincent et al., 2002; Hazel, 2009; Costa et al., 2010; Hoenner, 2012; Ferreira et al., 2018).

In the 1990s, archival tags were initially implemented and have since spread worldwide (Hussey et al., 2015). Pop-up satellite archival transmitters (PSATs), as

their name implies, are often used to track animals such as sharks that do not spend enough time at the surface during day-today movements (Sims, 2010; Hammerschlag et al., 2011; Ferreira et al., 2018). PSATs tags have sensors for temperature, depth, and ambient light levels that once deployed, the tag will record and archive data at pre-programmed sampling rates (Hill & Braun, 2001; Ferreira et al., 2018). The tag delays transmission to Argos satellite networks until they release from the shark at a pre-programmed date varying from a few months to a year and float to the surface (Hammerschlag et al., 2011; Ferreira et al., 2018). Therefore, archived data summaries are transmitted through the Argos satellite network; and if the tag is physically recovered, all raw data can be downloaded. While the depth and temperature data are very reliable (Sims, 2010; Hammerschlag et al., 2011), geolocations are estimated from the light-level measurements by the tag during deployment. Daily estimates of latitude are determined by the time between sunrise and sunset and the longitude using the midpoint between sunrise and sunset (Hill & Braun, 2001; Ferreira et al., 2018). Thus, many factors can influence the accuracy of the light-level measures such as turbidity, light attenuation, and shark behaviour (Hammerschlag et al., 2011; Musyl et al., 2011). As a result, the spatial accuracy of the PSAT tag estimates has a large error (hundreds to thousands of kilometers) (Ferreira et al., 2018). Retrieving the tag floating in the ocean can be complex in reason to poor weather conditions (currents, waves, white caps, strong winds) (Hammerschlag et al., 2011; Ferreira et al., 2018). Also, the PSAT tags must be located and retrieved when is still transmitting, for a limited period of 1 to 2 weeks, where very high frequency (VHF) transmitters are attached into the tag and a handheld VHF receiver is used to access the tag position for recovery (Ferreira et al., 2018).

Recently, the development of multi-sensor biologging tags with tri-axial sensors (i.e., accelerometers, magnetometers, gyroscope) provided novel knowledge about the fine-scale swimming behaviour in sharks due to complementing software and data processing tools (Sakamoto et al., 2009; Whitney et al., 2019).

Accelerometers

Accelerometers have been attached to animals, such as sharks (Brown et al., 2013; Davis et al., 1999; Rutz & Hays, 2009; Wilson et al., 2015; Yoda et al., 1999; Whitney et al., 2019), with at least one of three types of motion sensors that provides a slightly different perspective on animal movement.

Accelerometers which record both static acceleration (the constant acceleration due to gravity) useful to infer shark pitch or posture, and dynamic acceleration, which is due to the shark movements and a proxy of swimming performance (Shepard et al., 2008; Payne et al., 2014) that results in the total body acceleration (Whitney et al., 2019). Thus, the other two types of motion sensors can be coupled with accelerometers to provide more accuracy and/or detail in the estimation of shark kinematics. Gyroscopes that measure angular velocity of the animal but not its posture, allowing for impartial assessment of an animal's dynamic acceleration during unstable movements. But when linked to accelerometers, offer a more accurate estimate of attitude and kinematics while also improving the precision of behavioural classification (Noda et al., 2012; Noda et al., 2014; Whitney et al., 2019). Magnetometers that record the direction relative to the Earth's magnetic field provided in reference on the shark posture (Williams et al., 2017). When combined with the accelerometer in the context of the shark pitch and roll, it may provide a compass heading that, when paired with an estimate of velocity, can help to reconstruct their swimming paths or "pseudo-track" (Williams et al., 2017; Whitney et al., 2019). The three-dimensional (3D) data can be used to estimate metabolic rates and determine the energy expenditure (Hussey et al., 2015) since it provides a reliable assessment of swimming activity (Halsey et al., 2011; Wright et al., 2014). Furthermore, it can also be combined with video-camera loggers enabling 3D dive profiles to be linked with prey aggregations, thus estimating predator–prey encounter rates and foraging behaviour (e.g., Watanabe and Takahashi, 2013; Watanabe et al., 2014). Therefore, accelerometers loggers provide the total body acceleration data that can be used to determine the fine-scale behaviour and activity patterns, as well as shark tailbeat frequency (TBF), amplitude and body posture (Whitney et al., 2012).

Measurements must be taken at a sufficient frequency for all of these motion sensors to produce reliable behavioural data and many studies have chosen frequencies of 30 Hz as effective sampling rates for sharks, once they usually exhibit smaller acceleration values and lower tailbeat frequencies when compared to smaller fishes (Whitney et al., 2019). Since it is not common for most sharks to experience fast dynamic changes in environmental parameters, it is usual to sample at a lower frequency (1 Hz) for swimming speed, depth, and temperature sensors (Whitney et al., 2019). While the loggers will provide data at higher resolution (raw values) and the accelerometer need to be retrieved to recover data

(Houghton et al., 2009; Watanabe et al., 2012), the transmitters record acceleration data summaries, but it doesn't need to be retrieved (Payne et al., 2011; Payne et al., 2013; Payne et al., 2014). Double tagging, or the use of complementary tag types in the same individual, such as acceleration data loggers and PSATs tags, allows for the collection of both position, acceleration, and other environmental parameters.

Objectives

The aim of this study is to understand the fine-scale behaviour (i.e., tailbeat, shark orientation and heading) and the metabolic costs (overall dynamic body acceleration) associated with foraging movements of blue shark – the pelagic shark most commonly caught by commercial fisheries – under environmental gradients (temperature and oxygen). Furthermore, given a scenario of climatic warming, deoxygenation, and overfishing, to address some of the possible future perspectives in the sustainable management and conservation plan for the studied species. The objectives of this project align with the Sustainable Development Goals 13 and 14 of the 2030 Agenda.

Materials and methods

Tagging

In total 11 blue sharks were tagged between July 2020 and June 2021 in Faial Island (Table 1), located in the central group of the Azores archipelago. Sharks were caught using a 4 km drifting longline set by a fiberglass vessel with low gunnels (7m long) above the slope of the Condor seamount with a soak time of 3.5 h. They were placed alongside to be fitted with the Dissolved Oxygen Measuring (DOME) archival tag a resin-based flotation package with 135 mm in length, 85 mm in diameter and 30 g (weight in water; Fig. 2). The multisensor logger contains a tri-axial accelerometer, gyroscope, magnetometer that recorded data at 20 – 30Hz and environmental sensors recording at 1 Hz. Each of type of tri-axial motion sensors will give different information about shark movement: accelerometers provide the total body acceleration; gyroscopes measure the angular velocity and magnetometers give the posture of the shark in relation to the orientation of the Earth's magnetic field. The environmental sensors record pressure, water temperature and dissolved oxygen (DO). The loggers will also have GPS (global positioning system) unit for geolocalization and recovering

procedures (deployment time of 1 to 3 days to ensure high return rates) since the tags have to be recovered to download archived data – previously satellite tracked sharks showed coastal residence for ~ 30d (Queiroz et al., 2010; Queiroz et al., 2012; Vandeperre et al., 2014).

A timed-release cable tie was used to secure the tag to a 3D-printed polylactic acid (PLA) mounting plate attached by a loop through a small hole made in the base of the first dorsal fin (Fig. 2). The entire procedure, including body-length measurements and sex identification, took 5-7 minutes (Queiroz et al., 2016), after which the vessel moved slowly forward for 1-3 minutes to aerate the gills, during which time the caudal fin loop was removed. The sharks were released by taking out the hook when they returned to their normal swimming patterns. The cable used to attach the tag to the PLA mounting plate was released at the pre-programmed time, and the tag floated to the surface. Following 45 minutes on the surface, the tag switched to satellite mode and repeatedly sent coordinates of its location to satellites (Fig. 3). All the tags were then located and retrieved by a boat. Tagging procedures have been approved by institutional ethical review boards and carried out by licensed, qualified, and experienced individuals, with no evident harmful effects on the fish.

Data processing

The tri-axial data were initially processed using the Igor Pro software (version 9.0, Wavemetrics Inc., Lake Oswego, OR, USA) with the Ethographer extension (Sakamoto et al., 2009) to extract basic swimming metrics. Subsequent analyses were conducted in R (version 4.1.3; R Development Core Team, 2022).

Dive profile analysis

The analysis of two-dimensional dive time series was visualized performed, since we had a small sample size (n=11), supported by a literature review (e.g., Seminoff et al., 2006; Wilson and Block, 2009; Cook et al., 2011; Thomson et al., 2011; Queiroz et al., 2017; Andrzejaczek et al., 2018). The standard dive shape classes consistently performed by the sharks were defined and were afterwards visually assigned to every dive by the same person. Shape classification was performed using the method set out by Queiroz et al. (2017). V-shaped dives were defined as having little to no time spent at the maximum depth of the dive prior to ascent. U-shaped dives were defined as square or parabolic with a

distinctive descent followed by a relatively flat bottom phase and a steep ascent. W-shaped dives presented 2–4 undulations during the bottom phase. LV-shaped dives (“left-V”) consisted of a V-dive with a “stop” phase in the ascent, while RV-shaped dives (“right-V”) were the opposite of LV. Dives that did not fit within one of these shapes received the designation "Other". Lastly, dives were classified as starting when blue sharks descended below a depth of 50m (Queiroz et al., 2017).

Figure 2. Double tagging. DOME (Dissolved Oxygen Measuring) archival tag with oxygen, temperature and accelerometer sensors using a zip-tie with an explosive timed release (48h) and a PSAT tag attached to the dorsal fin of a 272cm TL female blue shark (*P. glauca*) in Azores archipelago. Photo: CIBIO/Luana Coelho.

Tri-axial sensor data

Tri-axial accelerometer, gyroscope and magnetometer data recorded by multisensor loggers were used to define the fine-scale behaviour of blue shark. Using a low-pass filter, the static components of the acceleration data were separated from the dynamic components. The dynamic component of acceleration was calculated by subtracting the gravitational component from the

raw acceleration for each axis. Overall dynamic body acceleration (ODBA), a proxy for energy expenditure of the animals, was calculated by summing the absolute value of dynamic acceleration from all three axes (Wilson et al., 2006). Accelerometer data and/or angular velocity gave insights about shark kinematics, including tailbeat and angle of orientation (pitch and roll).

