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Mestrado em Biologia Marinha

Supervisors:
Nuno Queiroz
David Maria Aguiar Abecasis

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Abstract

Large pelagic predators have distinct physiologies (Block, 2005), extensive movements, and broad distributions, and they exert top-down control in open ocean ecosystems (Heithaus et al., 2008; Block et al., 2011), shaping the ecological structure and habitat use of communities and providing an indication of ocean state (Sims and Quayle, 1998; Sims, 2003; Campana, 2016; Boerder et al., 2019). Climate changes are expected to alter existing environments and generate new ones, potentially leading to local loss of organisms and their related ecosystem function (Corrales et al., 2018; Pinsky et al., 2019; Yeruham et al., 2020). Marine ecosystems are characterized by vertical gradients, defined by physical (e.g., temperature, light level, oxygen concentration) (Brill and Lutcavage, 2001) and biological properties (e.g., primary production). Temperature is one of the most significant abiotic factors influencing animals' distribution, behavior, and physiological performance, especially for ectotherms that cannot regulate their body temperature internally (Angilletta et al., 2002). Large marine ectotherms are generally adapted to live within a narrow temperature range, resulting in a thermal optimum that optimizes their physiological performance (Neill, 1979; Costa, 2018). We used archival tags to record the diving behavior, and muscle temperature of six blue sharks, *Prionace glauca* (Linnaeus, 1758). Consistent dive patterns were observed for all sharks, with a wide variation of depth (1.60 - 711.10 m). The thermal gradient of the water column was proportional to the depth. All individuals had a similar ambient temperature on average (between 17.06 ± 4.53 ºC and 20.06 ± 2.19 ºC). Although the muscle temperature showed slower and smoother fluctuations, was directly influenced by the ambient temperature). Their high thermal inertia allows blue sharks to make short foraging trips to deep cold waters without significantly reducing their body temperature, as they warm up again at shallow depths (Watanabe et al., 2019). In general, muscles presented a higher and stricter range of temperature. Blue sharks shift vertical swimming directions (descending or ascending) before their body temperature reaches the ambient water temperature, presenting a greater whole-body heat transfer coefficients during the warming (ascendent) phase. Thus, this thermoregulatory behavior linked to the search for food explains blue sharks' vertically and geographically broad thermal niches. Understanding how species' physiology, behavior, and ecology interact with environmental temperature is critical for predicting changes in their movement, distribution, and ecological function in response to climate change and improving conservation measures.

Keywords: Climate change, Ectothermic, Thermoregulation, Muscle temperature, Heat exchange

Resumo

Os grandes predadores pelágicos têm fisiologias distintas (Block, 2005), movimentos extensos, amplas distribuições e exercem um controlo de topo nos ecossistemas de oceano aberto (Heithaus et al., 2008; Block et al., 2011), moldando a estrutura ecológica e a utilização do habitat das comunidades e fornecendo uma indicação do estado do oceano (Sims e Quayle, 1998; Sims, 2003; Campana, 2016; Boerder et al., 2019). Prevê-se que as alterações climáticas alterem os ambientes existentes e gerem novos, conduzindo potencialmente à perda local de organismos bem como, da sua função ecossistémica (Corrales et al., 2018; Pinsky et al., 2019; Yeruham et al., 2020). Os ecossistemas marinhos são caracterizados por gradientes verticais, definidos por propriedades físicas (por exemplo, temperatura, nível de luz, concentração de oxigénio) (Brill e Lutcavage, 2001) e biológicas (por exemplo, produção primária). A temperatura é um dos fatores abióticos mais significativos influenciando a distribuição, o comportamento e o desempenho fisiológico dos animais, sobretudo no caso dos organismos ectotérmicos, que não conseguem regular internamente a sua temperatura corporal (Angilletta et al., 2002). Os grandes ectotérmicos marinhos são geralmente adaptados para viver dentro de uma faixa estreita de temperatura, resultando num ótimo térmico que potencia seu desempenho fisiológico (Neill, 1979). Utilizámos etiquetas de arquivo para registar o comportamento de mergulho e a temperatura muscular de seis tubarões-azuis, *Prionace glauca* (Linnaeus, 1758). Foram observados padrões de mergulho consistentes para todos os tubarões, com uma grande variação de profundidade (1,60 - 711,10 m). O gradiente térmico da coluna de água foi proporcional à profundidade. Contudo, todos os indivíduos apresentaram uma temperatura ambiente média semelhante (entre 17,06 ± 4,53 ºC e 20,06 ± 2,19 ºC). Embora a temperatura muscular tenha apresentado flutuações mais lentas e suaves, foi diretamente influenciada pela temperatura ambiente. A sua elevada inércia térmica permite que os tubarões azuis façam migrações curtas de forrageamento para águas frias mais profundas sem a necessidade de reduzir significativamente a sua temperatura corporal, uma vez que reaquecem novamente à superfície (Watanabe et al., 2019). Em geral, os músculos apresentam uma gama de temperaturas mais elevada e restrita. Os tubarões-azuis mudam as direções verticais de natação (descendente ou ascendente) antes da sua temperatura corporal atingir a temperatura da água ambiente, apresentando maiores coeficientes de transferência de calor de corpo inteiro durante a fase de aquecimento (ascendente). Assim, este comportamento termorregulador conjuntamente com a procura de alimento explica os nichos térmicos verticais e geograficamente alargados dos tubarões azuis. Compreender a forma como a fisiologia, o comportamento e a ecologia das espécies interagem com a temperatura ambiental é fundamental para prever alterações no seu movimento, distribuição e função ecológica em resposta às alterações climáticas e melhorar as medidas de conservação.

Palavras-chave: Alterações climáticas, Ectotérmico, Termorregulação, Temperatura muscular, Troca de calor

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List of Abbreviations

ATL - Atlantic Ocean

Av - Average

DO – Dissolved oxygen

DSL - Deep scattering layer

DVM - Diel vertical migration

et al. - And others

e.g. - For example

IUCN - International Union for the Conservation of Nature

i.e. That is

m - Meters

min - Minutes

MultiS - MultiSensor archival tag

Sec - Seconds

s.d -.Standard deviation

TAD - Time-at-depth

TAT – Time-at-temperature

PSAT - Pop-off satellite archival transmitters

Chapter I

1. General introduction

Large pelagic predators have distinct physiologies (Block, 2005), extensive movements, and broad distributions, and they exert top-down control in open ocean ecosystems (Heithaus et al., 2008; Block et al., 2011), shaping the ecological structure and habitat use of communities and providing an indication of ocean state (Sims and Quayle, 1998; Sims, 2003; Campana, 2016; Boerder et al., 2019). Climate changes are expected to alter existing environments and generate new ones, potentially leading to local loss of organisms and their related ecosystem function (Corrales et al., 2018; Pinsky et al., 2019; Yeruham et al., 2020). Climate-driven alteration to the movements of large predators, such as sharks, could change their likelihood of interactions with recreational water users (Chapman and McPhee, 2016) and may alter ecosystem dynamics through novel trophic cascades (Bastille-Rousseau et al., 2019; Hammerschlag et al., 2019; Rosenblatt et al., 2017). Moreover, quantifying climate-associated changes to the space use and movements of upper trophic-level predators is particularly crucial given that they exhibit relatively high extinction risk (Myers and Ottensmeyer, 2005) and changes to their distributions could make them more vulnerable to exploitation (Selden et al., 2020).

1.1. Physiology and climate change

Marine ecosystems are characterized by vertical gradients, defined by physical (e.g., temperature, light level, oxygen concentration) (Brill and Lutcavage, 2001) and biological properties (e.g., primary production). The vertical distribution of marine animals is determined by these gradients, as well as the eco-physiological characteristics of each species and intra- and interspecific interactions (Longhurst, 1967; Giske et al., 1990). The threat that climate change represents to species and ecosystems around the world has led to its recognition as an environmental emergency (Lenton et al., 2019; Ripple et al., 2019). Major climatic stresses for ocean ecosystems include warming, acidification, and deoxygenation (Gruber, 2011). Ocean warming can be induced by both long-term climate change and short-term climate variability, such as marine heat waves. According to Pörtner et al. (2019), many of the habitats in the oceans that are experiencing the fastest rates of climate-driven change are productive regions with significant economic value (e.g., coastal shelves) and biodiversity hotspots (e.g., coral reefs). Therefore, a higher rate of ocean warming could have an impact on the distribution, abundance, and life history traits of fish (Pauly and Cheung, 2018) and invertebrates (McLachlan and Defeo, 2018).

According to some research (Fey et al., 2019; Wolff et al., 2020), behavioral responses, such as changes in activity in time and place, may help species adapt to thermally demanding settings and maintain their functional roles in the ecosystem despite changing temperatures. Therefore, moving throughout the water column will serve to maintain the surrounding temperature within the limits necessary for survival (Neill, 1979; Andrzejaczek et al., 2018). Nevertheless, reports of species responses to these climatic phenomena in marine ecosystems are increasing (Brown et al., 2016; Pinsky et al., 2013, 2020; Poloczanska et al., 2013, 2016; Scheffers et al., 2016). Temperature is one of the most significant abiotic factors influencing animals' distribution, behavior, and physiological performance, especially for ectotherms that cannot regulate their body temperature internally (Angilletta et al., 2002). Large marine ectotherms are generally adapted to live within a narrow temperature range, resulting in a thermal optimum that optimizes their physiological performance (Neill, 1979). Thus, when conditions deviate from the optimum, an organism's growth, reproduction, foraging, or competitiveness declines (Aspillaga et al., 2017; Pörtner and Farrell, 2008). The potential of ectotherms to buffer the deleterious effects of suboptimal temperatures is becoming more widely acknowledged (Kearney et al., 2009; Sunday et al., 2014). The ability to access prey resources in thermally disparate habitats allows ectothermic predators to broaden their ecological niche and ultimately increase their fitness (Huey and Kingslover, 1989; Block et al., 1993; Dickson and Graham, 2004). To do so, they must cope with the high thermal conductance of water and avoid body temperature changes that are detrimental to physiological performance. As ectotherms, sharks [e.g., tiger shark (*Galeocerdo cuvier*), blue shark (*Prionace glauca*) and escolar shark (*Lepidocybium flavobrunneum*)] could be influenced by climate change (Bernal et al., 2012; Rosa et al., 2014, 2017; Syndeman et al., 2015; Watanabe et al., 2015; Pinsky et al., 2019), with their metabolism and oxygen requirement are both being increased by higher temperatures (Pistevos et al., 2015; Lawson et al., 2019). Contrarily, the ability of an organism to retain metabolic heat and keep its internal temperature higher than that of the environment (endothermy) increases reaction rates, muscle power output, and the capacity for long-term aerobic performance.

Particularly for organisms that live in habitats with low or fluctuating temperatures, this mechanism offers clear advantages (Bennet, 1984; McNab, 2002). Because of this, endothermic species [e.g., Swordfish (*Xiphias gladius)*, bigeye tuna (*Thunnus obesus*), salmon shark *(Lamna ditropis)* and Lampris spp.) show a greater ability for niche expansion and frequently have an advantage over creatures that thermoconform to their environment (as in predator-prey interactions) (Bennet and Ruben, 1979; Ruben, 1995; McNab, 2002; Hillenius and Ruben, 2004; Watanabe et al., 2015; Coffey et al., 2017).

In a wide range of marine and terrestrial ecosystems, recent modeling of biodiversity under various future climate change scenarios indicates dramatic and permanent ecosystem damage by the late 21st century (Trisos et al., 2020). The rate and magnitude of future change is expected to increase even further from current levels (Cheng et al., 2019), with global ocean surface temperatures expected to rise by between 1.0 and 6.0 ºC by 2100, according to models assessed by the Intergovernmental Panel on Climate Change (IPCC Climate Change 2007; Rosenzweig et al., 2008). Understanding spatial patterns of change is essential for identifying the ecosystems that are most at risk because the speeds and intensity of climate impacts will not be consistent across the world's oceans (Hazen et al., 2012). An interdisciplinary approach is intrinsically necessary for thorough evaluations of the impacts of climate change. To evaluate and forecast how animals interact with their surroundings, a habitat-modeling framework can incorporate data from remote sensing of the environment and animal distribution.

1.2. Biologging

The linking of behavioral data with environmental features has been made possible by improvements in satellite telemetry and the growing accessibility of remotely sensed environmental data (Whitford and Klimley, 2019; Francisco et al., 2020). This has made it possible to research migratory marine species' habitat preferences even in remote regions like the open ocean (Humphries et al., 2010; Guzman et al., 2018; Sequeira et al., 2018). For centuries, conventional tagging systems based on capture-mark-recapture have been employed as markers on marine and freshwater fishes (Kohler and Turner, 2001). Longline surveys and mark-recapture experiments in the Atlantic have shed light on how pelagic sharks respond to dynamic changes in ocean habitat type, for blue sharks in particular (Kohler and Turner, 2001).