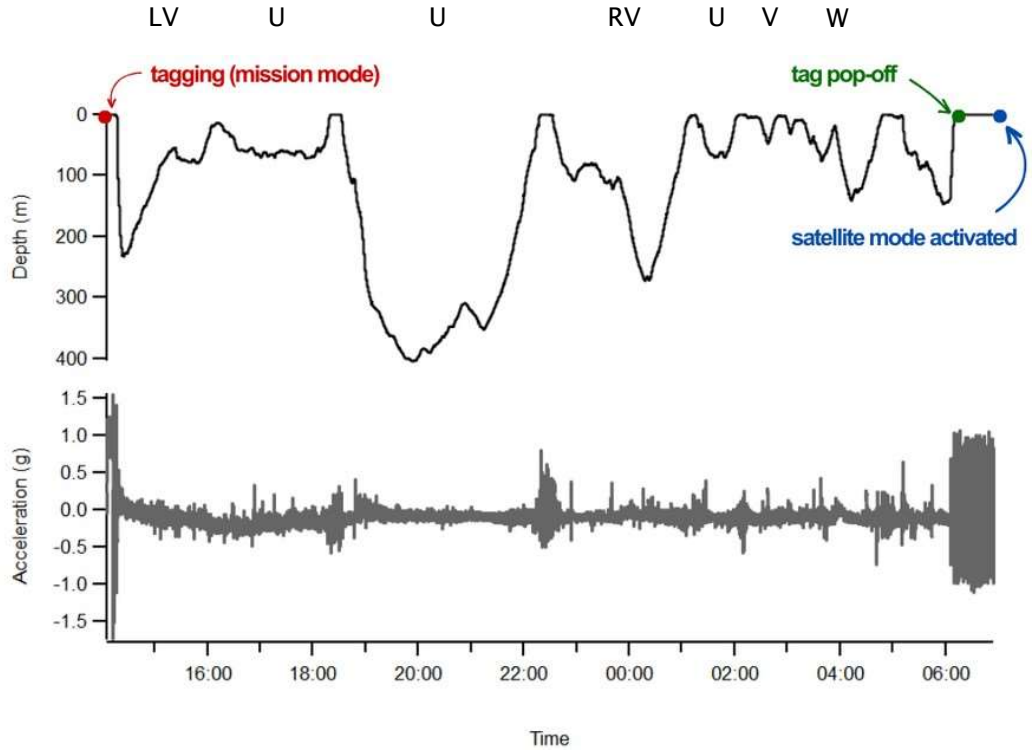


Figure 3. Example of tagging and pop-off with the five dive shape classes. During the tagging we turn on the tag in mission mode (red dot) which is already recording data. After 24-48h (pre-programmed) the tag pops-off and reaches the surface (green dot). After 45 minutes on the surface, the tag will activate satellite mode and begin sending positions.

The angles of pitch (i.e., angle of the body through the longitudinal axis relative to the horizon) and roll (i.e., angle of the body through the lateral axis relative to the horizon) were calculated by the static elements of the signal, and these were corrected for the attachment angle of the tag to the horizontal plane of the shark's longitudinal axis using the method set out by Kawatsu et al. (2009). A single tailbeat was defined as the time taken for the caudal fin to move from one extreme lateral position to the other and back again to its starting position (Watanabe et al., 2019). Then, shark orientation was integrated with

magnetometer data (posture in relation to magnetic field) to produce compass heading information that can be used to reconstruct the swimming paths of each shark tagged.

Table 1. Data summary of tagging and biological information of the tagged blue sharks (F: female; M: male; * 48h tag deployment; TRIDENT: DOME tag).

Shark ID	Tag ID	Sex	Fork length (cm)	Total length (cm)	Weight (kg)	Deployment date
blue2	TRIDENT_204	M	173	210	32,6	08/07/2020 16:00
blue3	TRIDENT_204	M	194	235	46,5	14/07/2020 14:37
blue4	TRIDENT_203	M	182	220	37,8	14/07/2020 16:05
blue5	TRIDENT_204	M	207	250	56,6	20/07/2020 14:20
blue6	TRIDENT_203	M	180	215	36,7	05/10/2020 17:00
blue7*	TRIDENT_203	M	187	225	41,4	08/10/2020 14:00
blue8	TRIDENT_204	M	230	275	79,1	08/10/2020 16:00
blue9	TRIDENT_205	M	205	240	55,2	08/10/2020 16:33
blue10 + 181752*	TRIDENT_202 + ATS1	F	224	272	72,8	22/06/2021 10:46
blue11 + 181753	TRIDENT_206 + ATS2	M	217	262	65,6	23/06/2021 14:27
blue12 + 181754*	TRIDENT_203 + ATS3	M	232	270	81,3	23/06/2021 15:58

Using both the acceleration and angular velocity data, a continuous wavelet transformation (CWT) was used on the dynamic acceleration of the sway (i.e., lateral) axis to calculate the signal amplitude and tailbeat frequency (TBF) of the shark (i.e., the number of cycles per second (Hz); Sakamoto et al., 2009). Data recorded by the tags were processed to obtain a number of parameters classifying shark movements and behaviours.

Results

Fine-scale swimming behaviour records were successfully obtained for 11 blue sharks (Table 1). Tagged blue sharks ranged in length from 215 to 275 cm (total length) and weight from 32,6 to 81,3 kg. A total of one female and ten male blue sharks were tagged off Azores archipelago, above the slope of the Condor seamount. The 11 blue sharks were tagged in this study (table 1): blue2 to blue9 and blue11 were tracked for over 24 h each, whereas blue10 and blue12 tags were tracked for 48h. The blue11 tag was prematurely released 2 hours earlier. The blue3 tag activated earlier the satellite mode (pop-up only in the next day). Table 1 summarizes the information about all the individuals tracked in this study.

Vertical space use

We recorded the fine-scale swimming behaviour, ambient water temperature, depth, and dissolved oxygen (DO) of the 11 blue sharks tagged (173–232 cm in fork length range) for 24 – 48 h, depending on the pre-programmed time (Fig. 4). Swam at a mean depth of 145.5 m ± 43.5 m, reaching wide range of depths (<669.3 m) with up and down movements (Table 2 summary, e.g., Fig. 4). They experienced an overall mean water temperature of 17.2 ºC and, since blue sharks are thermally tolerant, a temperature range of 10.3–22.8 ºC (Table 2). The mean DO was 234.6 µmol/l with a range of 185.2–271.9 µmol/l (Table 2). For other summary statistics of vertical movements, see table 2.

Swimming behaviour

Blue sharks displayed negative buoyancy, as evidenced by lower amplitudes of lateral acceleration (i.e., tailbeat activities) during descents compared to ascents (Fig. 5). Except for slight gliding behaviour during descents and increased ascents during burst swimming, tailbeats were constant throughout the recordings. The dominant TBF across all recordings were 0.23–0.43 Hz (Table 2) and sharks displayed a mean TBF of 0.34 Hz ± 0.06 Hz. A decrease in tailbeat amplitude is notable as the shark oscillates from descent to ascent phase. During the descent phase of the dive there was almost no sign of the tailbeat, and it is possible to observe the transition from the descent to the ascent phase by looking at the pitch angles (negative to positive values), in addition to the increase in the TBF. The burst-swimming events were based on the 99th percentile of ODBA data and

it occurred during the day and night over a wide depth range without centering around a particular depth (Fig. 6). We presumed that these burst swimming events recorded in the present study indicate foraging attempts. In response to tagging, the first dive of blue sharks exhibited more burst swimming events during descent than usual.

Table 2. Summary statistics calculated for the entire dataset (11 blue sharks), and each tagged individual. TBF: tailbeat frequency.

	Overall	Blue2	Blue3	Blue4	Blue5	Blue6	Blue7	Blue8	Blue9	Blue10	Blue11	Blue12
Mean depth (m)	145.5 ± 43.5	29.5 ± 25.7	286.7 ± 122.2	36.5 ± 31.1	131.7 ± 117.1	85 ± 83.1	186.8 ± 167	123 ± 129.6	78.2 ± 59.1	463.9 ± 121.9	84.8 ± 108.7	94.1 ± 109.2
Maximum depth (m)	669.3	132.1	406.5	123	403.9	322.5	666.7	411.8	230	669.3	491.3	506.6
Mean temperature (ºC)	17.2 ± 0.56	19.6 ± 1.4	14.4 ± 2.4	19.7 ± 1.9	17 ± 2.6	18.4 ± 2.3	16.6 ± 3.2	18 ± 2.9	18.7 ± 2.4	12.5 ± 1.3	17.6 ± 2.2	17.2 ± 2.1
Temperature range (ºC)	10.3 – 22.8	16 – 21.8	12.7 – 22-2	15.9 – 22.8	12.9 – 22.2	13.9 – 21.8	10.3 – 21.7	12.8 – 21.5	14.4– 21.5	10.4 – 20.8	12.2 – 21.3	12.1 – 21.7
Mean oxygen (µmol/L)	234.6 ± 2.4	243.7 ± 5.6	225.2 ± 12.4	247.2 ± 6.7	241.8 ± 11.6	243.6 ± 9.5	239.2 ± 13.2	233 ± 10.2	229.2 ± 7.9	210.4 ± 11	240.9 ± 11.4	226.7 ± 10
Oxygen range (µmol/L)	185.2 – 271.9	225.7 – 253.8	212.0 – 271.6	231.7 – 271.9	218.5 – 266	225.7 – 260.4	199.9 – 269.8	213.6 – 252.4	216.2 – 247.7	185.2 – 255.6	207.9 – 259.6	203.7 – 247.4
TBF (Hz)	0.34	0.35	0.41	0.35	0.35	0.39	0.39	0.23	0.31	0.29	0.43	0.29
Pitch (º)	0 – 87.2	0 – 68.7	0 – 40.8	0 – 42.5	0 – 32.8	0 – 65.7	0 – 63.9	0 – 52.7	0 – 42.6	0 – 51.8	0 – 87.2	0 – 59.2
Roll (º)	0 – 88	0 – 42.1	0 – 36	0 – 34.5	0 – 35.1	0 – 75.1	0 – 57.2	0 – 44.3	0 – 62.8	0 – 88	0 – 80.7	0 – 77.4

The scatterplot showed that blue sharks inhabited a wide vertical habitat, and many of them exhibited regular diving behaviour with a preference for surface waters. This surface-oriented behaviour was observed in most sharks, where they usually spent high percentages (75 to 100%) of their time near or at the surface, with some of them making frequent dives below 200 m. Likewise, they also frequented the surface-air interface (Fig. 5-c), displaying highly irregular vertical behaviour and not occupying surface layers for as long. In contrast, depth-oriented behaviour was observed in blue3 and blue10. The blue10 spent ~96% of time below 200 m, while the blue3 made frequent dives to the mesopelagic zone (~200–600 m) spending high percentages of time below 200 m (~79%). Profiles of water temperature at depth indicated sharks were diving through stratified water, with a thermocline at approximately 50 m (Fig. 4 and 7). The deployment of accelerometers with oxygen sensors provided an understanding of how blue

sharks responded directly to oxygen gradients, encountering a range (185.2 - 271.9 µmol/l) of available DO along with changes in temperature throughout the water column when moving vertically (Fig. 7). In addition, the scatterplot (Fig. 4-b) showed that oxygen decreases as depth increases, but around 50 m, there is a large increase in comparison to the surface layer. This maximum DO is associated with thermocline (~50 m) and, thus, a strong water column stratification.