Alternative approaches, such as acoustic telemetry, began to emerge in the 1960s. Acoustic tags can be linked to a variety of sensors that transmit data about water temperature, swimming depth, fish muscle temperature, cranial temperature, swim speed, tail beat frequency and heart rate (Lowe and Goldman, 2001). During the 1970s and 1980s, acoustic tracking of blue sharks in the North Atlantic provided insights into their vertical movements (Carey et al., 1990). Carey et al. (1990) concluded that blue sharks displayed seasonal depth oscillations, with sharks during late summer, autumn and winter making regular vertical oscillations from the surface to 400 meters (m) at daylight and moving to depths near the thermocline at night, in which did not happen during the summer.

Micro dataloggers, or 'archival tags', were developed and applied to a few free-ranging fishes during the 1990s (Boehlert, 1997; Metcalfe and Arnold, 1997; Block et al., 1998 a, b; Tanaka et al., 1998, 2000; Gunn et al., 1999; Lutcavage et al., 1999; Kitagawa et al., 2000; Naito et al., 2000). These transmitters were small enough to not obstruct the normal fish's movements and were still equipped with powerful batteries capable of storing high-quality data. Also in the 1990s, several studies (Holland et al., 1990,1992; Holland and Sibert, 1994) made use of ultrasonic transmitters attached to the bigeye tuna, to simultaneously measure swimming depth and muscle temperature. The advent of electronic tags capable of relaying stored data via satellites allowed scientists to obtain ecological information without dependence on fisheries returns. Termed pop-off satellite archival transmitters (PSAT) these tags provide useful information, particularly on the characterization of the thermal habitat used by fish, with data transmitted to Argos satellite receivers (Block et al., 1998b). More recent generations of PSAT allow the storage of data on depth and light levels, which is extremely important and has transformed our understanding of the behavior of large fish.

To increase the accuracy and obtain time data series without temporal gaps, several studies applied new methodologies. For example, the Argos system started to use the GPS constellation of satellites to obtain movement tracks with greater accuracy in turtles, pinnipeds, and seabirds (Schofield et al., 2007; Soanes et al., 2013). To overcome the temporal gaps issue and to construct movement tracks with more accuracy, new methods have been used, such as tags that incorporate tri-axial accelerometer sensors (Brownscombe et al., 2014). Accelerometers quantify mechanical work done by animals (Gleiss et al., 2011; Wilson et al., 2006), and have shown potential as a tool for evaluating temperature's influence on locomotor activity, at least in several estuarine fish species (Gannon et al., 2014; Payne et al., 2016).

Electronic tags provide fundamental knowledge of the movement ecology of marine predators. Tracking migrations of predators has helped scientists understand migration patterns, habitat preferences, and a species' susceptibility to commercial fishing on a global scale in teleosts and sharks (Block et al., 2011; Queiroz et al., 2016, 2019; White et al., 2019). Pelagic species' exploitation of their local environment has been quantified in terms of vertical habitat usage, relating to prey availability and physiological restrictions, and characterized the water column's physical parameters that significantly influence the region- and species-specific depth preferences of pelagic fish. (Block et al., 2001; Brill and Lutcavage, 2001; Bernal et al., 2017).

1.3. Thermoregulation strategies

Accordingly, key research priorities in climate change ecology are to determine and forecast the rate, direction, and timing of associated shifts in the space function and movements of species of corresponding climate variability and change. Climate change has raised the need to investigate how organisms adapt to temperature variations by directly influencing the thermal environment (Pacifici et al., 2015; Sinclair et al., 2016). Thermal performance curves (Huey and Stevenson, 1979) offer a theoretical foundation for comprehending this thermoregulatory behavior. These curves show how body temperature affects physiological performance and are bounded by the minimum and maximum critical temperatures at which an organism can survive, as well as the temperatures at which performance is optimal (Martin and Huey, 2008). Thermoregulatory strategies allow species to migrate from scorching surface waters to cooler deeper waters in order to, exploit food resources found at greater depths. The physiological mechanisms that enable this can include whole-body endothermy (Holland et al., 1992; Weng et al., 2005; Bernal, 2005; Madigan et al., 2015; Watanabe et al., 2015), regional endothermy, such as cooling of the brain or eyes (Weng and Block, 2004; Thorrold et al., 2014), or changes in blood flow rates (Carey and Gibson, 1987; Nakamura and Sato, 2015; Stoehr et al., 2018).

Due to their increased physiological function linked to regional heat retention, regionally endothermic fish like tunas (family Scombridae), lamnid sharks (family

Lamnidae), which heat the aerobic swimming muscles as well as other regions in some species (Dickson et al., 2004; Block et al., 1993; Bernal et al., 2001; Bernal et al., 2005), and billfish (families Istiophoridae and Xiphiidae, which heat only the eye and brain region) (Carey, 1982), are frequently referred to as "high-performance". In order to keep certain organs or tissues warm during extended dives into cold water, some species use counter-current vascular heat exchangers to maintain body heat (3–7). However, these fish fall far short of whole-body endothermy mainly because a large portion of their body (including vital organs such as the heart) remains at ambient temperature, which limits aerobic performance in cold water (Shiels et al., 2011). In addition, the diving capacity of large pelagic fish can be limited by the dependence of cardiac function on temperature (Watanabe, 2021). However, practically all species (including regionally endothermic species and ectothermic) have this physiological ability of the heart to maintain itself at ambient temperature (Wegner et al. 2015). For instance, compared to other species, salmon sharks and sibling taxa of the Lamnidae, are presumably less influenced by water temperature and DO on their vertical distributions due to their unique anatomy and physiology (Weng et al., 2005; Weng et al., 2008). Salmon sharks have a physiological advantage over ectothermic predators that enables them to take advantage of prey resources at higher latitudes more successfully (Weng et al., 2005).

Some sharks (Lamnidae and Alopiidae) and tunas (Scombridae) are able to thermoregulate through the retia mirabilia, which contains warm venous blood that returns to the heart from the swimming muscles. Consequently, the efficiency of the heat exchanger can be altered passively without any physiological manipulation of the vasculature (Holland et al., 1992), and thermoregulation is only activity-dependent. For example, regarding activity-independent thermoregulation or thermoconservation mechanisms, despite spending most of the daylight hours below the thermocline, bigeye tuna regularly makes brief excursions into the mixed layer. This suggests that when these tunas ascend from cold waters to warmer surface waters, the heat exchangers are deactivated to allow rapid warming and are reactivated to conserve heat when they descend to depth (Holland et al., 1990, 1992; Holland and Sibert, 1994; Brill et al., 1994). In addition, Dewar et al. (1994) found that yellowfin tuna can regulate the efficiency of their thermal conservation mechanisms to adjust the rate at which muscle temperature changes by more than an order of magnitude.

During fish migrations to deeper waters, the greatest and fastest loss of body heat to the environment occurs through the gills. As the blood passes through the gill lamellae, the metabolic heat produced in the muscle tissue is transferred and rapidly dissipated to the environment (Stevens and Sutterlin, 1976; Carey and Gibson, 1987). However, blue sharthe k does not have retia mirabilia, so Carey and Gibson (1987), as well as Carey and Scharold (1990), carried out studies to understand the physiological thermoregulation strategies developed by the species. Neill et al. (1974) pointed out that thermoregulation cannot be unequivocally separated from the simple effect of thermal inertia in such a large fish. To maintain body temperature during these dives, Kitagawa et al. (2001) noted that internal (metabolic) heat production during the day, or thermal inertia, is crucial. Thermal inertia is the ability of an animal to passively resist changes in body temperature in the face of changing external (environmental) conditions and reduce the rate of heat exchange with the environment (Schmidt-Nielsen, 1984). Once thermal inertia has been overcome, the body temperature of strict ectotherms must equilibrate with their environment, but some deep-diving species have developed strategies to reduce heat transfer (Royer, 2020). Large fish have a certain advantage due to their size alone (Schmidt-Nielsen, 1984). Due to their high thermal inertia, large body sizes allow species such as whale sharks, leatherback sea turtles (and possibly dinosaurs) to take advantage of a diverse range of thermal habitats (Paladino et al., 1990; Meekan et al., 2015; Nakamura et al., 2020). This may allow them to achieve a faster rate of warming than cooling, as previously demonstrated by the ectothermic blue shark (Carey and Gibson, 1987; Carey and Sharold, 1990). The blue shark is an ectothermic species, lacking the parallel arrangement of arteries and veins that function as counter-current heat exchangers in the muscles (Carey and Gibson, 1987). However, although large body sizes can passively dampen the rate of change in body temperature, most fish, including the hammerhead shark (*Sphyrna lewini*), are ectotherms that lack morphological and vascular adaptations to actively conserve heat. In ectotherms, the internal body temperature is determined by the surrounding environment. Due to the effect of temperature on metabolism, burst speeds in ectotherms typically increase with increasing temperature up to a point of optimal performance (fish, Wardle 1980; lizards, Zhang & Ji 2004). Some marine ectotherms navigate between thermal environments to take advantage of foraging habitats and select optimal ambient temperatures for bioenergetic efficiency (Sims et al., 2006; Di Santo and Bennet, 2011). Their performance of diel vertical movements (DVM) may also represent a behavioral mechanism that balances higher energetic costs associated with night-time foraging activity in shallow, warm waters, with reduced activity in deep cold waters during daytime that lowers metabolic rate (Sims et al., 2006). According to Weihs (1973) and other researchers (Gleiss et al. 2011; Watanabe et al. 2019) fishes denser than water, such as sharks, could migrate from one place to another with less energy costs by adopting negative buoyancy through a swim-glide progression mode. Animals experience less hydrodynamic drag during gliding than active swimming; therefore, in theory, animals with negative buoyancy could save locomotion costs by alternating passive gliding on descents and active swimming on ascents compared to continuous swimming over the horizon (Weihs, 1973). However, as with tiger sharks, the blue shark's dive patterns not an energy-saving tactic, gliding only during a small portion of descents and exhibiting dive and ascent angles not suitable for efficient progression, indicating that saving locomotion costs is not the primary explanation for deep dives (Watanabe, 2021). A previous study, tracking blue shark body temperature and diving behavior showed that they shift vertical swimming directions (descending or ascending) before their body temperature reaches the ambient water temperature (Carey and Scharold, 1990). Thus, shark body temperature falls within a narrow range, thereby supporting the thermoregulatory function of repeated deep dives (Carey and Scharold, 1990). Consequently, it is generally assumed that ectothermic fish have narrower thermal niches than regional endothermic fish with well-developed heat exchangers (e.g. tunas, lamnid sharks) (Block et al., 1993; Weng et al., 2005), but recent research challenges this assumption (Harding et al., 2021). This species (blue shark) is an interesting example, as it dives to great depths [occasionally >1000 m, with a maximum record of 1706 m (Queiroz et al., 2017)]. Furthermore, despite their ectothermic physiology, blue sharks tolerate a wide range of water temperatures (Stevens et al., 2010; Campana et al., 2011; Queiroz et al., 2012). This is achieved by modulating blood flow and, consequently, convective heat transfer in the gills (Carey and Gibson, 1987; Carey and Scharold, 1990; Kitagawa and Kimura, 2006). Furthermore, it has been shown in other studies (Carey and Gibson 1987; Nakamura et al., 2015) that the amount of heat transferred by fish bodies to the surrounding water is significantly reduced in the absence of convective heat transfer caused by blood flow. In other words, for a given temperature difference, the temperature gradients between the surface of the body and the place where the body temperature is measured tend to be smaller in large fish.

In addition, the hammerhead shark is an exceptional example of thermoregulation in ectothermic species. Contrary to what would be expected of an ectothermic species, it has been observed that individuals of this species maintain a high body temperature during most of each dive (Royer et al., 2023). One possible response to this thermoregulation mechanism is to limit heat loss by convection by closing the mouth and/or gill slits, drawing blood away from the gills, or decreasing the flow of water through the gills. In addition, adult hammerhead sharks have high body masses that provide them with sufficient thermal inertia to slow down the rate of heat exchange with the environment (Royer et al., 2023). Royer et al., (2023) suggest that this physiological capacity, which is similar to the active physiological thermoregulation techniques used by other elasmobranchs and teleosts, may be useful. On the other hand, as in the case of shortfin mako sharks (Royer, 2020), the analysis of the heat transfer coefficient revealed a constant rate of heat exchange between the muscle and the ambient water temperature, which indicates that blue shark's resort to passive thermoregulation when moving between different thermal environments. Regardless of the specific pathways by which temperature regulates activity or growth, the response of ectotherms to their environment is crucial for informing mechanistic distribution models and establishing management strategies through extrapolating projections to future climate scenarios (Schlaff et al., 2014; Payne et al., 2018).