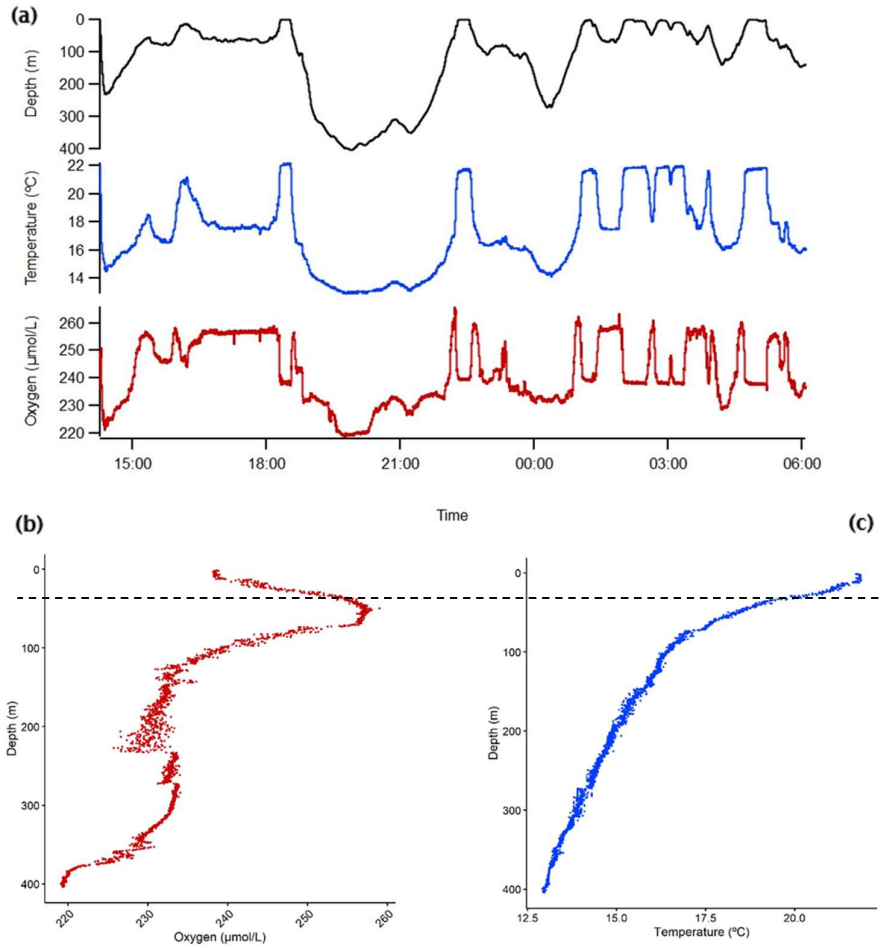


Figure 4. Full time-series of the depth profile, temperature, and oxygen from a blue shark (blue5) in Azores fitted with an acceleration data logger package displaying a regular diving behavior. Scatterplot shows the relationship between depth and oxygen (red), and depth and temperature (blue). Dashed line: thermocline.

A total of 145 individual dives were identified and they were categorized into five general types common to blue sharks, labeled U-, V-, W-, LV-, and RV-shaped dives (Table 3). It is noteworthy that no discrete dives were identified for blue3

and blue10 once they displayed depth-oriented behaviour, spending large amounts of time continuously submerged at depth. The depth record was mainly made up of V- and U-shaped dives (~70% of the total number of dives). V-shaped dives alone represented ~45% of total dives in frequency, whereas U-shaped dives ~25%. The W-, LV- and RV- shaped dives accounted for a low percentage of total dives representing together < 20%. Irregular dives (class "Other") represented around 12% dive time for blue sharks. U-shaped dives represented the longest dive durations with some dives extending for several hours, whereas V dives were usually short (Fig. 5-d). The dives were performed to a wide range of depths, from the top 50m to < 500 m. W, LV and RV dives showed intermediate duration when compared to U or V dives.

Table 3. The dive shape classes considered in this study for tagged blue sharks.

	V		U		W		LV		RV		Other		
ID	%	Dives	%	Dives	%	Dives	%	Dives	%	Dives	%	Dives	**Total dives**
blue2	50	4	12.5	1	25	2	12.5	1	-	0	-	0	8
blue4	33.3	2	-	0	-	0	-	0	-	0	66.7	4	6
blue5	14.3	1	42.8	3	14.3	1	14.3	1	14.3	1	-	0	7
blue6	30	3	30	3	10	1	-	0	20	2	10	1	10
blue7	70.3	26	5.4	2	10.8	4	2.7	1	2.7	1	8.1	3	37
blue8	35.7	5	64.3	9	-	0	-	0	-	0	-	0	14
blue9	66.6	4	16.7	1	-	0	-	0	-	0	16.7	1	6
blue11	36.1	13	30.6	11	8.3	3	-	0	8.3	3	16.7	6	36
blue12	33.3	7	33.3	7	14.3	3	-	0	4.8	1	14.3	3	21

Additionally, a scatterplot showed the relationship of ODBA and environmental variables of the 11 sharks analyzed (Fig. 8). Pearson's correlation coefficient was used to measure the strength between the ODBA and environmental variables indicating a highly significant negative correlation between these variables. Pearson's correlation coefficient between ODBA and depth was r=-0.0335, p<0.001; between ODBA and oxygen was r=0.0445, p=0.000; and between ODBA and temperature was r=0.0399, p<0.001.

Discussion

Blue sharks experienced a temperature range of 10.3–22.8 ºC (Table 2) and despite having an ectothermic physiology, they are thermally tolerant and can tolerate temperatures ranging from 4˚C to 30˚C in the water (Howey et al., 2017). However, they prefer a much narrower temperature range (Kohler et al., 2002; Queiroz et al., 2005). Our results revealed a wide vertical space used by blue sharks, with many of them exhibiting frequent diving behavior and a preference for surface waters, which is totally normal given that most of the recording time was at night. According to Carey et al. (1990) results, blue sharks (*Prionace glauca*) might oscillate from the surface to depths of 200–400 m, inhabiting deeper waters in the daytime and shallower at night. This behaviour pattern of spending more time in the warmer upper layers at night and at moderate depths during the day, with repeated deep-diving behaviour into cooler waters associated with stratified water columns has been also reported in other multiple previous studies with blue sharks (Stevens et al., 2010; Campana et al. 2011; Queiroz et al., 2012; Howey et al., 2017; Queiroz et al., 2017; Braun et al., 2019; Vedor et al., 2021a). Some studies suggest that it is a response to the DVM of the deep (or sound) scattering layer (SSL) (Carey, 1990). SSL is defined by the migration of small fishes and invertebrates to depth at sunrise and rise to surface layers near the thermocline at sunset to feed (Andrzejaczek et al., 2019b). DVM may depend on species and environment (e.g., foraging, locomotion cost-saving, thermoregulation, navigation), yet their drivers have only recently begun to be investigated in sharks with the development of sophisticated technologies such as archival tags (Weihs, 1973; Carey and Scharold, 1990; Klimley, 1993; Andrzejaczek et al., 2019b) and being a complex behaviour with some species either not performing or performing reverse DVM, which in turn were influenced by the regional oceanography (Sims et al. 2005). While the DVMs have been linked to zooplankton avoiding visual predation, pelagic predators are then mimicked throughout the food chain to optimize prey encounter effectiveness (Hays, 2003) and more recently, associated with thermoregulation and/or foraging (Pade et al., 2009; Campana et al., 2011; Queiroz et al., 2012; Andrzejaczek et al., 2019b; Watanabe et al., 2021). Although DVM is a mechanism for apex predators to maintain an optimal body temperature (Teo et al., 2006) diving into deep colder waters to reduce metabolic costs and swimming near the surface to rewarm, maintaining their optimal temperature (Campana et

al., 2011) and therefore behaviourally thermoregulate at the surface (Thums et al., 2013). Ectotherms may boost their fitness in the absence of high levels of predation by selecting an optimum combination of thermal and foraging resources (Sims et al., 2006). Thus, representing a behavioral mechanism that balances the increased energy costs linked to night-time foraging in shallow and warm waters with reduced activity in deep and cold waters during the daytime that decreases their metabolic rate (Sims et al., 2006; Vedor et al., 2021b). There is also evidence that these may improve navigation by using magnetic, chemical, topographic, electric, and light signals that change along the vertical gradient (Watanabe et al., 2021).

Blue sharks adopted either a surface-oriented or a depth-oriented diving pattern, often switching between both. In the surface-oriented period, sharks usually spent more time at or near the surface, making frequent deep dives below 200 m (e.g., Fig. 6), and often associated with thermally stratified waters (e.g., Fig. 8-b). Likewise, some of them spend a significant amount of time at the warm surface layer above the thermocline as shown for blue sharks in the Pacific Ocean (Weng et al. 2005), where they spend 65% of their time above 50 m. Blue sharks off Hawaii often moved within the upper 220 m, with infrequent dives below 500 to 600 m (Moyes et al. 2006). Surface-oriented behaviour has been reported in other studies (e.g., Sepulveda et al., 2004; Weng et al., 2005; Queiroz et al., 2010), seeming to be a result of higher probability of prey abundance or encounter (Sims et al. 2003). Thus, suggesting that the epipelagic zone is an important foraging habitat for oceanic predators (Queiroz et al., 2010; Vedor et al., 2021b). Other studies associated this behaviour with areas where prey typically aggregates near the surface (Sims et al., 2006; Campana et al., 2011; Vedor et al., 2021b). Additionally, by linking dive profiles with horizontal movements and environmental gradients, it was shown that blue sharks appear to forage near the surface in productive areas of the north Atlantic, where surface longliners also concentrate their activities (Queiroz et al., 2012). The depth-orientated behaviour (e.g., blue3 and blue10) was observed when sharks spent a brief amount of time or no time on the surface and performed widespread deep dives, demonstrating oscillatory movements at depths ranging from 200 – 669.3 m. The blue10 is the only female tagged and showed fresh mating scars. Previous research on the north Atlantic blue shark aggregation hypothesised that mating scars on subadult and immature females indicate opportunistic mating and

subsequent sperm storage during this seasonal aggregation (Casey, 1985; Nakano and Stevens, 2008; Calich et al., 2015; Howey et al., 2017). Studies indicate that intermediate SST levels occur around the Azores, with large mature females lacking in catch data from July to November (Vandeperre et al., 2014b; Coelho et al., 2018; Druon et al., 2022). Howey et al. (2017) showed that female blue sharks occupied cooler temperatures than males, indicating that temperature has sex specific biological significance in this species. Due to the aggressive behaviour of mating males and the risk of injury (Sims, 2005), females may venture into these areas only when mating is crucial (Druon et al., 2022). This separation reduces the chance of encountering an unnecessary mate without increasing the likelihood of prey encounter (Howey et al., 2017). Additionally, the skin of females is thicker than male skin (Pratt, 1979; Druon et al., 2022), resulting in higher tolerance to low temperatures (Vandeperre et al., 2014a) and, ultimately, an expanded fundamental niche (Howey et al., 2017). A late spring/early summer breeding season for blue sharks in the north Atlantic has been hypothesized (Pratt 1979; Queiroz et al., 2010). Longline fisheries catch records verified the presence of dense, adult male blue shark aggregations in offshore waters and submerged seamounts south of the Azores, which are most likely used as mating areas (Litvinov, 2006; Queiroz et al., 2010).

The “V” and “U” shaped dives presented in our study have been identified in several species of mammals (Beck et al., 2003; Halsey et al., 2007), seabirds (Tremblay and Cherel, 2000; Cook et al., 2011), marine turtles (Hochscheid et al., 1999; Seminoff et al., 2006) and sharks (Gleiss et al., 2011b; Queiroz et al., 2017). These combined behaviours were often observed prior to prey investigation events suggesting that blue sharks may have been searching for visual or olfactory cues through the water column (Carey et al, 1990: Klimley et al., 2002; Nakamura et al., 2011; Andrzejaczek et al., 2019a). As shown by some research with harbor seals and penguins, eating habits and an extended bottom phase in U-shaped dives are positively correlated (Carroll et al., 2014; Viviant et al., 2014). Our results demonstrated that U-shaped dives of blue sharks occurred when sharks dived and remained at a specific depth for extended periods of time, probably to forage on prey aggregated in discrete horizontal layers (Wilson and Block, 2009). Additionally, the V dives in this study were performed at a wide range of depths with short durations, further suggesting an exploratory or transiting behaviour (Horodysky et al., 2007; Wilson and Block, 2009; Gleiss et

al., 2011b, 2013; Queiroz et al., 2017). Likewise, high-resolution dive depth profiles were analyzed for two pelagic shark species with contrasting feeding strategies in the north Atlantic (Queiroz et al., 2017). They aimed to examine blue (*P. glauca*) and basking sharks' (*Cetorhinus maximus*) movement patterns in relation to environmental heterogeneity, and as the results in this present study showed, U- and V-shaped dives were the most performed by both species (~70% of total dives). V-shaped dives have been attributed to transiting or prey searching behaviours through the water column, across different depth layers. Since the trails of different odours propagate horizontally, marine animals may increase their chances of detecting olfactory cues (Carey and Scharold, 1990; Pade et al., 2009; Queiroz et al., 2017). The U-shaped dives are defined by typifying foraging behaviour (Queiroz et al., 2017) once they are characterized by a bottom phase of an extended duration at a constant depth, perhaps reflecting foraging on aggregated prey areas (Austin et al., 2006). Queiroz et al. (2017) suggested that U-shaped dives of tracked basking and blue sharks emerged when sharks dived and remained at a specific depth, most likely to forage on prey aggregations. Also, their results showed that in blue and basking sharks, characteristics of "V" and "U" shaped dives changed with environmental field gradients, with mean depth and changes in mean depth generally decreasing with increasing levels of chlorophyll, whereas ascent speeds displayed a positive correlation. Thus, confirming the optimal foraging theory which implies that a predator duration in a particular prey patch is probably associated with its richness (Stephens and Krebs, 1986). Although we performed a visual analysis, for larger datasets, the 'diveMove' package and custom-written programming techniques in R can be implemented.

Blue sharks demonstrated negative buoyancy, as indicated by reduced tailbeat activity (i.e., lateral acceleration) during decent in relation to ascent. According to Schmidt-Nielsen (1972), especially for the ram-ventilating fishes that never stop swimming, locomotion is one of the most energetically costly and important behaviours. In that way, motion sensors such as accelerometers have been implemented to the study of swimming energetics and kinematics (Payne et al., 2016b; Whitney et al., 2019). Previous studies have shown that several shark species, to reduce the mechanical cost of swimming, often gliding during descents, whilst ascents are characteristic of active swimming due to their negative buoyancy (Weihs, 1973; Gleiss et al., 2011a, 2011b; Nakamura et al.,

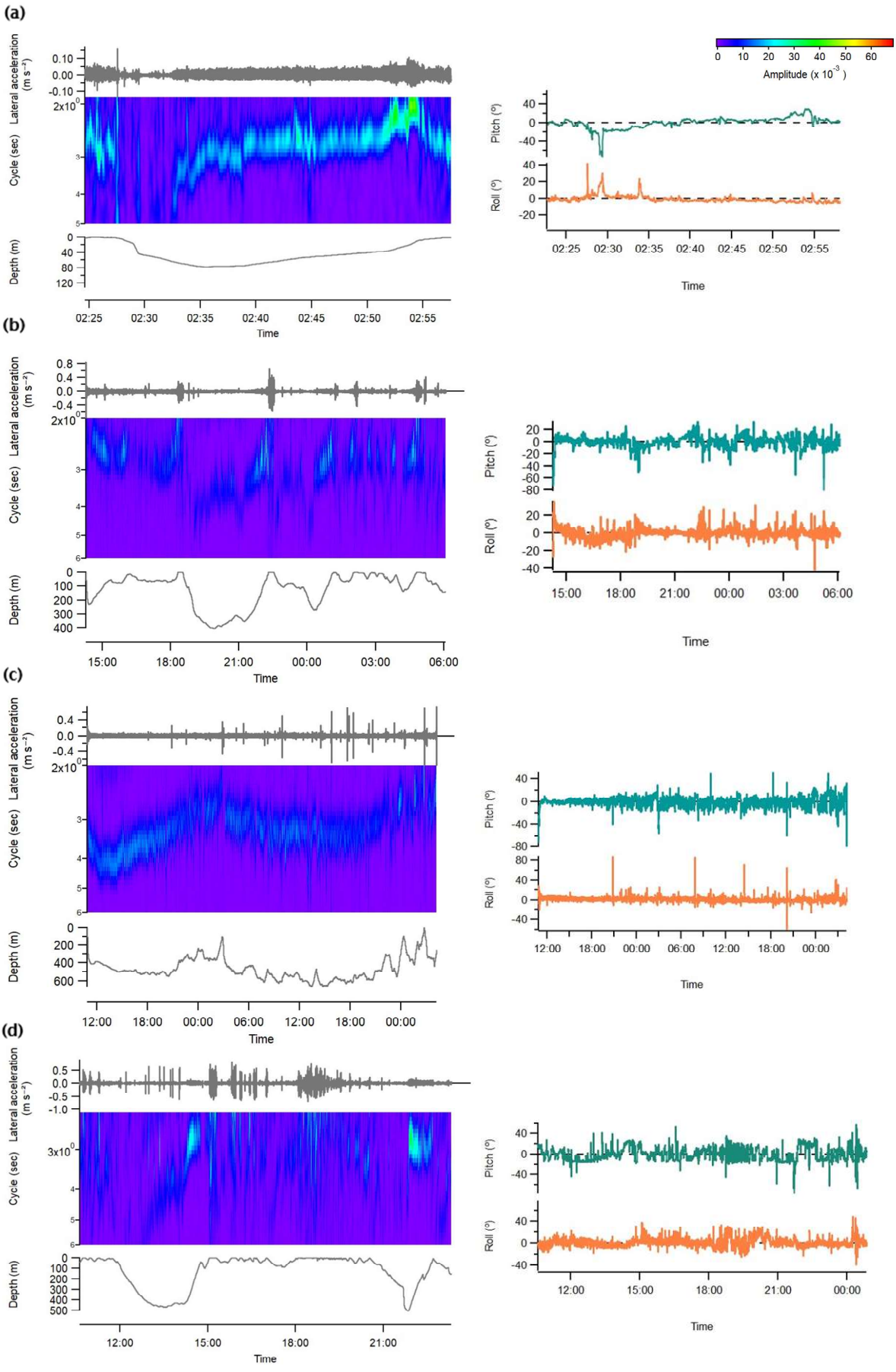

(a)
Lateral acceleration (m s⁻²)
Cycle (sec)
Depth (m)
Time
Amplitude (x 10⁻³)
Pitch (°)
Roll (°)
(b)
(c)
(d)

Figure 5. Lateral (i.e., surging) acceleration, spectrogram and depth profile. Negative buoyancy during dive phases in blue sharks (*Prionace glauca*) with a decrease in tailbeat amplitude as the shark oscillates from descent to ascent phase. (a) Example of decrease in tailbeat amplitude, from blue2, with associated decreases in pitch angle. (b) Example of lower tailbeat amplitudes in descents during U-shaped dive followed by V-shaped vertical movement and higher tailbeats amplitudes during ascents, from blue5, with decreases or increases in pitch angles. (c) Example of depth-oriented diving pattern from blue10 (d) Example of U-shaped dive with long bottom durations followed by V-shaped vertical movement from blue12. Grey lines above the spectrogram represent the dynamic lateral acceleration (g); spectrograms are coloured based on the signal amplitude at a given TBF (i.e., the number of cycles per second (Hz)); grey lines below the spectrograms represent depth (m) profile. On the left, green lines in the angle plot denote the pitch angle of the shark (transition from the descent (-) to the ascent (+) phase); and the orange line represents the roll angle of the shark.

2011; Whitney et al., 2019). For deep-sea sharks that are positively buoyant, Nakamura et al. (2015) demonstrated the reverse pattern. As reported for tiger sharks (*Galeocerdo cuvier*; Nakamura et al., 2011) and Greenland sharks (*Somniosus microcephalus*; Watanabe et al., 2012), Watanabe et al. (2021) showed that gliding behaviour in blue sharks was observed during only 10 to 20% of total descent durations. This suggests that reducing energy expenditures by moving is not the primary reason for deep dives despite the decrease in sharks' tailbeat amplitude in our study.

The burst swimming events in our results, similarly to earlier studies (e.g., Watanabe et al., 2021), suggests that blue sharks may increase prey encounter rates by moving vertically. Therefore, selecting swimming strategies that maximize their energy surplus while foraging (Saraiva et al., 2023). Feeding episodes in several species have been observed and linked to bursts of speed to grab prey items, as well as potentially different body postures, thanks to acceleration and depth data. These variations in surging acceleration may be more consistent if we had the animal-borne video camera to confirm prey aggregations and foraging linked to these high-energy events (Watanabe and

Takahashi, 2013; Watanabe et al., 2014; Whitney et al., 2019). Thus, enabling us to detect equivalent burst swimming events as indications of prey capture attempts and contrasting prey searches from fine-scale habitat use (Heithaus et al., 2002; Nakamura et al., 2011; Papastamatiou et al., 2018). Another study examined the Greenland sharks, *Somniosus microcephalus*, that present very low stroke frequency and burst acceleration, actively predate seals that are faster swimming (Watanabe et al., 2012). Probably, this occurs because when sleeping in surface waters to avoid polar bear predation, it makes them more vulnerable to Greenland shark predation (Watanabe et al., 2012; Payne et al., 2014). For example, Nakamura et al. (2011) observed that tiger sharks (*Galeocerdo cuvier*) during consecutive V-shaped dives (i.e., "yoyo"), displayed burst swimming and prey capture events. W-shaped dives frequently occur coupled to V-dives and are typically linked to the same behaviour and functions. According to Queiroz et al. (2017), LV and RV dives may be related to feeding on aggregated prey at certain depth, resulting in the "stop" phase before or following exploratory V-type events. Despite that, we cannot exclude the possibility that burst swimming events recorded in this study may represent foraging attempts or even evasions from bigger predators (e.g., bigger sharks). Nevertheless, considering the size of the sharks tagged in our study, encounter rates with predators are probably very rare.

The vertical diving behaviour of blue sharks may be associated with physical properties of the water column, which might directly or indirectly impact the depth and spatial distribution of prey resources (Sims et al., 2005; Queiroz et al., 2010). Therefore, this pattern in vertical distribution of the studied species fluctuated significantly within and between individuals, with behavioural phases mainly associated with environmental variables (e.g., DO and temperature) and likely variations in prey distribution, density, or type in deeper water. Endotherms (e.g., tunas) disable heat exchangers during ascent throughout the day to allow quick warming at the surface and reactivate them on descent to save heat, influencing how far they migrate vertically to rewarm after eating at depth (Holland et al., 1992; Andrzejaczek et al., 2019b). Since blue sharks lack similar heat exchange structures, they cool at a more rapid rate, diving back to the surface every few hours, supposedly to rewarm (Carey and Scharold, 1990). The blue sharks tracked in this study spent a significant amount of their time at the warm surface layer, suggesting that spending considerably time at the surface is