1.4. Thermal modeling – heat exchange model

Behavioral and physiological thermoregulation strategies can be employed to manage the exchange of body heat with the surrounding environment both passively and actively (Holland et al., 1992; Hight and Lowe, 2007; Pépino et al., 2015; Stoehr et al., 2018). Convective and conductive heat transfer allows fish to exchange heat between their bodies and their surroundings. Convective heat transfer takes place at the location of respiratory gas exchange (the gills), where heat is exchanged between the blood and the surrounding water via the thin gill lamellae. Due to the high thermal conductance of water, it is assumed that most of the metabolic heat generated in muscle tissue is carried away by the blood and rapidly lost to the environment as blood flows through the gill lamellae (Stevens and Fry, 1974; Stevens and Sutterlin, 1976; Carey and Gibson, 1987; Wegner et al., 2015). Conductive heat exchange occurs between the body and the surrounding water across the body wall (Neill et al., 1974; Fechhelm and Neill, 1982; Dewar et al., 1994;

Bernal et al., 2001; Stoehr et al., 2018). Heat exchange models based on Newton's law of cooling have been used to predict the rate of heat exchange between the body of fish to their ambient environment (Stevens and Fry, 1974; Stevens and Sutterlin, 1976). The rate of heat exchange between the body and its surrounding environment determines an individual’s ability to occupy habitats beyond their thermal optimum. The whole-body heat transfer coefficient predicts the rate of heat exchange between an organism and the environment, with a greater coefficient indicating a higher rate of heat exchange (Neill et al., 1974, Stevens and Sutterlin, 1976). A thermal coefficient analysis can be used to distinguish between passive (thermal inertia) and active thermoregulation in fishes and to calculate whole-body heat transfer coefficients (Holland et al., 1992; Holland and Sibert, 1994).

1.5. Specie description

With a vast geographic range, the blue shark can be found in all tropical and temperate oceans. The distribution of the Atlantic population is complex, with sexes and ages being segregated spatially and temporally, as well as seasonal and annual migrations, including Trans-Atlantic and Trans-Equatorial movements (Stevens, 1990). During the winter, mature females, many of which are pregnant, can be found in the eastern Atlantic close to the Canary Islands and North Africa (Stevens, 1990). Along with juveniles and sub-adult females, which migrate into the western English Channel and Irish waters throughout the summer, adult males are found further north, particularly off the coast of Portugal (Stevens, 1976; Fitzmaurice et al., 2005). Offshore, notably off of the Azores, adult males and juveniles are also common (Litvinov, 2006).

Movement patterns and vertical distribution of large pelagic fish can be very complex, reflecting not only thermoregulation behaviors but also, foraging, energetics, navigation, and reproduction behaviors (Weihs, 1973; Carey et al., 1990; Klimley, 1993; Shepard et al., 2006; Queiroz et al., 2012; Andrzejaczek et al., 2019). Empirical records of fish body temperature suggest that thermoregulation linked to foraging is a major function of diving behavior, at least in bigeye tunas (Holland et al., 1992) and ocean sunfish, *Mola mola* (Nakamura et al., 2015). Additionally, recently Watanabe et al., (2021) suggested that behavioral thermoregulation linked to foraging is key to the vertically and geographically expanded thermal niches of blue sharks. On the other hand, tiger sharks are willing to move in response to (or alongside) patterns in sea surface temperature (SST), as demonstrated by Andrzejaczek et al. (2018), and their spatial distribution will potentially be constrained by future changes in SST. Diel vertical movements (DVM) have been identified as a particularly characteristic cyclic behavior for a variety of pelagic species, ranging from zooplankton to apex predators (e.g., Hays, 2003; Sims et al., 2005; Baird et al., 2008; Weng et al., 2009; Coffey et al., 2017; Hafker et al., 2017). Shifts in DVM patterns could be associated with changes in prey distribution or peak productivity, environmental variations or physical oceanographic features including fronts, eddies, and stratification (Nelson et al., 1997; Labat et al., 2009). In general, the thermocline divides the warmer, isothermal waters of the mixed layer from the deeper, colder waters that reach into the mesopelagic (Madigan et al., 2020). This oceanic layer, where temperature rapidly drops with depth, acts as a barrier to contain prey (Sogard and Olla, 1993) and may help to explain shifts in top predator distribution and diving patterns. Several species of marine megafauna perform diel vertical migrations, and a significant portion of their diet includes mesopelagic fish and diel vertically migrating species, supporting the theory that DVM increases foraging success (Sims et al., 2005; Pade et al., 2009; Braun et al., 2019). Research on blue sharks (Queiroz et al., 2010) and basking sharks, *Cetorhinus maximus*, (Sims et al., 2000) shows how thermal fronts influence the behavior of large predators. For blue sharks, the movement patterns corresponding to the Northeast Atlantic detected a higher prevalence of sharks in highly productive regions characterized by the presence of oceanic fronts. In frontal regions with high productivity, cold surface temperatures, and distinct water-column stratification, both blue and salmon sharks have demonstrated greater surface occupancy (Queiroz et al., 2012; Coffey et al., 2017).

Since movement at particular locations strongly determines temporal changes in population density, information on movements and behavior is an often overlooked but essential component of assessing population trends of mobile animals (Turchin, 1998). Understanding the patterns of horizontal and vertical habitat use in marine predators about environmental physical features is crucial because they have a significant impact on the movements and distribution of predators (Simns et al., 2003) and help us predict how animals will behave in the face of shifting environmental conditions (Humphries et al., 2010). Commonly reported as the most abundant and widely distributed pelagic shark species (Nakano and Stevens, 2008) the blue shark is probably the most frequently caught large shark in the world oceans (Walker, 1998; Stevens et al., 2000), and is certainly the most frequently caught large pelagic shark in the North Atlantic (International Commission for the Conservation of Atlantic Tunas, 2008). Their populations have decreased by about 40% since the 1970s (Baum et al., 2003; Pacoureau et al., 2021) due mostly to the high mortality risk from fishing (Queiroz et al., 2016, 2019). Virtually all the North Atlantic blue shark catch is pointed as undirected bycatch in the pelagic longline fishery for swordfish, and tuna, where it accounts for up to 50% of the total catch weight (Mandelman et al., 2008; Mejuto et al., 2008). Shark populations are a concern for bycatch fisheries, although their decline is mainly due to their slow recovery compared to catch numbers, as they have slow growth rates, late age at sexual maturity, and low fecundity (Heithaus et al., 2007). 16.6% of shark species are estimated to be threatened with extinction, and another 37.9% of shark species are categorized as “Data Deficient” by the International Union for Conservation of Nature (IUCN, 2020). Despite recently established fishing quotas for blue sharks in some regions and is assessed as Near Threatened by the IUCN (International Union for the Conservation of Nature) Red List of Threatened Species 2019, the uncertainty in current stock assessments makes understanding shark fine-scale behavior a priority for effective conservation management (Hammerschlag et al., 2016; Robinson et al., 2017; Boerder et al., 2019). The identification of regions and intervals of greater susceptibility to fisheries has also been made possible by a knowledge of how environmental changes affect the migrations and behavior of pelagic fish (Song et al., 2009; Queiroz et al., 2016, 2019; Hays et al., 2019). This spatial and behavioral information must be considered collectively to create more successful conservation policies (Hammerschlag et al., 2016; Sequeira et al., 2019; Hindell et al., 2020).

1.6. Thesis objectives

Due to its erratic population trends employed by climate change and fishing pressure, the blue shark has recently been listed as "near threatened" (Dulvy et al., 2008), highlighting the need for in-depth knowledge of its behavior and movement patterns to implement effective conservation and management measures. To better understand diel vertical movements and thermoregulation mechanisms of blue sharks, we used archival tags capable of directly measuring depth, ambient water temperature, activity rates and swimming muscle temperature. In this context, the specific aims were to:

(1) Describe the movements and diving behavior of blue sharks at varying spatial and temporal scales across thermal gradients.

(2) Understand the possible physiological thermoregulation strategies that can be employed to manage the exchange of body heat with the surrounding environment.

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Chapter II

Title: Behavioral thermoregulation of the ocean’s widest ranging ectothermic shark, *Prionace glauca* (Linnaeus, 1758)

Authors: Maria J. M. Mendes [1], Nuno Queiroz[2,3], David M. A. Abecasis[4]

[1] Faculdade Ciências e Tecnologia, Universidade do Algarve, Faro, Portugal
[2] Centro de Investigação em Biodiversidade e Recursos Genéticos/Rede de Investigação em Biodiversidade e Biologia Evolutiva (CIBIO/InBIO), Universidade do Porto, Vairão, Portugal
[3] Marine Biological Association of the United Kingdom, Plymouth, United Kingdom
[4] Centre of Marine Sciences (CCMar), Universidade do Algarve, Campus de Gambelas 8005-139 Faro, Portugal

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Abstract

Large pelagic predators have distinct physiologies (Block, 2005), extensive movements, and broad distributions, and they exert top-down control in open ocean ecosystems (Heithaus et al., 2008; Block et al., 2011), shaping the ecological structure and habitat use of communities and providing an indication of ocean state (Sims and Quayle, 1998; Sims, 2003; Campana, 2016; Boerder et al., 2019). Climate changes are expected to alter existing environments and generate new ones, potentially leading to local loss of organisms and their related ecosystem function (Corrales et al., 2018; Pinsky et al., 2019; Yeruham et al., 2020). Marine ecosystems are characterized by vertical gradients, defined by physical (e.g., temperature, light level, oxygen concentration) (Brill and Lutcavage, 2001) and biological properties (e.g., primary production). Temperature is one of the most significant abiotic factors influencing animals' distribution, behavior, and physiological performance, especially for ectotherms that cannot regulate their body temperature internally (Angilletta et al., 2002). Large marine ectotherms are generally adapted to live within a narrow temperature range, resulting in a thermal optimum that optimizes their physiological performance (Neill, 1979; Costa, 2018). We used archival tags to record the diving behaviour, muscle temperature of six blue sharks, *Prionace glauca* (Linnaeus, 1758). Consistent dive patterns were observed for all sharks, with a wide variation of

depth (1.60 - 711.10 m). The thermal gradient of the water column was proportional to the depth. All individuals had a similar ambient temperature on average (between 17.06 ± 4.53 ºC and 20.06 ± 2.19 ºC). Although the muscle temperature showed slower and smoother fluctuations, was directly influenced by the ambient temperature). Their high thermal inertia allows blue sharks to make short foraging trips to deep cold waters without significantly reducing their body temperature, as they warm up again at shallow depths (Watanabe et al., 2019). In general, muscles presented a higher and stricter range of temperature. Blue sharks shift vertical swimming directions (descending or ascending) before their body temperature reaches the ambient water temperature, presenting a greater whole-body heat transfer coefficients during the warming (ascendent) phase. Thus, this thermoregulatory behavior linked to the search for food explains blue sharks' vertically and geographically broad thermal niches. Understanding how species' physiology, behavior, and ecology interact with environmental temperature is critical for predicting changes in their movement, distribution, and ecological function in response to climate change and improving conservation measures.

2.1. Introduction

Climate changes are expected to alter existing environments and generate new ones, potentially leading to local loss of organisms and their related ecosystem function (Corrales et al., 2018; Pinsky et al., 2019; Yeruham et al., 2020). Climate-driven alteration to the movements of large predators, such as sharks, could change their likelihood of interactions with recreational water users (Chapman and McPhee, 2016) and may alter ecosystem dynamics through novel trophic cascades (Bastille-Rousseau et al., 2019; Hammerschlag et al., 2019; Rosenblatt et al., 2017). Ocean warming can be induced by both long-term climate change and short-term climate variability, such as marine heat waves. The rate and magnitude of future change is expected to increase even further from current levels (Cheng et al., 2019), with global ocean surface temperatures expected to rise by between 1.0 and 6.0 ºC by 2100, according to models assessed by the Intergovernmental Panel on Climate Change (refs. 1, 2). Understanding spatial patterns of change is essential for identifying the ecosystems that are most at risk because the speeds and intensity of climate impacts will not be consistent across the world's oceans (Pecl et al. 2017). According to Pörtner et al. (2019), many of the habitats in the oceans that are experiencing the fastest rates of climate-driven change are productive regions with significant economic value (e.g., coastal shelves) and biodiversity hotspots (e.g., coral reefs). Therefore, a higher rate of ocean warming could have an impact on the distribution, abundance, and life history traits of fish (Pauly and Cheung 2018) and invertebrates (McLachlan and Defeo 2018). According to some research (Fey et al., 2019; Wolff et al., 2020), behavioral responses, such as changes in activity in time and place, may help species adapt to thermally demanding settings and maintain their functional roles in the ecosystem despite changing temperatures. Therefore, moving throughout the water column will serve to maintain the surrounding temperature within the limits necessary for survival (Neill, 1979; Andrzejaczek et al., 2018).

Large marine ectotherms are generally adapted to live within a narrow temperature range, resulting in a thermal optimum that optimizes their physiological performance (Neill, 1979; Costa, 2018). Thus, when conditions deviate from the optimum, an organism's growth, reproduction, foraging, or competitiveness declines (Aspillaga et al., 2017; Pörtner and Farrell, 2008). The ability to access prey resources in thermally disparate habitats allows ectothermic predators to broaden their ecological niche and ultimately increase their fitness (Huey and Kingslover, 1989; Block et al., 1993; Dickson and Graham, 2004). To do so, they must cope with the high thermal conductance of water and avoid body temperature changes that are detrimental to physiological performance. As ectotherms, sharks [e.g., tiger shark (*Galeocerdo cuvier*), blue shark (*Prionace glauca*) and escolar shark (*Lepidocybium flavobrunneum*)] could be influenced by climate change (Bernal et al., 2012; Rosa et al., 2014, 2017; Syndeman et al., 2015; Watanabe et al., 2015; Pinsky et al., 2019; Hammerschlag et al., 2021), with their metabolism and oxygen requirement are both being increased by higher temperatures (Pistevos et al., 2015; Lawson et al., 2019). Contrarily, the ability of an organism to retain metabolic heat and keep its internal temperature higher than that of the environment (endothermy) increases reaction rates, muscle power output, and the capacity for long-term aerobic performance. Particularly for organisms that live in habitats with low or fluctuating temperatures, this mechanism offers clear advantages (1, 2). Because of this, endothermic species [e.g., Swordfish (*Xiphias gladius)*, bigeye tuna (*Thunnus obesus*), salmon shark *(Lamna ditropis)* and Lampris spp.) show a greater ability for niche expansion and frequently have an advantage over creatures that thermoconform to their environment (as in predator-prey interactions) (2–5)(Watanabe et al., 2015; Coffey et al., 2017).

Electronic tags provide fundamental knowledge of the movement ecology of marine predators. Tracking migrations of predators has helped scientists understand migration patterns, habitat preferences, and a species' susceptibility to commercial fishing on a global scale in teleosts and sharks (Block et al., 2011; Queiroz et al., 2016, 2019; White et al., 2019). Pelagic species' exploitation of their local environment has been quantified in terms of vertical habitat usage, relating to prey availability and physiological restrictions, and characterized the water column's physical parameters that significantly influence the region- and species-specific depth preferences of pelagic fish. (Block et al., 2001; Brill and Lutcavage, 2001; Bernal et al., 2017).

Thermal performance curves (Huey and Stevenson, 1979) offer a theoretical foundation for comprehending this thermoregulatory behavior. These curves show how body temperature affects physiological performance and are bounded by the minimum and maximum critical temperatures at which an organism can survive, as well as the temperatures at which performance is optimal (Martin and Huey, 2008). The physiological mechanisms that enable this can include whole-body endothermy (Holland et al., 1992; Weng et al., 2005; Bernal, 2005; Madigan et al., 2015; Watanabe et al., 2015), regional endothermy, such as cooling of the brain or eyes (Weng and Block, 2004; Thorrold et al., 2014), or changes in blood flow rates (Carey and Gibson, 1987; Nakamura and Sato, 2015; Stoehr et al., 2018). Due to their increased physiological function linked to regional heat retention, regionally endothermic fish like tunas (family Scombridae), lamnid sharks (family Lamnidae), which heat the aerobic swimming muscles as well as other regions in some species (6–12), and billfish (families Istiophoridae and Xiphiidae, which heat only the eye and brain region) (13, 14), are frequently referred to as "high-performance" (8, 15). In order to keep certain organs or tissues warm during extended dives into cold water, some species use counter-current vascular heat exchangers to maintain body heat (3–7). However, these fish fall far short of whole-body endothermy mainly because a large portion of their body (including vital organs such as the heart) remains at ambient temperature, which limits aerobic performance in cold water (16, 17). During fish migrations to deeper waters, the greatest and fastest loss of body heat to the environment occurs through the gills. As the blood passes through the gill lamellae, the metabolic heat produced in the muscle tissue is transferred and rapidly dissipated to the environment (Stevens and Sutterlin, 1976; Carey and Gibson, 1987). Some sharks (Lamnidae and Alopiidae) and tunas (Scombridae) are able to thermoregulate through the retia mirabilia, which contains warm venous blood that returns to the heart from the swimming muscles. Consequently, the efficiency of the heat exchanger can be altered passively without any physiological manipulation of the vasculature (Graham, 1983; Holland et al., 1992), and thermoregulation is only activity-dependent. However, the blue shark does not have retia mirabilia, so Carey and Gibson (1987), as well as Carey and Scharold (1990), carried out studies in order to understand the physiological thermoregulation strategies developed by the species. Neil and Stevens (1974) pointed out that thermoregulation cannot be unequivocally separated from the simple effect of thermal inertia in such a large fish. Thermal inertia is the ability of an animal to passively resist changes in body temperature in the face of changing external (environmental) conditions and reduce the rate of heat exchange with the environment (Schmidt-Nielsen, 1984). Once thermal inertia has been overcome, the body temperature of strict ectotherms must equilibrate with their environment, but some deep-diving species have developed strategies to reduce heat transfer (Royer, 2020). Large fish have a certain advantage due to their size alone (Schmidt-Nielsen, 1984). The blue shark is an ectothermic species, lacking the parallel arrangement of arteries and veins that function as counter-current heat exchangers in the muscles (Carey and Gibson, 1987). However, although large body sizes can passively dampen the rate of change in body temperature, most fish, including the hammerhead shark (Sphyrna lewini), are ectotherms that lack morphological and vascular adaptations to actively conserve heat. In ectotherms, the internal body temperature is determined by the surrounding environment. Some marine ectotherms navigate between thermal environments to take advantage of foraging habitats and select optimal ambient temperatures for bioenergetic efficiency (Sims et al., 2006; Di Santo and Bennet, 2011). Their diel performance of vertical movements (DVM) may also represent a behavioral mechanism that balances higher energetic costs associated with night-time foraging activity in shallow, warm waters, with reduced activity in deep cold waters during daytime that lowers metabolic rate (Sims et al., 2006). A previous study, tracking blue shark body temperature and diving behavior showed that they shift vertical swimming directions (descending or ascending) before their body temperature reaches the ambient water temperature (Carey and Scharold, 1990). Thus, shark body temperature falls within a narrow range, thereby supporting the thermoregulatory function of repeated deep dives (Carey and Scharold, 1990). In addition, the hammerhead shark is an exceptional example of thermoregulation in ectothermic species. Contrary to what would be expected of an ectothermic species, it has been observed that individuals of this species maintain a high body temperature during most of each dive (Royer et al., 2023). One possible response to this thermoregulation mechanism is to limit heat loss by convection by closing the mouth and/or gill slits, drawing blood away from the gills or decreasing the flow of water through the gills. In addition, adult hammerhead sharks have high body masses that provide them with sufficient thermal inertia to slow down the rate of heat exchange with the environment (Royer et al., 2023). Royer et al., (2023) suggest that this physiological capacity, which is similar to the active physiological thermoregulation techniques used by other elasmobranchs and teleosts, may be useful. Regardless of the specific pathways by which temperature regulates activity or growth, the response of ectotherms to their environment is crucial for informing mechanistic distribution models and establishing management strategies through extrapolating projections to future climate scenarios (Schlaff et al., 2014; Payne et al., 2018).

Behavioral and physiological thermoregulation strategies can be employed to manage the exchange of body heat with the surrounding environment both passively and actively (Holland et al., 1992; Hight and Lowe, 2007; Pépino et al., 2015; Stoehr et al., 2018). Convective and conductive heat transfer allows fish to exchange heat between their bodies and their surroundings. Heat exchange models based on Newton's law of cooling have been used to predict the rate of heat exchange between the body of fish to their ambient environment (Stevens and Fry, 1974; Stevens and Sutterlin, 1976). The rate of heat exchange between the body and its surrounding environment determines an individual’s ability to occupy habitats beyond their thermal optimum.

In this study, to better understand diel vertical movements and thermoregulation mechanisms, we copulate with the six blue sharks’ archival tags capable of directly measuring depth, ambient water temperature, activity rates and swimming muscle temperature. We aimed to describe the movements and diving behavior of blue sharks at varying spatial and temporal scales across thermal gradients and physiological thermoregulation strategies that can be employed to manage the exchange of body heat with the surrounding environment. This information allows us to deepen our understanding of the movements of blue sharks along thermal gradients in the water column, as well as the thermoregulation strategies employed and the potential consequences of climate change on their physiology.

2.2. Material and methods

Blue shark handling and tagging procedures were performed according to national Portuguese laws for the use of vertebrates in research and were approved and authorized by the Azorean Directorate of Sea Affairs of the Autonomous Region of the Azores (AMP/2021/017), which oversees, and issues permits for scientific activities, and by the Azorean Directorate of Fisheries (SAI/DRP/2021/3534), which oversees and issues permits for scientific fishing. This research and operations were undertaken or supervised by trained personnel at the University of Azores and at MOVE (Movement Ecology) group.

2.2.1. Field experiments and shark tagging

Between July and October 2021, a total of six male blue sharks were tagged with biologging MultiSensor tags in the Azores archipelago, Portuguese Exclusive Economic Zone (EEZ) in the northeast of the Atlantic Ocean. All the sharks were caught on board longlines baited with mackerel (*Scomber scombrus*). Only individuals that met certain selection criteria, such as size, maturity, robustness, and health/physical condition, were captured. After capture, the animal was stabilized and placed in a supine position on the side of the boat in order to restrict its movements, the hook was fixed at the bow and another rope attached to the tail of the shark was fixed to the stern of the boat. All the handling provides for the least constraint and stress for the animal (at a maximum duration of 15 minutes they were measured, sexed, and tagged), and the position of the boat was kept to the swell, to allow water to pass through the gills. For each shark, a biologging package, the MultiSensor archival tag (MultiS), composed of an accelerometer data-logger (Model ORI400/1300-3MPD3GT, Little Leonardo Tri-axial accelerometer, Bunkyo-ku, Tokyo, Japan; diameter: 16.5 mm, length: 83.5 mm, mass: 42.4 g), video camera (Model DVL2000M, Little Leonardo Camera; diameter: 11.0 mm, width: 20.0 mm, length: 52.0 mm, mass: 16.0 g) and depth-temperature sensor (Model LAT2810S, Lotek Temperature Sensor; diameter: 11.0 mm, length: 38.0 mm, mass: 6.0 g) was attached (Figure 2.1).

Figure 2.1. **Pop- off MultiSensor (MultiS) archival tag.** (Photo by: Movement Ecology - MOVE, CIBIO).

The biologging package, MultiS, was attached using a clamp that passed through small holes drilled in the base of the first dorsal fin (which is mostly made of cartilage and hence has no detrimental impact on the shark). During the one-day deployment period, the Little Leonardo Tri-axial accelerometer measures vertical movements and swimming activity, measuring depth and ambient water temperature, as well as speed and tri-axial acceleration at one-second intervals. The Lotek temperature sensor was attached to the sharks using a monofilament line attached to a five cm long stainless-steel T-bar arrowhead inserted immediately lateral to the posterior end of the first dorsal fin at a 45° angle to a maximum depth of eight cm (Figure 2.2). This device was connected to the MultiS and measured the muscle/internal temperature over time. Before the sharks were released the boat was set in motion at a low pace, driving more water into the shark's gills, offering more oxygen to the animal's system, and ensuring the fish was released without any apparent adverse effects. The MultiS employs FastLoc GPS (GlobalStar Satellite Constellation) to help locate it. The GPS is pre-programmed (by the user via the wildtrack application) to send positions every five minutes after the animal is released. Before deploying the tag, the user specifies the date and time when they want the tag to start generating GPS signals. Therefore, the only spatial locations obtained are from the start datetime release and pop-up positions after release from the animal. After 20-22 hours of the animal's release, a fusible capsule severed the stainless-steel band, allowing the entire assembly, including the stalk temperature sensor, to detach from the shark and float to the surface.

***Figure 2.2*. The biologging package**. MultiS, deployment in base of the first dorsal fin of a Blue Shark (Sophie Prendergast supported by Movement Ecology - MOVE, CIBIO).

2.2.2. Data analysis

The data collected by the MultiS tags were processed, and analyzed with Excel software [Version 2304 (Build 16327.20248 Click-to-Run)], the RStudio program (2023.03.1,446, "Cherry Blossom"), and Matlab software. The depth and temperature profiles collected every second for approximately one day by the Little Leonardo Tri-axial accelerometer and Lotek (respectively) were optimized and aligned to select only the dive times from shark release to tag release. The initial alignment was considered as the time when the shark started recording depths gradually greater than 2.0 m and a dive speed greater than 0 m/s. The final alignment considered the last recorded deep dive, followed by a direct decrease in depth to the surface, as the tag release point (considering that naturally the shark oscillates during the ascending phase of the dive). The time series collection included data at high resolution (one sec), allowing for the analysis of possible distinct vertical habitat usage patterns for each individual at a very tiny scale. We calculated, from the readjusted data set, time-at-temperature (TAT), time-at-depth (TAD) and temperature-at-depth matrices, used later for dive analysis, thermocline, and whole-body heat transfer coefficient determination, and made comparisons to infer on potential differences between shark's profiles and how the profiles change throughout the entire day.

2.2.2.1. Data preparation

The time series datasets were processed in R Studio (R core team), and both environment and muscle data, were aligned and combined in a new dataset to allow analysis and comparison. The TAD and TAT data were used to produce matrices, from which plots (using the R package "ggplot2") were developed for profiles of depth and ambient temperature change over time. Conditions were developed using logic math functions to determine the various phases of the dives performed by the sharks. Depth averages were calculated with the *frollmean ()* function (in R program) every five points (corresponding to five seconds) to try to reduce the noise caused by small oscillations that did not coincide with any return point, preventing, the distortion of the original data. The math conditions were generated by employing the *lag ()* function from R package "stats". The rest phase of the dive was defined as the point at which two successive points assumed equal depth; the descending phase was considered the hypothetical positive slope phase, in which the points showed a constant increase in depth over time (considering a reverse scale, in which zero is the water surface, the increase in diving depth over time generates a positive slope line); the ascending phase was considered the hypothetical negative slope phase, in which the points showed a constant decrease in depth over time. These conditions, which define the different phases of the dive, have made it possible to see, in more detail, the number of oscillations that occur throughout the dive.