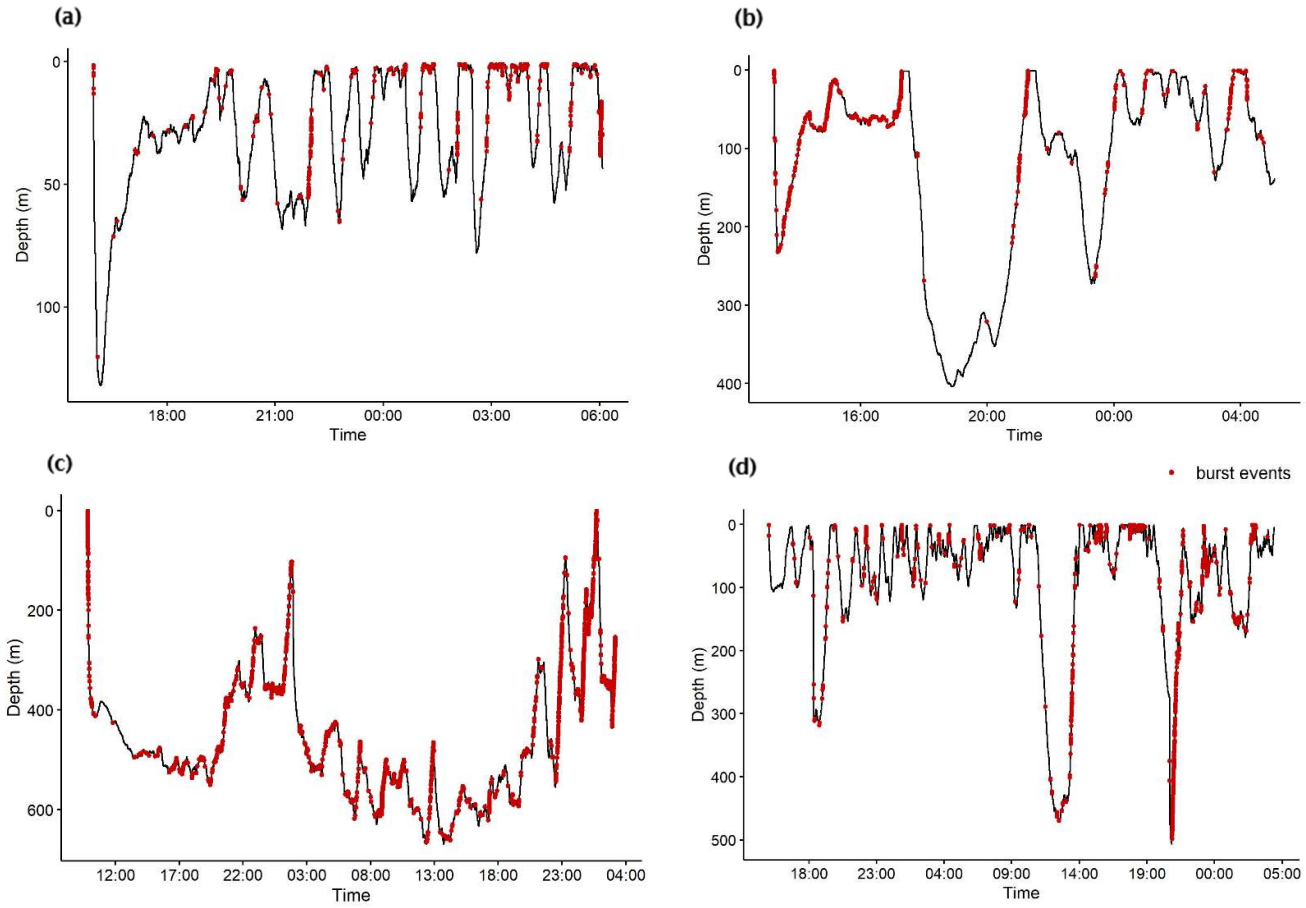
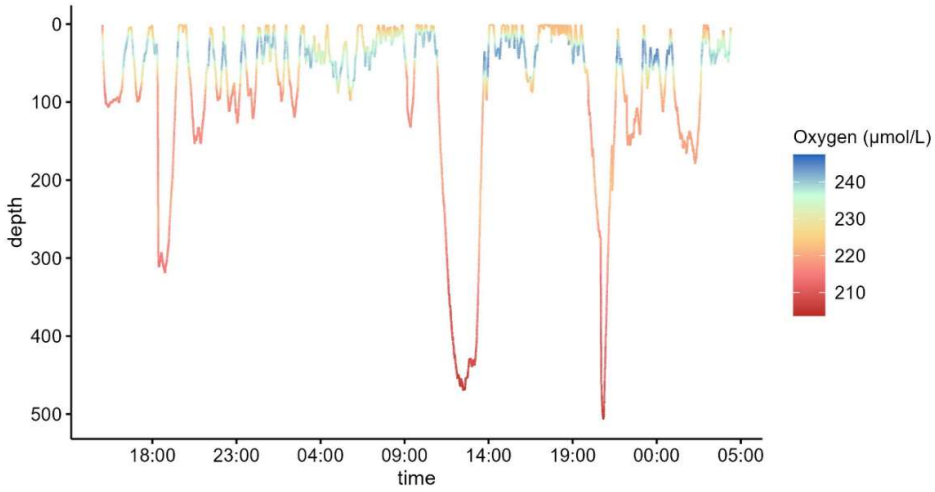


Figure 6. Example of bursting swimming events. Thermoregulation and/or foraging behaviours during depth profile. Red circles on the depth represent the timings of burst swimming events (i.e., signals of prey capture attempts) based on the 99th percentile of ODBA data. (a) blue2; (b) blue5; (c) blue10; (d) blue12.

linked to behavioural thermoregulation (Carey & Scharold 1990, Cartamil & Lowe 2004; Queiroz et al., 2010). For instance, Carey and Gibson (1987) studied blue shark swimming behaviour and proposed that when they stayed at the surface for extended periods of time, they performed deep dives until their bodies were fully rewarmed. In this approach, recurrent deep dives in blue sharks may be primarily driven by behavioural thermoregulation related to foraging (Watanabe et al., 2021). Blue sharks conclude their deep dives as soon as their muscle cools to 15°C, with water temperatures ranging from 7 to 26°C (Carey et al., 1990). As identifying the same minimum muscle temperature, Watanabe et al. (2021) concluded that blue sharks' regular deep-diving behaviour can be explained by their drive to maintain body temperature within a narrow range while foraging through the water column. Pelagic predators perform wide-ranging distributions

and are also efficient divers, exploring a multitude of vertical habitats from a range of depths (Schaefer and Fuller, 2002; Wilson et al., 2005; Howey-Jordan et al., 2013; Vedor et al., 2021b) according to environmental conditions and prey availability (Dagorn et al., 2006; Campana et al., 2011; Thorrold et al., 2014). As mentioned before, many shark species do not stay at a particular depth but exhibit vertical return movements with various cycles and amplitudes (Hays, 2003; Andrzejaczek et al., 2019b; Watanabe et al., 2021) with their depth profiles being similar to those of airbreathers (e.g., marine mammals) (Watanabe et al., 2019; Watanabe et al., 2021). DO sensor tag results to date confirm that a small range of high DO concentrations are encountered during their vertical movement. Thus, the blue sharks in this present study experienced vertical space use under normoxia conditions combined with shifts in temperature throughout the water column. Our study showed that depth-temperature profiles of the water column indicated blue sharks were diving through stratified water, with a thermocline at approximately 50 m (Fig. 4). The Azores archipelago display large-scale regional and seasonal fluctuations in oceanographic conditions (Lafon et al., 2004), with minimum chlorophyll-a concentrations observed during the summer, when SST is typically higher (maximum of 27ºC; Martins et al., 2007; Santos et al., 2013; Amorim et al., 2017). In contrast, the maximum chlorophyll-a concentrations correspond to periods of lower SST, usually occurring during winter (average of 15ºC) and spring (Martins et al., 2007; Santos et al., 2013; Amorim et al., 2017). A deep mixed layer is present at ~150 m depth during the winter, while a seasonal thermocline usually develops between 40 and 100 m depth in the summer (Santos et al., 1995; Amorim et al., 2017).



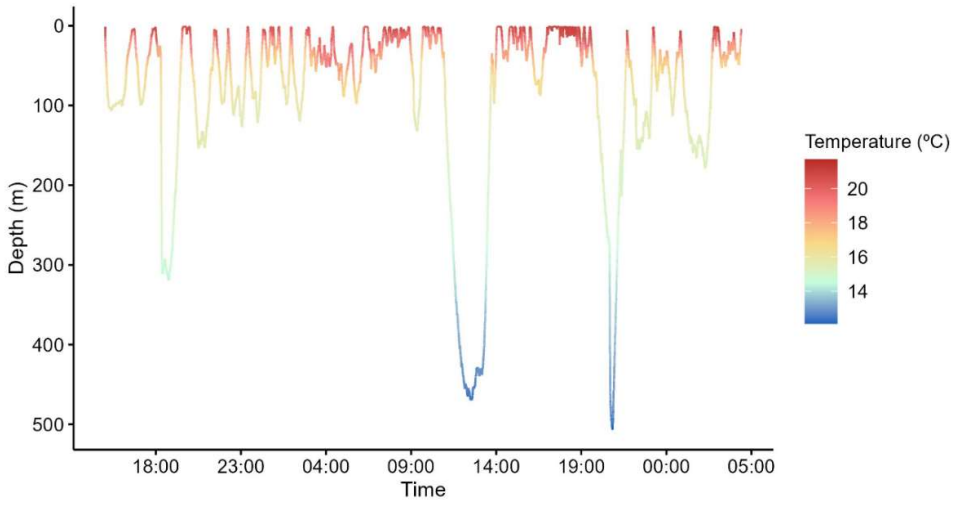


Figure 7. Depth-oxygen and depth-temperature profiles of the blue12.

The combination of water temperature and DO has been demonstrated to be a significant limitation influencing vertical range in previous research of pelagic fish (Nasby-Lucas et al., 2009; Abascal et al., 2011; Coffey et al., 2017; Vedor et al., 2021a). Biologging studies investigated a reduction in dive depth associated with OMZs for large pelagic predators, such as billfishes and sharks (Prince et al., 2010; Stramma et al., 2012; Coffey et al., 2020; Vedor et al., 2021a). Vedor et al. (2021a), using satellite tracking data, predicted that blue shark habitat will become even more compressed above OMZs in the future due to the combined effects of ongoing ocean deoxygenation (Breitburg et al., 2018), elevated sea surface temperature and increased surface-layer net primary production, resulting in higher shark exposure and susceptibility to capture by surface fisheries. They showed that blue and mako sharks swimming above the OMZ, linked to high SST and greater phytoplankton production, made fewer deep dives with reduced dive depth in comparison to oxygenated waters. Finally, they emphasized the importance of tighter fisheries restrictions to prevent deoxygenation impacts on sharks, as longliners currently target certain OMZ areas where shark catches are enhanced. Future studies might investigate how predators respond to oxygen gradients, OMZs, and consequently, habitat compression, deploying accelerometers equipped with oxygen sensors comparing areas with various DO profiles (e.g., normoxia and hypoxia conditions).

A lack of correlation between ODBA (i.e., swimming activity) and the environmental variables was not unexpected given that sharks predominantly

experienced normoxia conditions, with high DO concentrations. Despite our results, an understanding of the relationship between ODBA and environmental data is essential to developing spatial-temporal predictive maps as powerful indicators of the odds of the occurrence of blue sharks. Also, when comparing areas with different DO profiles, it allows us to know if the behavior of blue sharks is being affected by the lack of O2 and whether they or their prey are being compressed to the surface layers.