In order to investigate the influence of thermal structures on the vertical behavior of tagged fish, we calculated thermocline gradients by analyzing TAD and temperature-at-depth matrices. Following data processing at five m depth bins and one hour time bins for each dataset, we computed an interpolation (using R package "zoo") to obtain a smoother contour plot color-coded by the proportion between time and average temperature. The resulting matrices were transformed and the analysis of the depth-temperature profiles (.mat) was performed with the Mares algorithm in Matlab software. The algorithm clustered the data points into bins and extracted the mean value differences to obtain the temperature gradients. With an estimate of potential error, these bins were modified as a function of thermocline thickness, vertical fish velocity, and sample rate. The size of the bins can influence gradient detection; small bins can lead to high errors in gradient estimates, whereas larger bins can increase the smoothness of temperature variations. Several bin sizes were tested to determine the best range for calculating thermocline gradients, with five m bins having the better “mldindex” and spanning the thermocline depths most accurately. Briefly, the algorithm analyses and compares the vertical temperature gradient with a set threshold during a fish dive to establish the upper and lower limits of the thermocline (Figure 2.3). Following the definition of these limits, thermocline properties (namely, the maximum gradient and the thermocline depth and its limits) were retrieved from the preceding vertical profile and thermocline depth was plotted with TAD and TAT matrices to study potential changes in shark behavior.

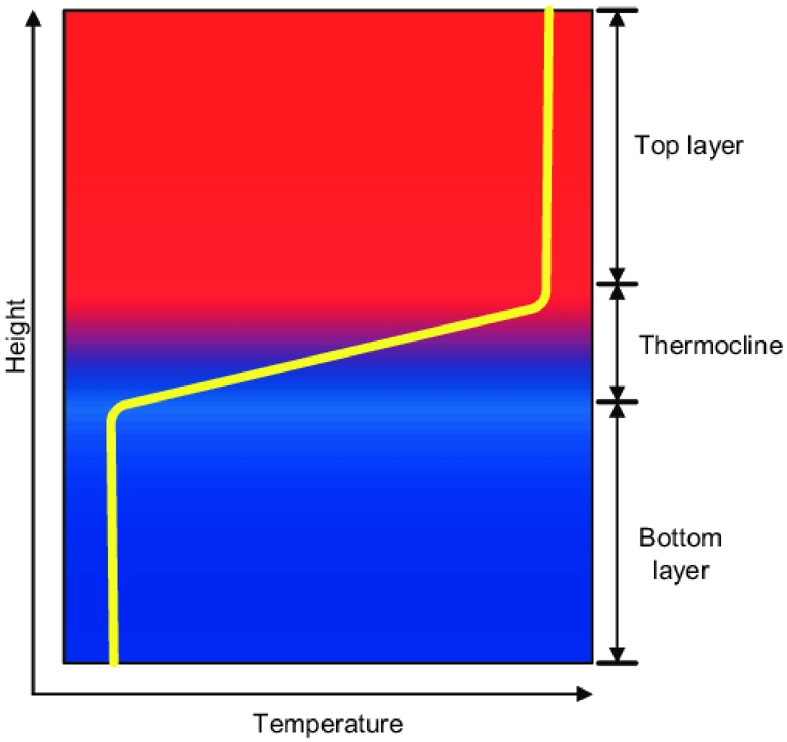

Figure 2.3. **Thermocline representation.** Thermal gradient of water column and stratification of thermal layers (Sinha, 2019).

2.2.2.2. Thermoregulation

The muscle temperature data was also optimized and then adjusted to the depth and water temperature data over time by using the lag () function from the R package "mergefile". Ambient and muscle temperature profiles were then constructed in order to understand the influence of water temperature on the shark, as well as possible thermoregulation strategies associated with its movement in the water column. Data on the depth of the thermocline layer obtained by the Matlab software and the muscle temperature recorded for each shark were also cross-referenced in order to verify potential thermoregulatory behaviors.

2.2.2.3. Thermal modeling – heat exchange model

To quantify the physiological thermoregulation capacity of blue sharks, a heat exchange model was used to estimate the instantaneous rate of change of muscle temperature in relation to the ambient temperature, as shown in equation (1):

$$\frac{dT_{\mathrm{m}}(t)}{dt} = k\left(T_{\mathrm{a}}(t) - T_{\mathrm{m}}(t)\right) + \dot{T}_0 \qquad \textit{Eq. 1}$$

where t is time (min); k is the whole-body heat transfer coefficient (Δ°C min^{-1} $°\mathrm{C}^{-1}$); $T_{\mathrm{a}}(t)$ is the ambient water temperature (ºC) as a function of time t; $T_{\mathrm{m}}(t)$ represents the core muscle temperature (ºC) as a function of time t; and $\dot{T}_0$ is the rate of temperature change as result of metabolic heat production (ºC.min^{-1}) by the swimming muscles (Weller et al., 1984; Holland et al. 1992; Nakamura et al., 2015; Royer, 2020; Watanabe et al., 2021), therefore $\dot{T}_0$ is considered zero in this study.

To apply this model to our dataset, muscle temperature and ambient water temperature were subsampled at one-minute intervals. Subsampling can be accomplished in at least two ways: using package "xts" (from R), which uses information captured for the final second of each minute, or by the *aggregate ()* function by mean from R program, for each minute. In this study, we chose to use the second method. We created mathematical conditions to define the different variables of the heat exchange model. To reduce noise associated with sensor resolutions, the derivative of muscle temperature as a function of time ($dT_{\mathrm{m}}(t)/dt$) was smoothed using a filter, *smooth.spline ()* from R "stats" package). The derivative of muscle temperature as a function of time was plotted as a function of the instantaneous rate of change of muscle temperature relative to ambient water temperature ($T_{\mathrm{a}}(t)$ - $T_{\mathrm{m}}(t)$) for the warming ($T_{\mathrm{a}}(t) - T_{\mathrm{m}}(t) \geq 0$) and cooling ($T_{\mathrm{a}}(t) - T_{\mathrm{m}}(t) < 0$) process. Since $\dot{T}_o$ was considered zero for ectothermic blue sharks, the plots were linearly regressed over the origin through the *stat_smooth ()* function from R “ggplot2” package ("lm" method). The slopes of the regression lines represented the initial estimates for k_{warming} and k_{cooling}.

These initial estimations for the whole-body heat transfer coefficient, combined with the time-series records of ambient temperature, allowed us to predict the changes in muscle temperature over time. Then, we constructed a new dataset containing the variables of the heat exchange model, for which initial values were simulated. Once our incognita was the muscle temperature and the rest of the variables changed in function of this, we assigned the recorded initial value of ambient temperature to the muscle temperature and estimated the remaining. The subsequent matrix values were computed from the preceding lines and adjusted consecutively autonomously by the real and constant values provided, ambient temperature and heat transfer coefficient, respectively (FIG). The predicted muscle temperature obtained was compiled with real muscle temperature recorded and plotted through time, allowing comparisons and evaluation of the fit._The predicted values of the whole-body heat transfer coefficient (k) were modeled to better fit the observed rates of warming and cooling of the body. Thus, we created a matrix with the previously estimated values for k_{warm} and k_{cool} and produced a set of predictions by changing the values around the initial estimates (± 0.002, 0.005, and 0.01). The added/subtracted values were chosen not only for their closeness to the values of k, but also because they did not change them illogically, considering studies previously done (Kitagawa and Kimura, 2006; Nakamura et al., 2020; Watanabe et al., 2021). Using the residual sum of squares method RSS [showed in Equation (2)] between observed [$T_{\text{m}}(i)$] and predicted muscle temperature measurements [$T_{\text{mp}}(i)$], we selected the combination of k_{warm} and k_{cool} that estimates the muscle temperature that best fits the muscle temperature recordings.

$$RSS = \sum_{i=1}^{n} (T\text{m}(i) - T\text{mp}(i))^2 \qquad Eq.2$$

The model that produces the lowest RSS with the fewest number of parameters was selected as the best, as it was expected to provide an estimate of the muscle temperature value that is closer to the real value. We re-run the models using the fitted heat transfer coefficients to produce an accurate and better prediction of muscle temperature and plot these values and the real muscle temperature, recorded by the archival tags, as function of time and the TAD profile.

2.3. Results

Diving behavior, ambient water temperature and muscle temperature data were collected from six male blue sharks tagged in Azores Island, Portugal, with fork length ranging between 190 and 240 cm and thus all mature (Pratt, 1979). There were possible tagging errors, associated with incorrect placement of the biologging devices and overlapping data on the devices. As a result, some data (particularly from the sharks Blue14 and Blue17) were not used in order to make the results more accurate. Data was collected by the archival tag for periods between 18 and 23 hours (except for the shark Blue14, which only recorded data for approximately five hours) (Table 2.1). The time and dive data considered already exclude inaccurate data acquired at the moment of shark release and tag release.

2.3.1. Dive behavior

Blue sharks inhabited a broad vertical range, from the surface to a maximum depth of 711.10 m and water temperatures spanning from 10.10 to 23.40 ºC (Figure 2.4). Consistent dive patterns were observed for all sharks, with a wide variation of mean depth use (from 35.87 ± 37.40 m to 233.40 ± 216.81 m). The shark Blue14 recorded the narrowest depth range (1.60 - 111.00 m) while Blue17 experienced the widest depth range of all the sharks (1.60 - 711.10 m), reaching the maximum depth recorded (Table 2.1). Overall, all sharks showed similar movement profiles, making regular excursions between the surface and the bottom (Figure 2.4). The thermal window of ambient temperatures reported was fairly large, with a recorded minimum of 10.10 ºC (Blue17) and a maximum of 23.40 ºC (Blue18). Nevertheless, all individuals had a similar ambient temperature on average (between 17.06 ± 4.53 ºC and 20.06 ± 2.19 ºC) (Table 2.1). Despite these evident disparities in range, all six blue sharks had a large thermal window. In the case of shark Blue14, the difference between maximum and minimum ambient temperature was 5.7 ºC, whereas shark Blue18 confronted a thermal range of 10.70 ºC. TAT profiles represented in Figure 2.4, demonstrate a clear similarity between the ambient temperature fluctuations and depth dive movements. The increase in depth is "directly" proportional to the temperature of the water column recorded during the dive. The lower the water temperature, the greater the depth reached (Figure 2.4).

Table 2.1. Descriptive information and data summary for the blue sharks, *Prionace glauca*, tagged.

Shark ID	Fork length (cm)	Recording duration (h)*	Depth (m)*		Ambient temperature (°C)*		Muscle temperature (°C)*	
			Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Blue13	240	20.07	35.87 ± 37.40	0 – 171.50	20.06 ± 2.19	15.50 – 22.60	20.82 ± 0.84	18.32 – 22.14
Blue14	214	5.28	42.23 ± 30.19	1.60 – 111.00	19.56 ± 2.21	16.40 – 22.10	20.56 ± 1.03	18.86 – 22.34
Blue15	240	22.05	63.32 ± 90.20	1.60 – 381.60	19.77 ± 2.91	13.70 – 22.90	20.38 ± 1.79	14.92 – 23.08
Blue16	234	22.96	93.60 ± 57.40	1.60 – 268.60	18.09 ± 2.57	14.40 – 22.70	19.42 ± 1.28	17.04 – 22.40
Blue17	190	22.93	233.40 ± 216.81	1.60 – 711.10	17.06 ± 4.53	10.10 – 23.30	17.81 ± 4.27	10.22 – 23.44
Blue18	232	18.89	74.61 ± 80.37	1.20 – 408.10	19.49 ± 2.95	12.70 – 23.40	20.79 ± 1.24	17.62 – 23.00

* The time and dive data considered already exclude distorted data acquired at the moment of shark-tag release and are considered as time 0.

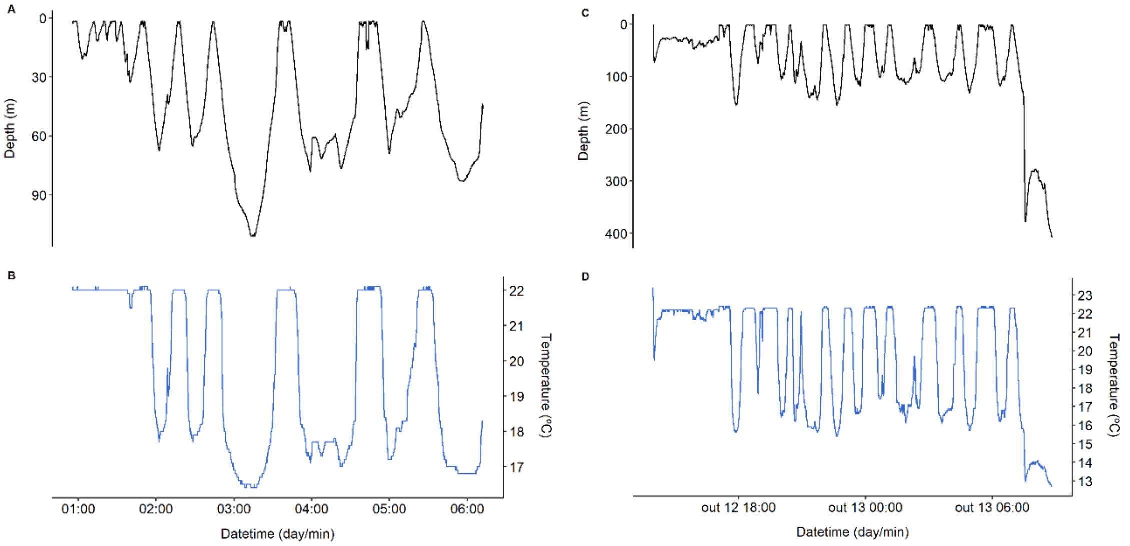

Figure 2.4. **Dive movement and ambient temperature profile**. Dive patterns of sharks Blue14 (A) and Blue18 (C), at each second during the entire recorded time. Ambient temperature profile recorded during the blue sharks dives across water column (B, D; shark Blue14 and Blue18 respectively).

According to the water column depth-temperature profiles presented in Figure 2.5, the six blue sharks showed a continuous residence time at depth during the day, spending an average of 61.30 % (± 12.53) of their time below the thermocline layer (potentially represented by the orange-yellow color of the ambient temperature gradient). Figure 2.5

shows not only a higher prevalence of individuals for deep dives (dives av. 90.51 ± 85.40 m), but also a higher occurrence of surface dives during the night. For example, sharks Blue13, Blue16, and Blue17 exhibited both daytime and nighttime movements in shallow waters. However, an increase in the number of deep dives (through thermocline) was observed during the day and a greater consistency of shallow dives at night (Figure 2.5; A, D, E). On the other hand, sharks Blue14 and Blue18 showed dives through the thermocline throughout the follow-up period, with more restricted depths (decreased deep excursions), reflecting increased thermal stratification of the water column (Figure 2.5; B, F).

Using the Matlab algorithm, the ambient temperature was interpolated every five m, allowing the depth values of the thermocline layer recorded during each shark's dive to be obtained. The amplitude and depth of the thermocline were estimated to characterize the water temperature stratification (Figures 2.5 and 2.6). Blue sharks not only showed a wide range of depth preferences, but also responded differently to the thermocline layer that showed a depth range between 22.0 and 188.0 m (av. 33.50 ± 7.01 m). In general, all sharks exhibited a shallow thermocline layer and a smooth water range between the reference values for the upper and lower limit, reflecting a weak thermocline. Based on interpolation graphs of temperature as a function of depth, it is possible to assume a "direct" proportion between depth and the ambient temperature recorded (Figure 2.6). The ambient temperature decreases as the shark dives into deeper waters. However, the greatest temperature variation occurs in the thermocline zone, where within a few tens of meters the temperature can vary by more than 5 ºC. For example, shark Blue15 recorded temperatures between 17 ºC and 22 ºC between 25 and 65 m (thermocline region), and ambient temperature variations of less than 3. 5 ºC between 65 m and around 400 m (region below the thermocline layer) (Figure 2.6; A). The Blue18 shark (Figure 2.6; B) showed a similar fluctuation in water temperature, with a sharp variation in ambient temperature associated with the thermocline layer, registering differences of almost 6.0 ºC in less than 60 m. In general, all the other sharks showed this pattern of water column temperature variation throughout the dive profile.

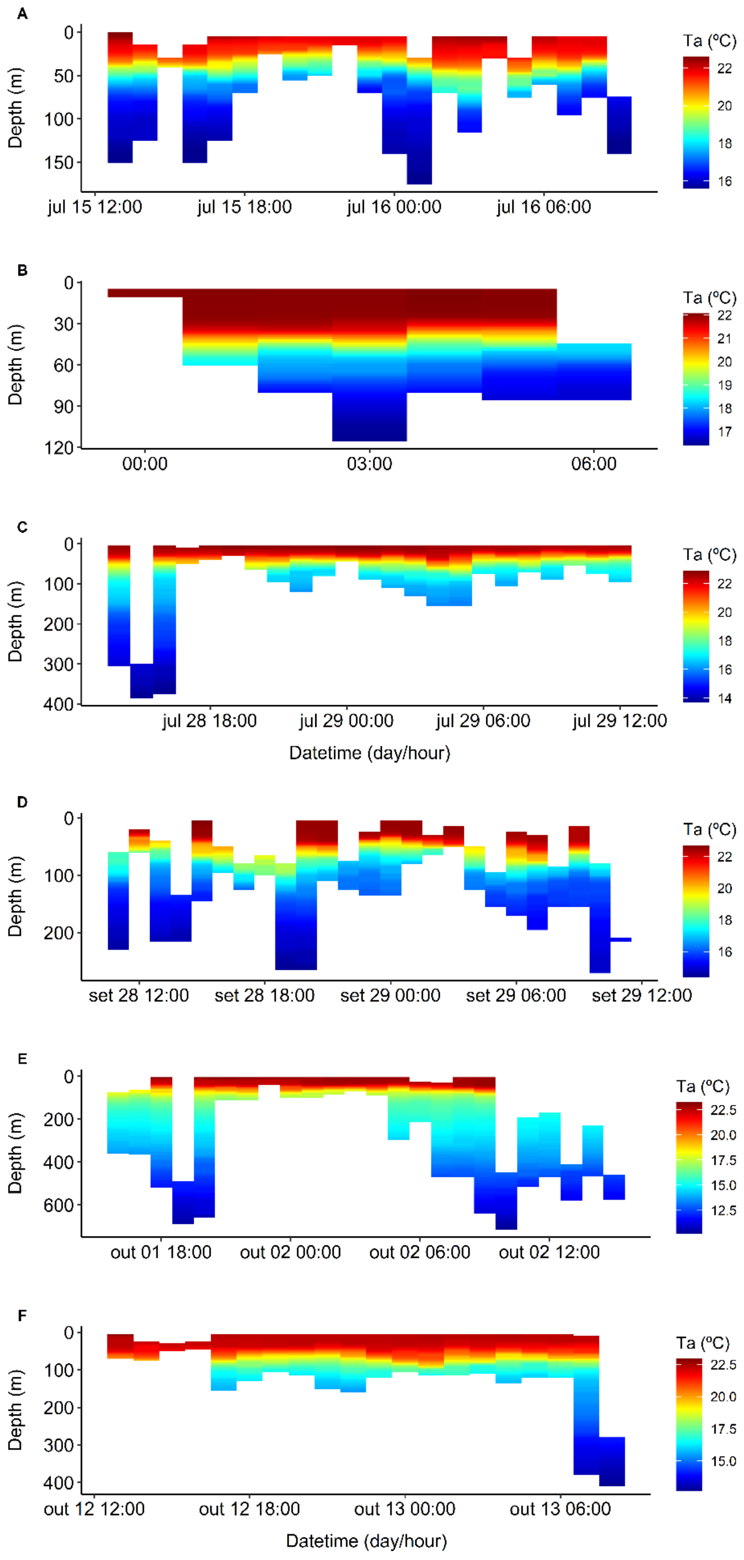

Figure 2.5. **TAD profile of the six blue sharks.** Temperature at depth profile at each hour, superimposed on the color-coded water temperature field from Matlab algorithm data. (A) Shark Blue13; (B) Shark Blue14; (C) Shark Blue15; (D) Shark Blue16; (E) Shark Blue17; (F) Shark Blue18.

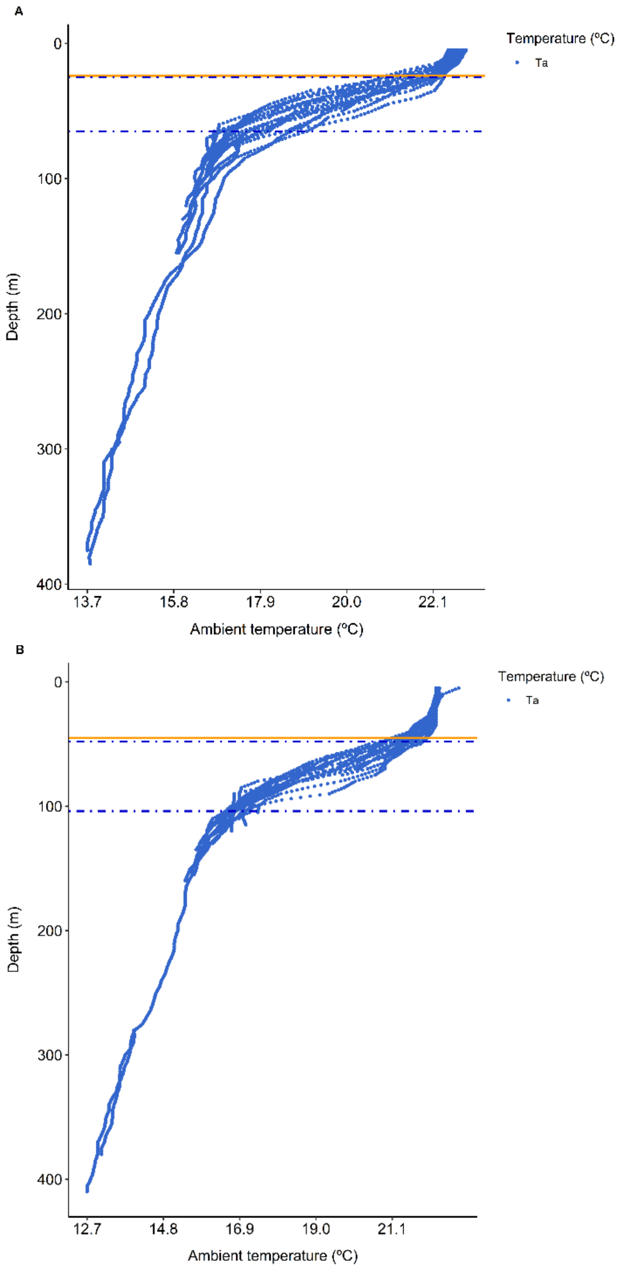

Figure 2.6. **Depth-temperature correlation during blue sharks movement.** Depth interpolation as function of water column temperature with thermocline limits defined by dashed blue lines and yellow full line. (A) Shark Blue15; (B) Shark Blue18.

2.3.2. Thermoregulation

While ambient temperature varies in depth, muscle temperature showed a profile with slower and smoother variations over time. For most of the sharks, the range of difference between minimum and maximum muscle temperature was relatively low (e.g., 5.70 ºC for Blue13), the exception was Blue17 which experienced a range interval of 13.20 ºC (Table 2.1). Regardless of this, the average muscle temperature recorded was similar between all blue sharks studied, with a difference of no more than 3 ºC between individuals. Blue17 recorded the lowest (10.22 ºC) and highest muscle temperature (23.44 ºC) observed (Table 2.1), exceptionally following the changes in ambient temperature and shark movement through the water column (Figures 2.7 and 2.8). The remaining five blue sharks described a smoother profile of body temperature change, decreasing body temperature slowly during descent and increasing it almost instantaneously during ascent.

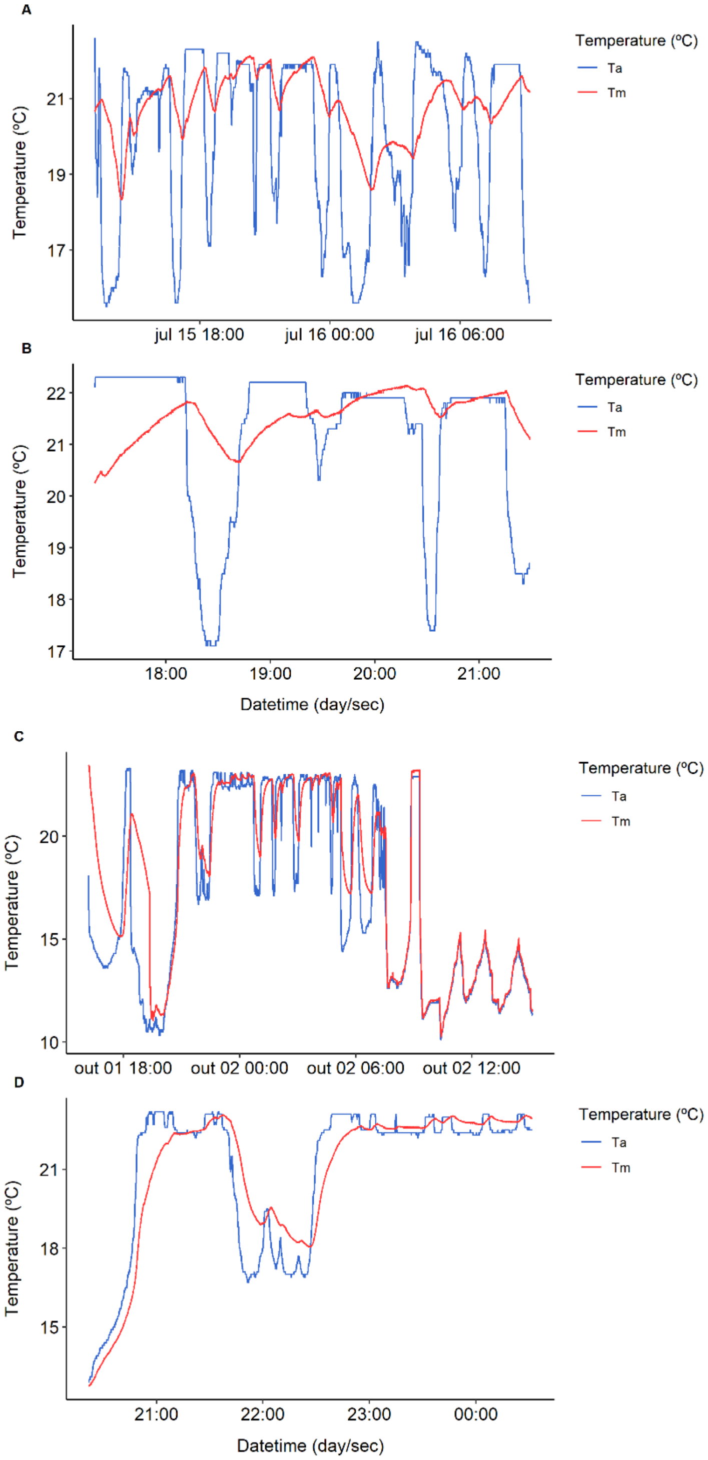

Figure 2.7. **Temperature profile**. (A, C) Ambient (blue line) and muscle (red line) temperature fluctuations of blue sharks during the entire day, recorded at each second. (B, C) Temperature profile over a constrained time period, highlighting more precisely how ambient temperature influences muscle temperature. (A, B) Shark Blue13; (C, D) Shark Blue17.