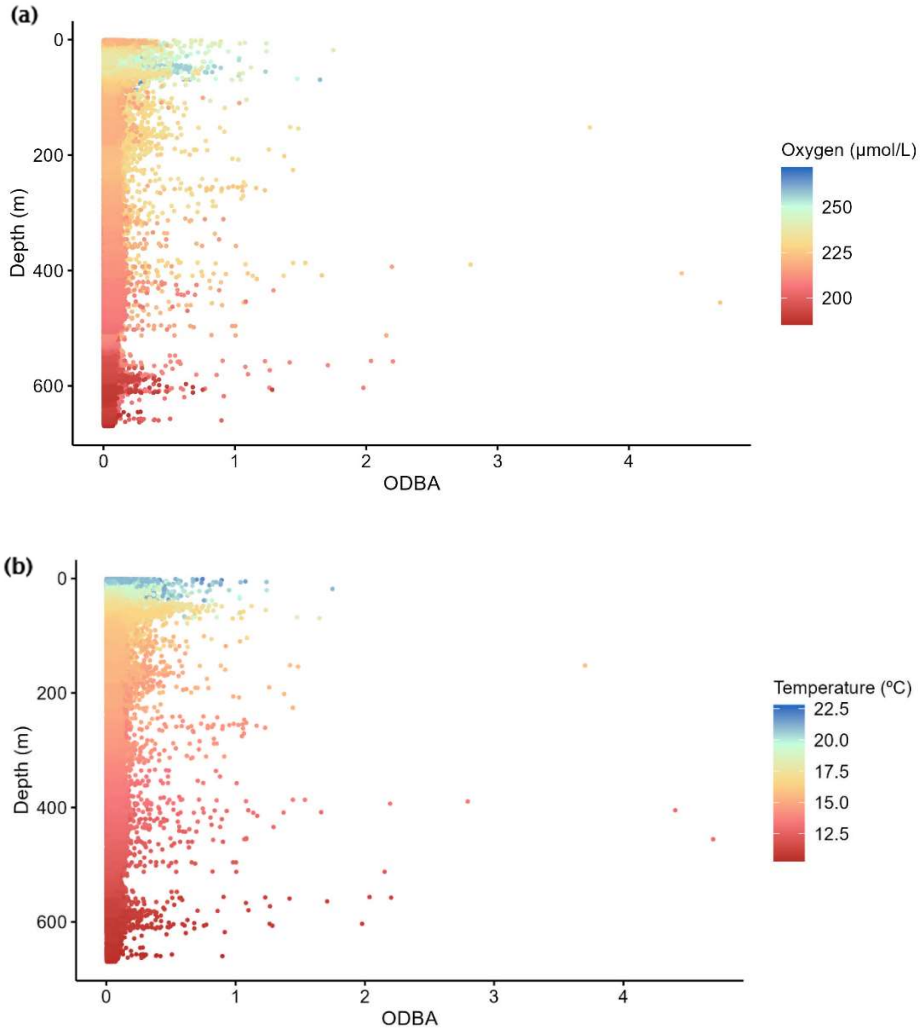


Figure 8. Scatterplot shows the relationship between overall ODBA and depth profile. (a) colour: oxygen; (b) colour: temperature.

By combining dive profiles with horizontal movements and oceanographic gradients, blue sharks were found to forage closer to the surface in productive areas of the north Atlantic, where surface longliners also concentrate their activities (Queiroz et al., 2012). Queiroz et al. (2019) showed that major high

seas fishing activities are currently centered on ecologically important shark "hotspots" worldwide and, therefore, these high productivity regions may be ideal habitat targets for the implementation of large-scale high seas marine protected areas (MPAs) around ecologically important hotspots not only for blue sharks, but also for other large pelagic predators' space-use. Also, satellite monitoring can give real-time signals of where sharks are aggregating (hotspots) and where fishermen interact with them helping to monitor these high-risk areas more efficiently, which will be important for their conservation and management in the face of high fishing pressure.

Conclusion and Future Perspectives

This study presented the first insights into the fine-scale movements of blue shark (*Prionace glauca*), thus, having implications in future assessments of their responses to climate-driven changes in the ocean environment. Since sharks are a species of special conservation concern due to its relatively sluggish life-history characteristics, commercial importance, and high capture rates, biologging techniques have been central to identifying how human threats and climate change conditions drive shifts to their patterns in the distribution and behaviour. Accelerometers allow to distinguish between the activity state of a shark by periods of swimming or resting according to the analysis of fine-scale tailbeat frequency and amplitude, having several main applications (Gleiss et al., 2009a; Whitney et al., 2019). Monitoring the foraging behavior of animals such as sharks in the wild is challenging since most species cannot be observed in the wild unless they are attracted by bait or chum (Payne et al., 2014).

Blue sharks, *Prionace glauca*, have extensive vertical niches (Vandeperre et al., 2014; Queiroz et al., 2017; Queiroz et al., 2019) and they appear to be tolerant to a wide variety of environmental situations, including water temperatures ranging from 4˚C to 30˚C (Howey et al., 2017; Vedor et al., 2021a). Therefore, they have been proposed as a model for studying foraging-thermoregulation relationships (Watanabe et al., 2021). Using accelerometer tags with video cameras, to monitor diving behaviour (e.g., foraging), and intermuscular temperature sensor, Watanabe et al. (2021), despite their small sample size, demonstrated that blue sharks during repeated deep dives behaviourally thermoregulate and forage. They keep their body temperature within a small range by beginning ascents before their bodies become too cold and beginning

descents before their bodies become excessively warm, resulting in a muscle temperature range that was narrower than ambient temperature. Additionally, it was established that blue sharks search for prey (e.g., fish and squids) distributed extensively in the water column by comparing burst swimming events and video. In that way, incorporating animal-borne video cameras and internal temperature sensors into our tags would be crucial once time-depth records alone would be insufficient to distinguish foraging and fine-scale habitat use. This data associated to the analysis of all the fine-scale behaviour data (3D movements, habitat, and prey field) would offer currently unavailable insights into the physiological processes behind foraging movements as well as how top predators react to variations in prey density in heterogeneous environments.

Most previous studies were limited by interpolated, modelled DO values from oceanographic data sets that were matched with locations along the shark' tracks (Sims, 2019; Vedor et al., 2021a), differing from actual DO concentrations in the selected habitats. A recent study predicted that blue shark habitat will become more constricted above OMZs in the future given to increasing ocean deoxygenation, being more prone to overfishing due to elevated fishing intensity leading to higher CPUE than in more oxygenated nearby areas (Vedor et al., 2021a). The deployment of accelerometers with oxygen sensors in this present study demonstrated how blue sharks respond directly to oxygen gradients. Thereafter, tagging sharks in areas with different DO profiles (i.e., normoxia and hypoxia) will enable future research on their physiological responses to low DO concentrations (Sims, 2019).

Under a scenario of global warming and decreasing oxygen levels, the combination of spatial-temporal predictive maps of the relationship between ODBA (i.e., swimming activity) and environmental data will highlight ocean spots of possible high shark occurrence. Such information is necessary to fully understand the potential effects of predicted climate changes on the vertical distributions of pelagic sharks. Additionally, a two-state Hidden Markov Model (HMM) could be used to identify behavioural states based on tailbeat or ODBA (Ferreira et al., 2018; Coffey et al., 2020) and to determine the probability of sharks switching or persisting within less active/more active behavioural states. Associating energy expenditure measures (e.g., ODBA) with distinct behavioural states and temperature data, would enable to determine the metabolic costs linked with foraging movements under different environmental gradients and

thus assess how foraging decisions (e.g., targeting a prey or opportunistic feeding, burst swimming and speed changes) are related to achieve an energetically optimal behaviour (Whitney et al., 2019; Wilson et al., 2015).

Blue sharks are the most commonly taken by commercial fisheries, with populations dropping by ~40% since the 1970s (Baum et al., 2003; Pacoureau et al., 2021), owing mostly to the significant mortality risk resulting from overfishing and making up ~90% of the total reported catch of pelagic sharks in the Atlantic Ocean (Oliver et al., 2015; Queiroz et al., 2016, 2019; Vedor et al., 2021a). Although several research have been conducted on blue shark vertical behaviour (e.g., Carey et al., 1990; Campana et al., 2011; Queiroz et al., 2012; Braun et al., 2019; Vedor 2021a), the understanding of the fine-scale behaviour of oceanic adult blue sharks and their vulnerability to fishing is limited. In spite of recent establishment of blue shark fishing limitations in certain areas, the lack of knowledge in existing population estimations makes understanding shark fine-scale behaviour a priority for successful conservation management (Hammerschlag et al., 2016; Robinson et al., 2017; Boerder et al., 2019). Due to increased fishing pressure in recent decades, there is an increasing demand for proper management of blue shark stocks (e.g., in the Atlantic by ICCAT, European Union, 2020; European Union, 2021; Druon et al., 2022). This study provided significant data into how physical oceanography (i.e., temperature and DO) influences the distribution and fine-scale behaviour of blue sharks (*Prionace glauca)* by associating their metabolic costs with foraging movements. Thus, emphasizing the potential vulnerability of this endangered species to the consequences of climate change (i.e., elevated sea surface temperature and deoxygenation). Such data is critical for adopting successful management strategies as well as projecting their future habitat loss or change (e.g., Queiroz et al., 2019 and Vedor et al., 2021).

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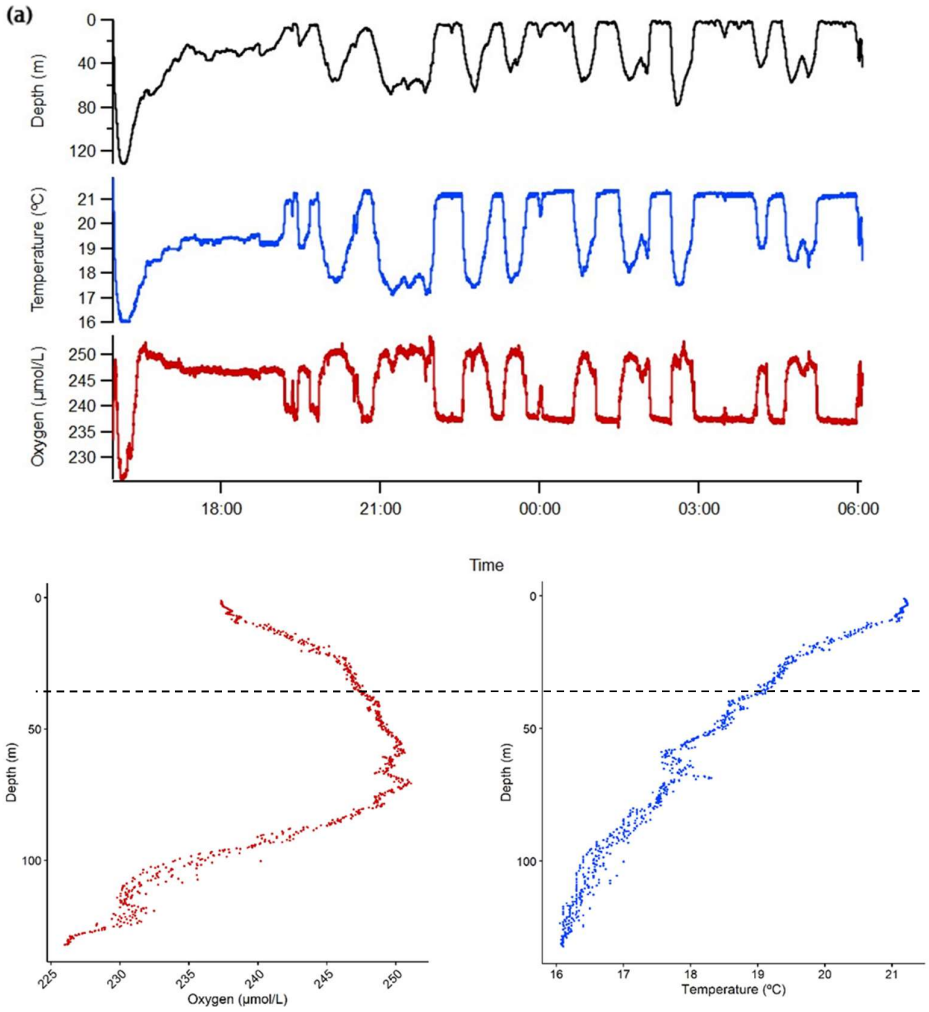
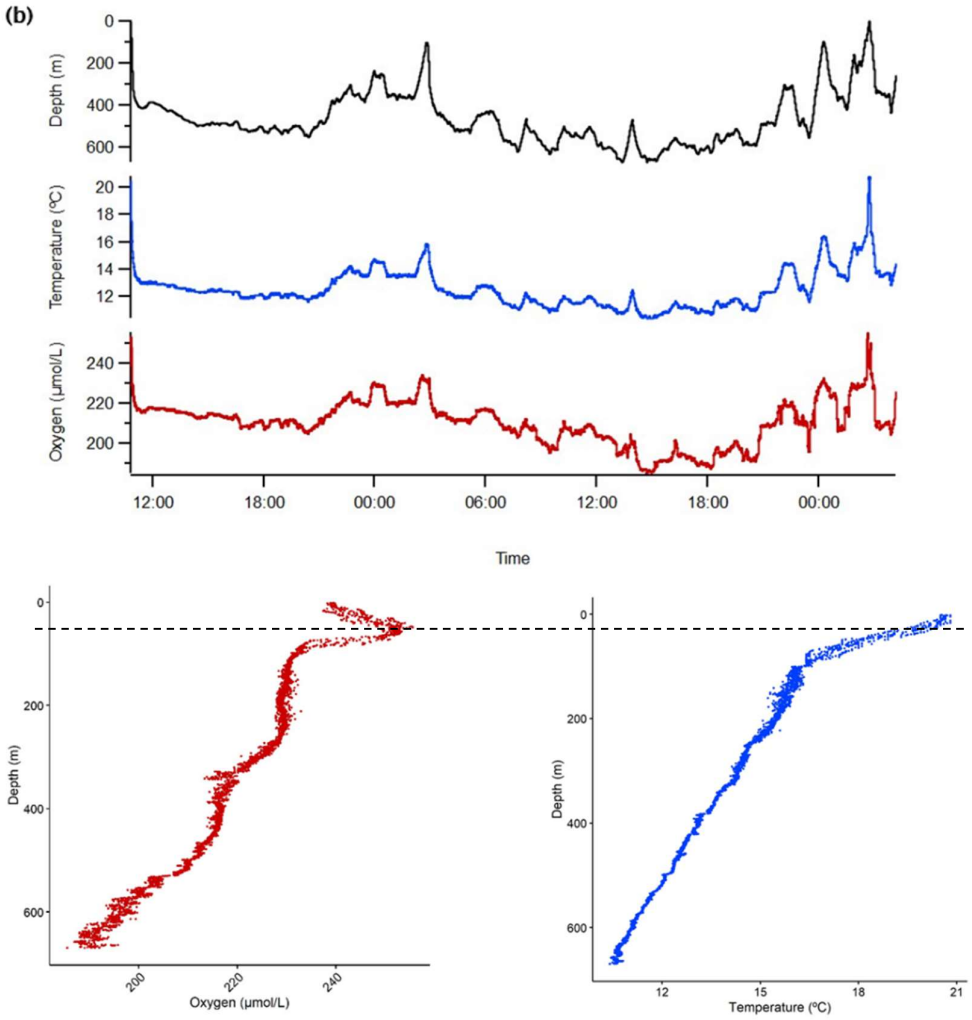
Supplementary materials