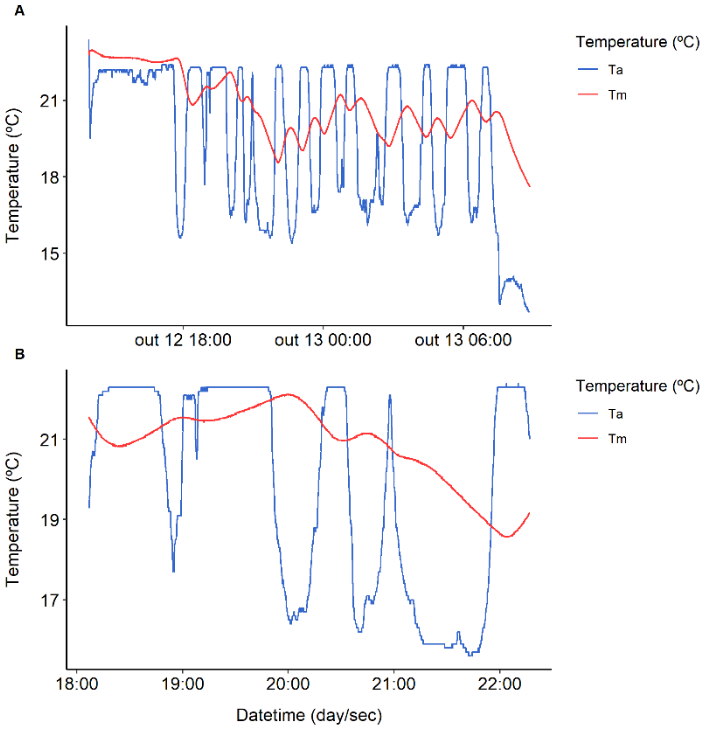

Figure 2.8. **Temperature profile of shark Blue18**. (A) Ambient (blue line) and muscle (red line) temperature fluctuations of blue shark during the entire day, recorded at each second. (B) Temperature profile over a constrained time period, highlighting more precisely how ambient temperature influences muscle temperature.

The descending phase of the movement always showed a slow and progressive decrease in the sharks' muscle temperature, which reached its minimum during the ascending phase. Also, during the ascending phase, the sharks abruptly increased their muscle temperature. Exceptionally, shark Blue17 recorded muscle temperatures like the ambient temperature. Muscle temperature varied in the same way as water column temperature, being proportional to the diving depth reached by the shark over time (Figure 2.7; C, D). In the case of shark Blue18, for two hours the shark's temperature gradually decreased, regardless of the occasional rise in ambient temperature associated with an upward diving movement. The absence of a muscle temperature adjustment during this period was a response to rapid variations in ambient temperature as well as a high prevalence of downward diving (Figure 2.8; B). Almost all individuals, however, showed a change in the direction of their movement before they had reached the peak of their minimum or maximum muscle temperature or the equilibrium with water temperature (Figures 2.7 and 2.8). Based on interpolation graphs of depth as a function of temperature, it is possible to assume a "direct" proportion between depth and the ambient temperature recorded. The ambient temperature decreases as the shark moves through the water column. However, muscle temperature is shown to vary within a narrower temperature range, independent of depth (Figure 2.9).

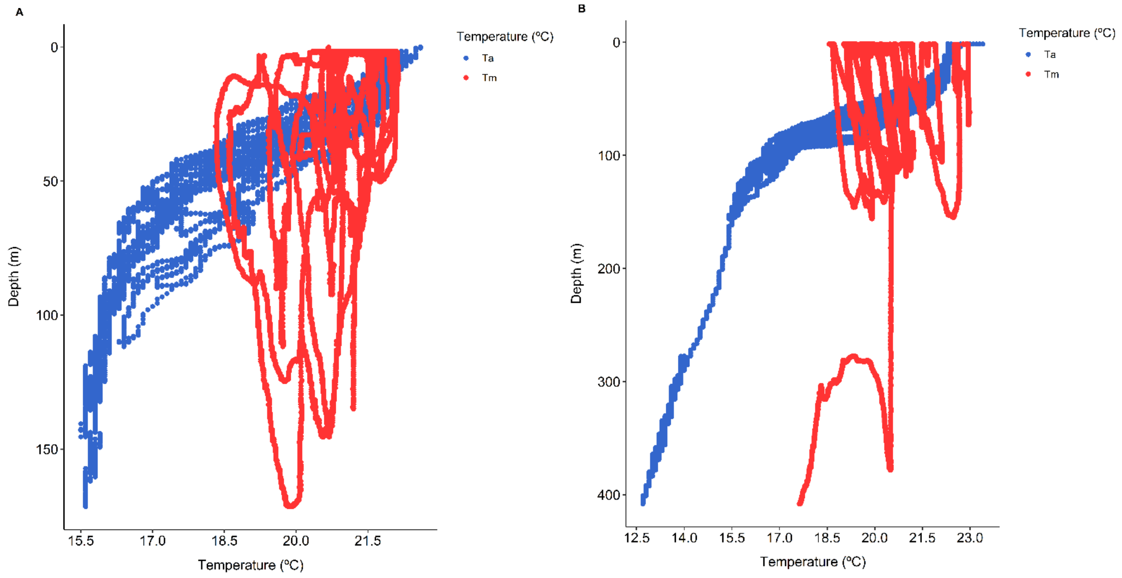

Figure 2.9. **Depth-temperature correlation**. Depth interpolation as function of ambient water (blue circles) and muscle temperatures of blue sharks (red circles). (A) Shark Blue13; (B) Shark Blue18.

Figure 2.10 shows a general representation of the stratification of the water column, with the demarcation of the thermocline layer and a representation of the temperature gradient in the water column. It also shows the fluctuations in body temperature recorded throughout the dive. The fluctuation of the ambient temperature throughout the water column is evident and its range is proportional to the range of diving depths explored by the shark throughout the day. The greater occurrence of deeper dives during the hours of greatest luminosity is consistent for both sharks represented in the figure, as well as for the others analyzed. The influence of water column temperature on muscle temperature is noticeable, although they do not show similar patterns of variation (Figure 2.10). Despite the different scales, figure 2.10 demonstrates the more restricted variation in muscle tissue temperatures in relation to the ambient temperature. For example, in the case of the Blue13 shark, its muscle temperature varies between around 18 and 22 ºC, while the ambient temperature varies between 10 and 23 ºC. The Blue16 shark has a muscle temperature variation of around 4 ºC and an ambient temperature variation of around 8 ºC. The shark tends to adjust its dive profile according to the thermal structure of the water column, never allowing its muscle temperature to balance with the ambient temperature.

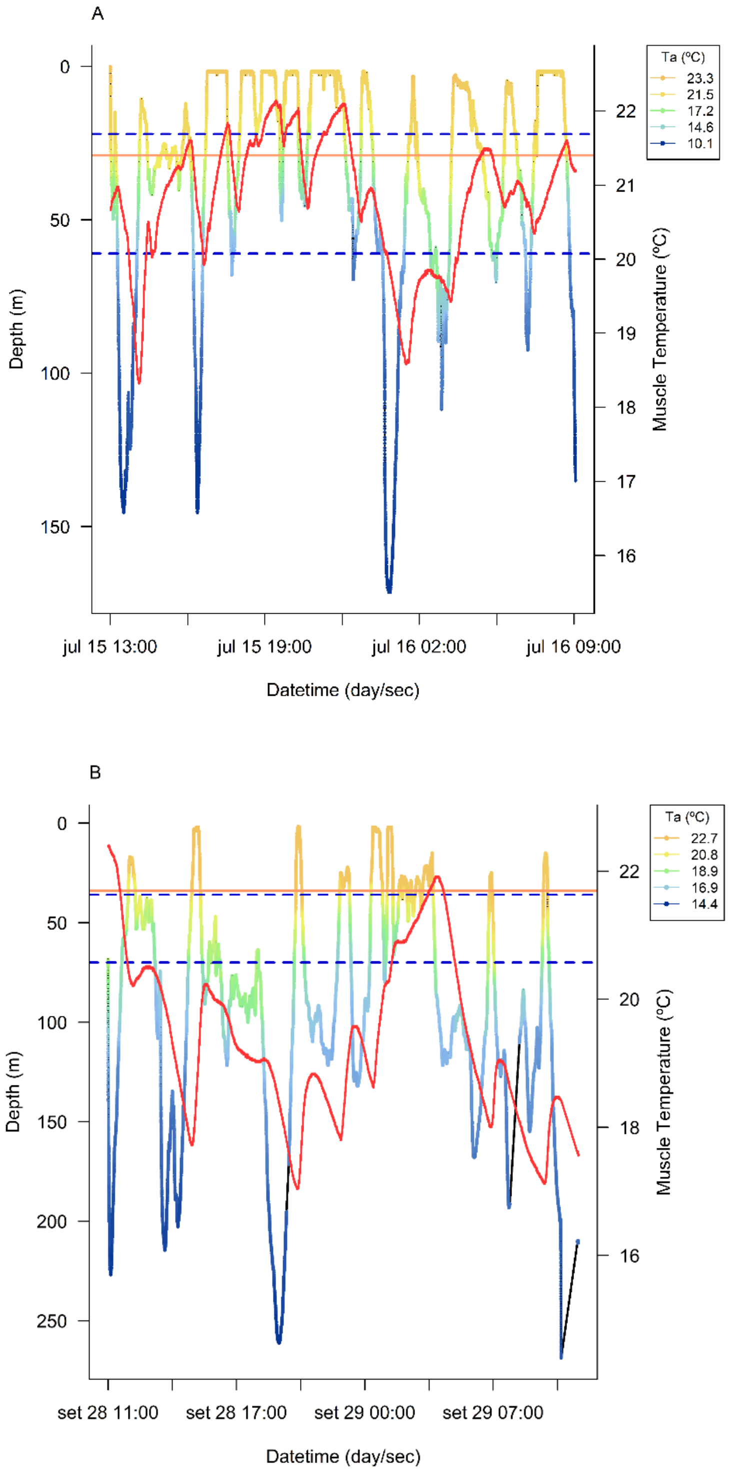

Figure 2.10. **TAD and TAT profiles of blue sharks**. Temperature-at-depth and both (ambiente and muscle) temperature-at-time performance profiles. Thermal gradient during swimming performance through the water column and definition of thermocline boundaries (blue dashed lines and yellow full line). Representation of flutuations in muscle temperature during the recording time. (A) Shark Blue13; (B) Shark Blue16.