(b)
Depth (m)
0
200
400
600
Temperature (°C)
20
18
16
14
12
Oxygen (µmol/L)
240
220
200
12:00
18:00
00:00
06:00
12:00
18:00
00:00
Time
Depth (m)
0
200
400
600
200
220
240
Oxygen (µmol/L)
Depth (m)
0
200
400
600
12
15
18
21
Temperature (°C)

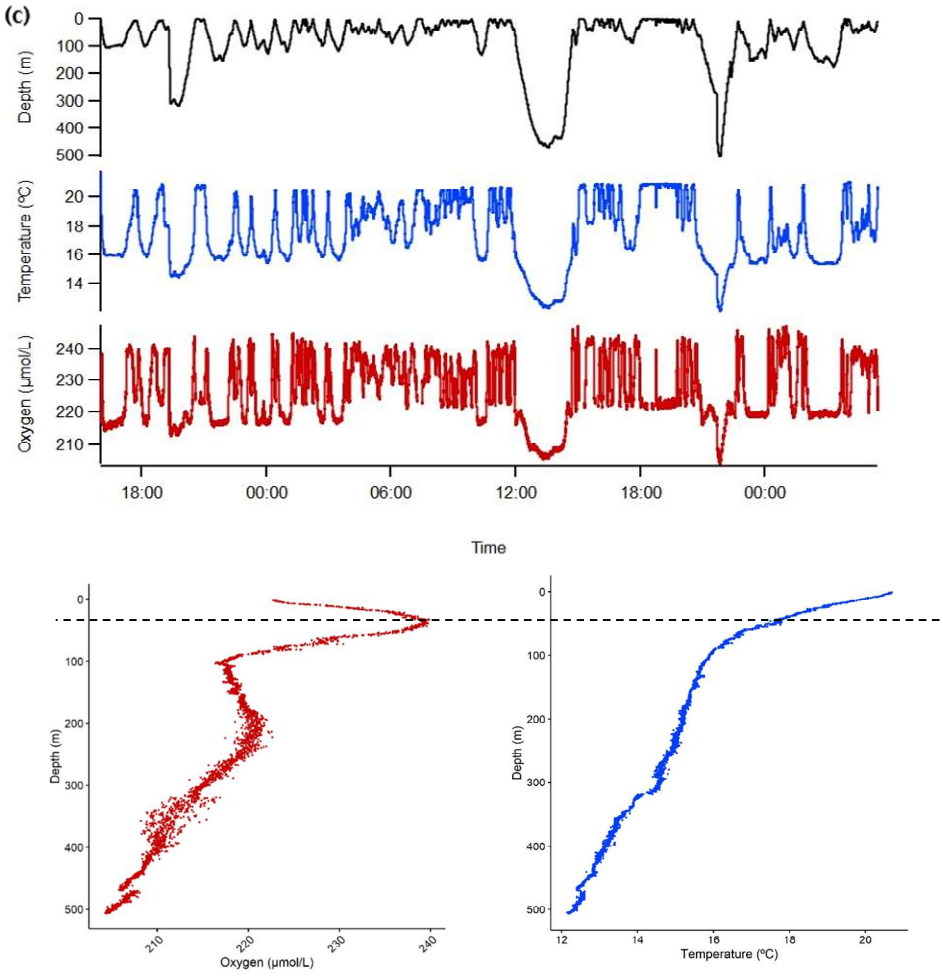


Figure S1. Full time-series of the depth profile, temperature, and oxygen from blue sharks in Azores outfitted with an acceleration data logger package displaying a regular diving behavior. Scatterplot shows the relationship between depth and oxygen (red), and depth and temperature (blue). (a) blue2; (b) blue10; (c) blue12. Dashed line: thermocline.

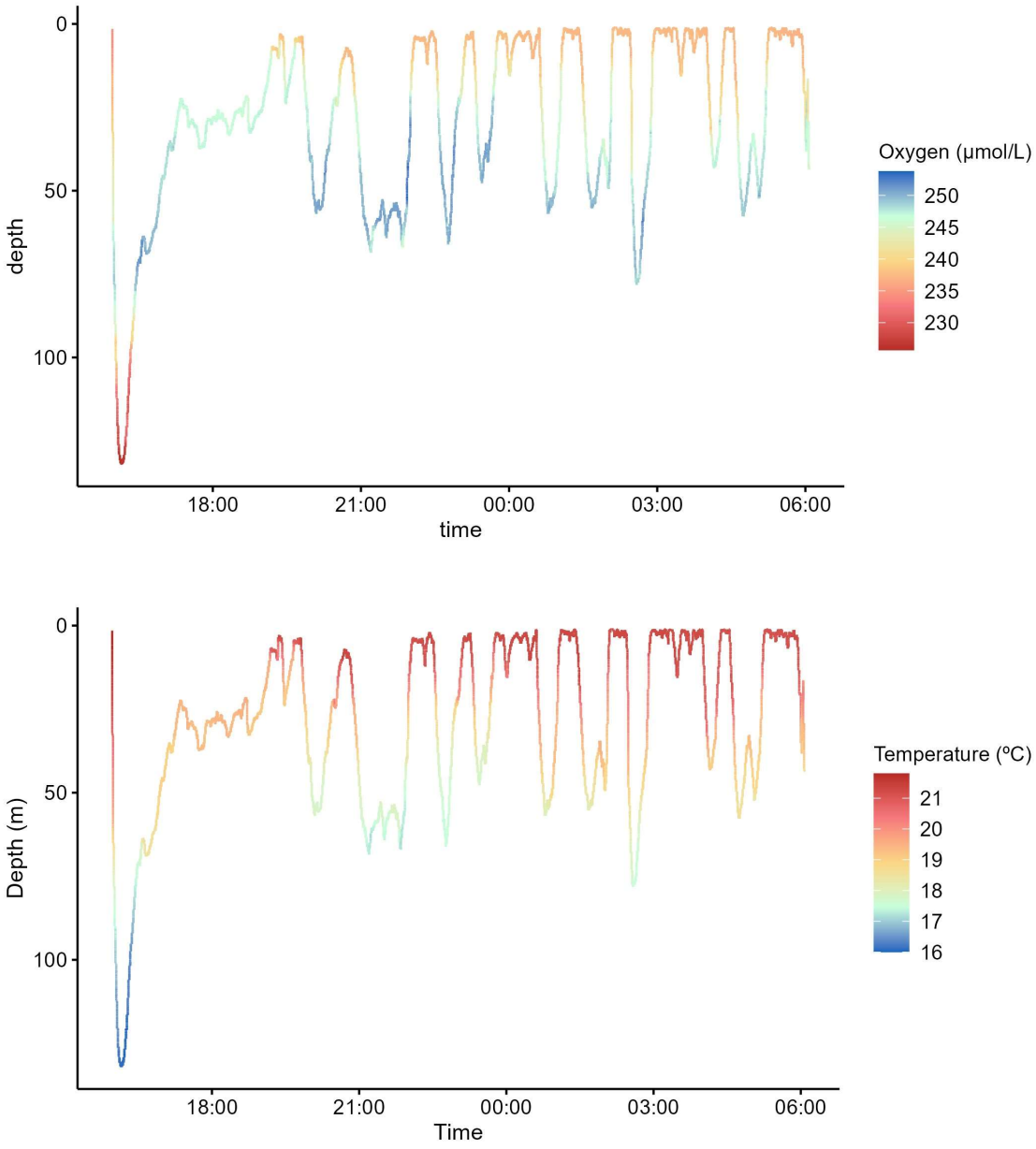


Figure S2. Depth-oxygen and depth-temperature profiles of the blue2.

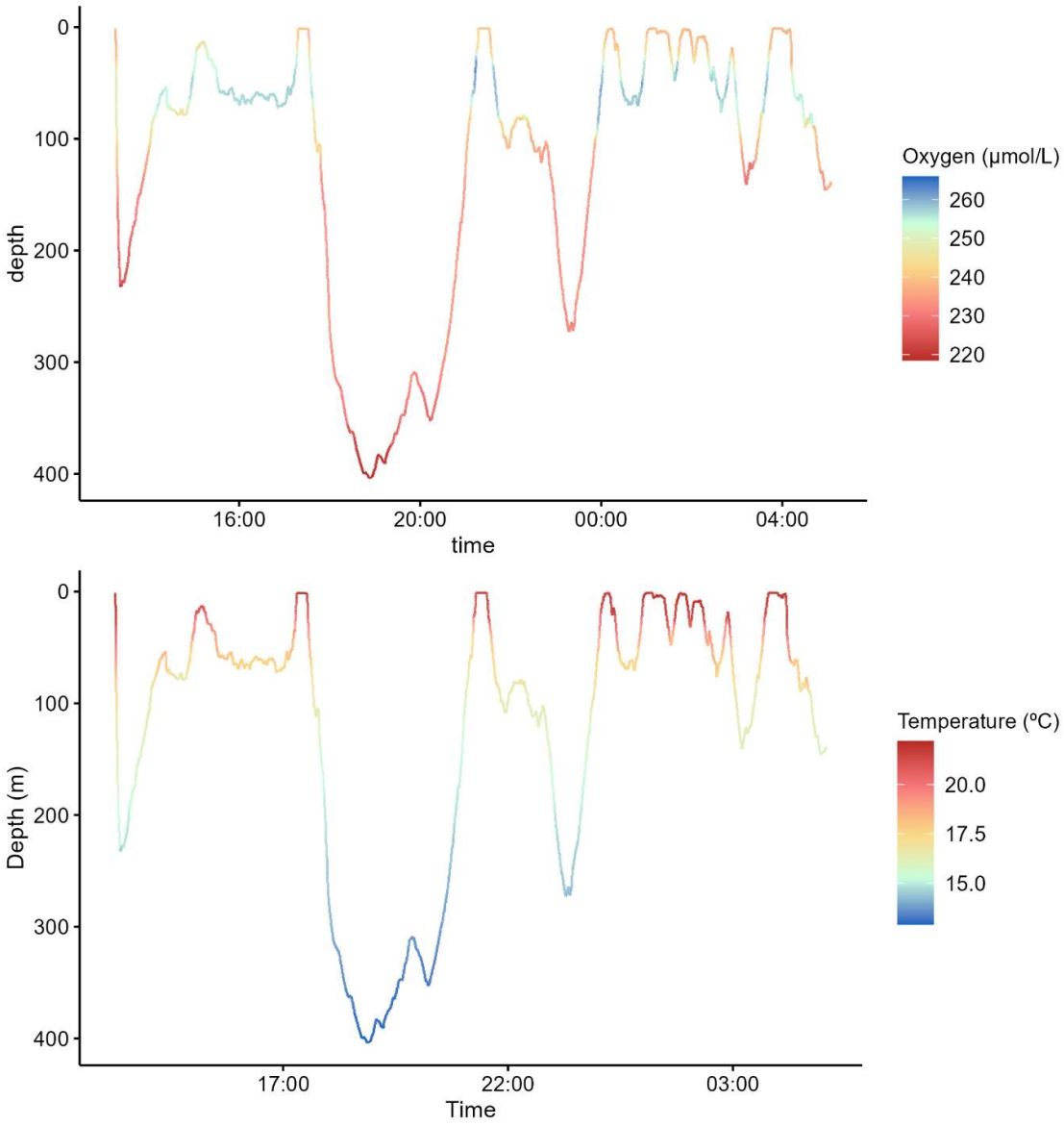


Figure S3. Depth-oxygen and depth-temperature profiles of the blue5.

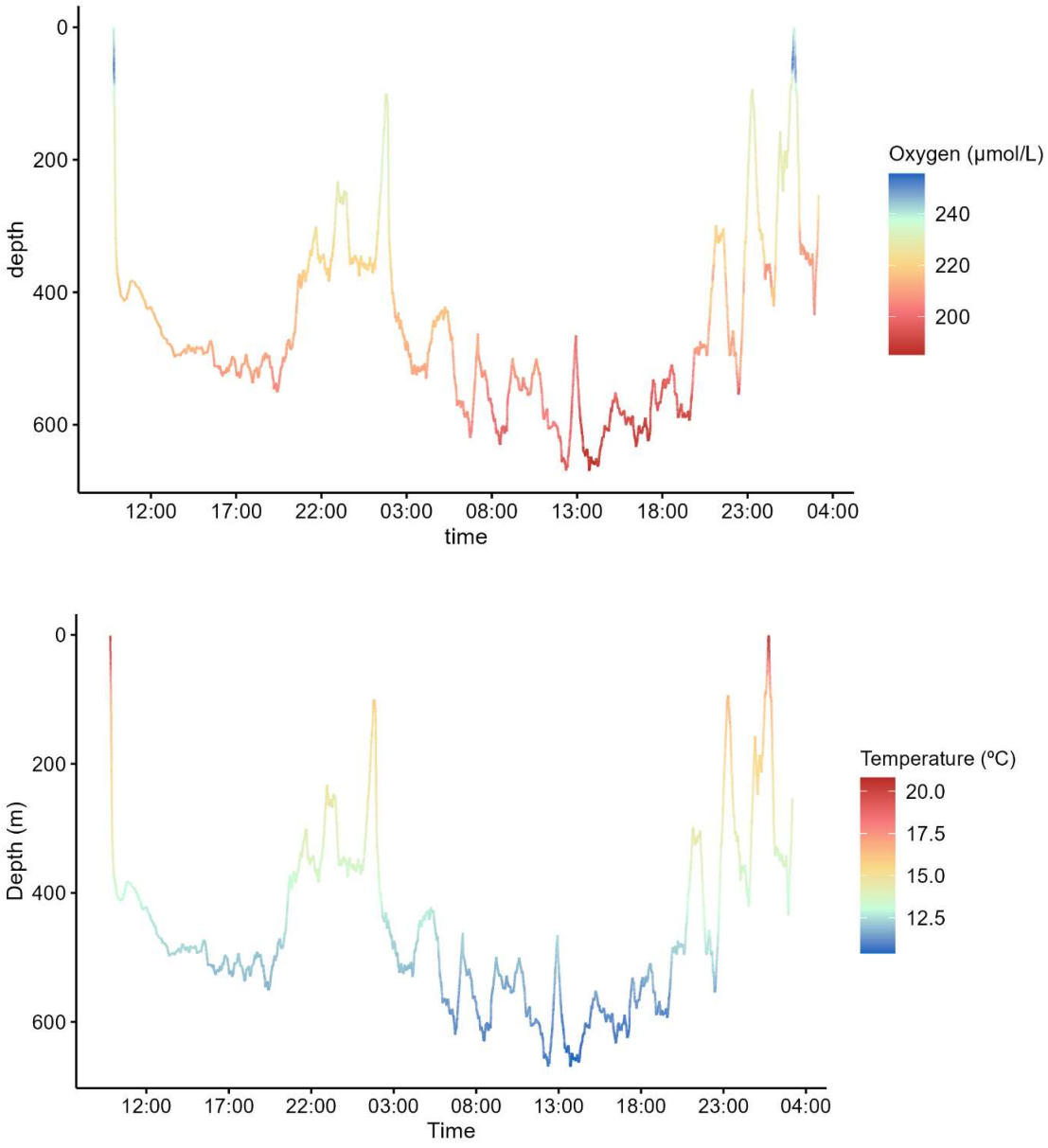


Figure S4. Depth-oxygen and depth-temperature profiles of the blue10.

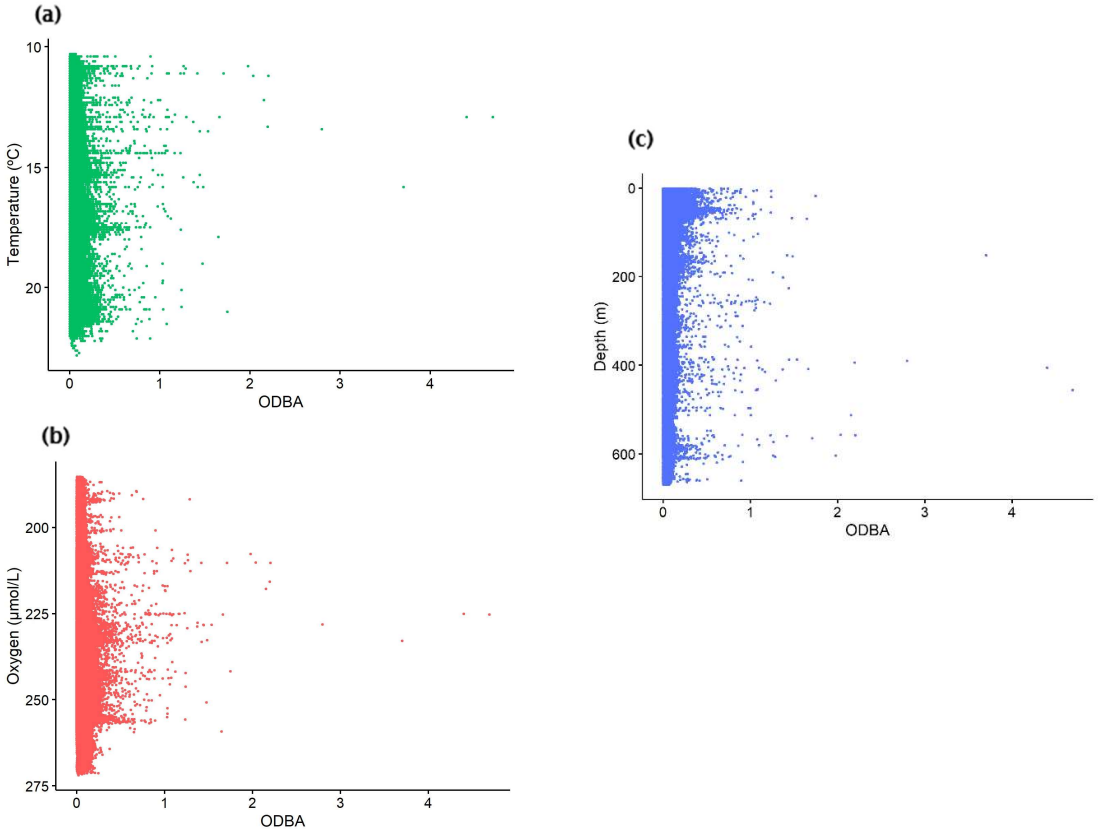


Figure S5. Scatterplots of the relationship between ODBA and environmental variables. (a) Temperature (ºC); (b) Oxygen (µmol/L); (c) Depth (m).

Table S1. Time-at-depth (%) for each tagged blue shark.

	Time-at-depth (%)										
Depth (m)	**blue2**	**blue3**	**blue4**	**blue5**	**blue6**	**blue7**	**blue8**	**blue9**	**blue10**	**blue11**	**blue12**
0–50	78.5	11.4	68.1	22.5	56	23.2	36.9	45	0.28	50.1	47.6
50–100	19.4	3.81	27	34.9	18	24.8	34.8	19.3	0.773	32.2	23.6
100–150	2.1	3.17	4.91	13.1	4.95	10.5	4.88	21.3	1.37	3.44	12.7
150– 200	–	3.1	–	4.62	4.51	5.87	1.68	10.1	1.6	2.41	4.26
200–250	–	4.32	–	4.88	8.38	3.07	1.83	4.32	2.06	2.67	1.93
250–300	–	4.86	–	3.55	6.41	4.42	2.26	–	2.69	0.382	2.02
300–350	–	29.3	–	7.98	1.8	6.73	2.75	–	8.22	2.07	1.96
350–400	–	35.9	–	7.35	–	3.84	8.73	–	11.4	1.5	0.947
400–450	–	4.2	–	0.996	–	5.28	6.13	–	8.56	4.43	2.66
450–500	–	–	–	–	–	8.98	–	–	17.8	0.788	2.16
500–550	–	–	–	–	–	1.37	–	–	20.9	–	0.188
550–600	–	–	–	–	–	1.12	–	–	13.3	–	–
600–650	–	–	–	–	–	0.389	–	–	8.72	–	–
650–700	–	–	–	–	–	0.434	–	–	2.33	–	–