2.3.3. Thermal modeling – heat exchange model

The rate of change in muscle temperature was correlated with the difference between ambient water temperature and muscle temperature, as predicted by the heat exchange model. The slopes of the regression lines over the origin provided preliminary estimates of whole-body heat transfer coefficients (in °C min^{-1} $°\mathrm{C}^{-1}$) during cooling (k_{cooling}) and warming (k_{warming}) processes (Figures 2.11 and 2.12). Cooling and warming processes were defined based on the thermal difference between the ambient temperature and the muscle temperature, cooling being the process where this difference is negative and warming being the process where this difference is equal to or greater than zero. In general, the cooling process takes place during the downward phase of the movement and the warming process during the upward phase. Without exception, all sharks demonstrated a positive relationship between the rate of change in muscle temperature and the surrounding temperature (Figures 2.11 and 2.12). For the majority of the sharks, the rate of change in muscle temperatures has not far exceeded ± 0.1 ºC/min, except

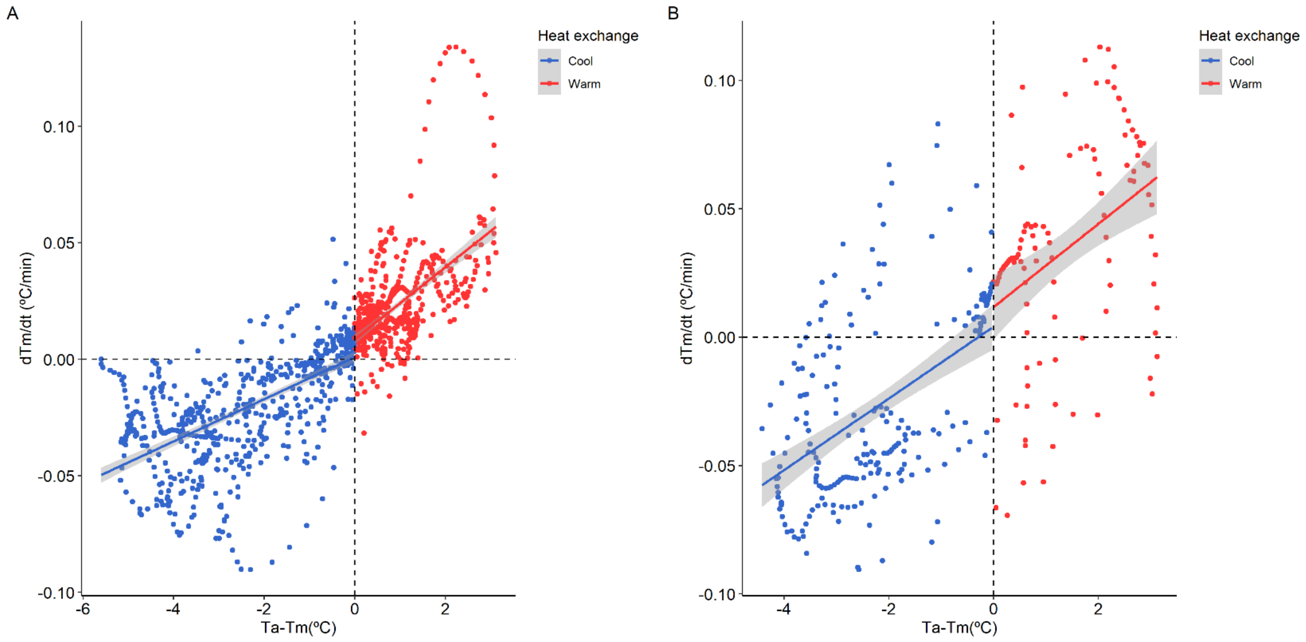

Figure 2.11. **Whole body heat exchange model applied to archival tag deployed in blue sharks.** The rate of changes in muscle temperature is plotted against muscle temperature subtracted from ambient water temperature. Red and blue circles represent the values of warming and cooling process, respectively. The slopes of regressions lines through the origin (thick lines) represent the initial estimates for whole-body heat transfer coefficients. (A) Shark Blue13; (B) Shark Blue14.

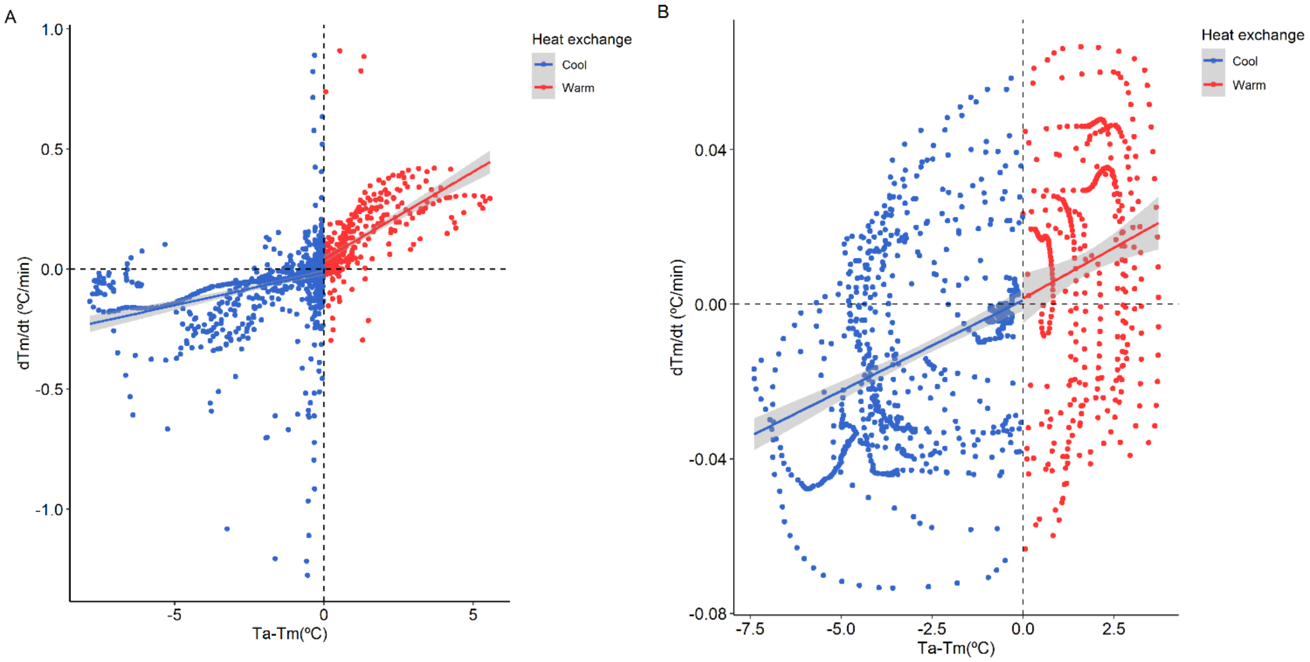

Figure 2.12. **Whole body heat exchange model applied to archival tag deployed in blue sharks.** The rate of changes in muscle temperature is plotted against muscle temperature subtracted from ambient water temperature. Red and blue circles represent the values of warming and cooling process, respectively. The slopes of regressions lines through the origin (thick lines) represent the initial estimates for whole-body heat transfer coefficients. (A) Shark Blue17; (B) Shark Blue18.

Blue17 which showed a rate of muscle temperature change of 1 ºC/min at certain points (Figure 2.12; A). The range of thermal difference between muscle and surrounding temperature did not go much further than ± 6 ºC for most sharks (Figures 2.11 and 2.12).

In comparison, the heat transfer coefficient (HTC) values during the cooling process were always lower than during the warming process (Table 2.2). Nonetheless, the differences in the rate of change in muscle temperature and the lag between the linear regressions during the cooling and warming processes (e.g., Figure 2.11; B), suggest that the estimates may not be the most accurate or suitable for determining changes in muscle temperature over time. By adjusting $k_{cooling}$ and $k_{warming}$ around the initial estimates, the best estimates for the whole-body heat transfer coefficient values were reached (Table 2.2). The adjusted $k_{cooling}$ and $k_{warming}$ estimates are more accurate and precise than the earlier estimates, as shown by the profiles described in Figure 2.10. The whole-body heat transfer coefficient values computed from the linear regressions for both cooling and warming processes revealed a low sum square residual (RSS) (< 0.05) for the majority of individuals. The shark Blue17 was the exception, showing a low RSS, although higher than 0.01, as presented. For both cooling and warming processes, several values close to

Table 2.2. Whole body heat transfer coefficient of all six blue sharks.

Shark ID	**Body mass (kg)**	**K cooling ± SE (°C min^{-1} °C^{-1})**	**K cooling RSS[a]**	**K warming ± SE (°C min^{-1} °C^{-1})**	**K warming RSS[a]**	**K cooling fitted (°C min^{-1} °C^{-1})**	**K warming fitted (°C min^{-1} °C^{-1})**	**RSS[b]**
Blue13	90.4	0.0087 ± 0.0003	0.0183	0.0212 ± 0.0006	0.0178	0.0107	0.0262	147.3142
Blue14	63.1	0.0126 ± 0.0008	0.0314	0.0217 ± 0.0022	0.0391	0.0146	0.0267	30.9397
Blue15	90.4	0.0174 ± 0.0005	0.0416	0.0239 ± 0.0009	0.0432	0.0224	0.0339	204.0857
Blue16	83.5	0.0045 ± 0.0002	0.0201	0.0088 ± 0.0005	0.0261	0.0065	0.0188	237.2875
Blue17	43.5	0.0306 ± 0.0021	0.1660	0.0891 ± 0.0040	0.1243	0.0405	0.0991	3164.7727
Blue18	81.3	0.0044 ± 0.0002	0.0225	0.0059 ± 0.0008	0.0291	0.0064	0.0159	170.2466

[a] Residual sum of squares obtained by the best combination of $K_{cooling}$ and $K_{warming}$.

[b] Residual sum of squares obtained by the addition of all RSS calculated for each muscle temperature prediction per minute.

the initial estimate of the whole-body heat transfer coefficient were merged. The best estimates for each shark's heat transfer coefficients were chosen based on the lowest sum of RSS that results from values of muscle temperature obtained from the better combination of k_{warm} and $k_{cooling}$ values (Table 2.2). The lowest RSS (for most sharks) was reached by adding 0.002 and 0.010 to the initial estimated values of $k_{cooling}$ and $k_{warming}$, respectively. The best estimates of the whole-body heat transfer coefficient value for both cooling and warming processes allowed us to infer the muscle temperature of each shark very accurately concerning the actual temperature recorded. When fitting the estimates with the other environmental and behavioral parameters, we observed that, compared to the actual values, the estimates followed more accurately and precisely the movement profile. The default values of the heat transfer coefficient for cooling and warming operations are 0.0107 and 0.0262, respectively. These values were carefully acquired and calculated based on the average of the best-estimated values, from which sharks Blue14 and Blue17 were removed. The blue sharks previously mentioned show irregularities in the parameters analyzed. For example, shark Blue14 shows substantial differences in the sampling times compared to the others, which may influence the variables due to a lower number of values. In the case of shark Blue17 (Figure 2.4; E), the high discrepancy of temperature profile compared with other sharks showed abnormal recorded and estimated values of muscle temperature.

Figure 2.13 shows the results of improving whole-body heat transfer coefficient estimates and merging these estimates with actual muscle temperature values. Despite the residual discrepancy between the estimated and actual value of muscle temperature, in general, the adjustment of the initial estimates allowed a higher accuracy and better approximation to the real values of muscle temperature. In comparison, the Blue15 shark was the one that showed the best accuracy in its muscle temperature estimates, both the original and the improved ones, with no difference of 0.50 ºC from the real muscle temperature recorded by the tag. The other sharks (e.g., Blue14 shark and Blue18; Figures 2.13 and 2.14; A and B) showed a greater approximation of the estimated values to the real values after the improvement of the heat transfer coefficients in the different phases of the dive. The differences between muscle temperature and estimated temperature did not exceed 1.0 ºC in the case of the Blue14 shark. In the case of the Blue18 shark, the model adjustment allowed the predicted muscle temperature to show a maximum difference of around 1.0 ºC compared to the real muscle temperature, instead of around 2.0 ºC (Figure 2.14).

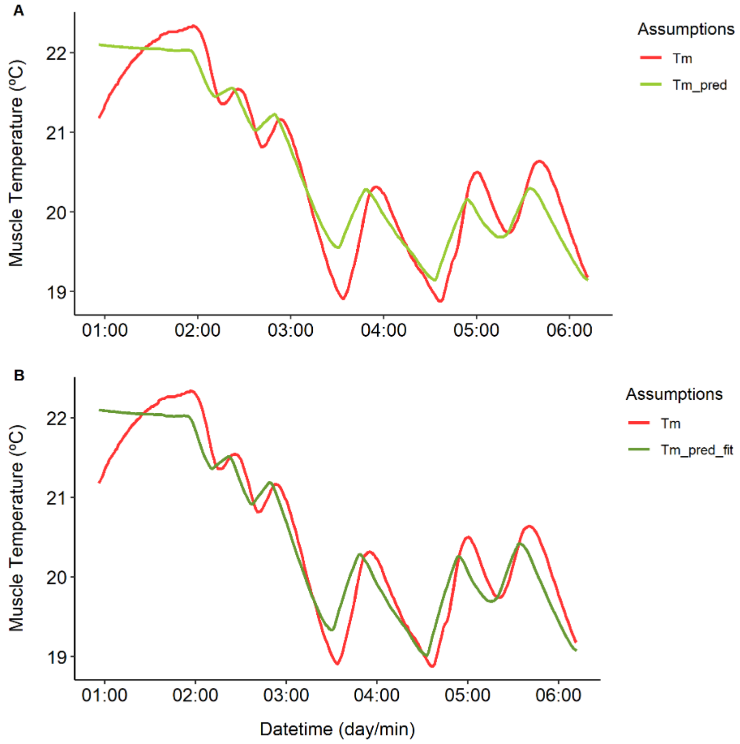

***Figure 2.13.* Blue shark muscle temperature flutuations, real prediction and fitted values**. Entire tracking period showing Tm, Tm_pred and Tm_pred_fit during descents, surface intervals and basking events. Simulated muscle temperature (Tm_pred) and improved simulated muscle temperature provided by the model (Tm_pred_fit), traces to the actual muscle temperature record (Tm). (A, B) Shark Blue14.

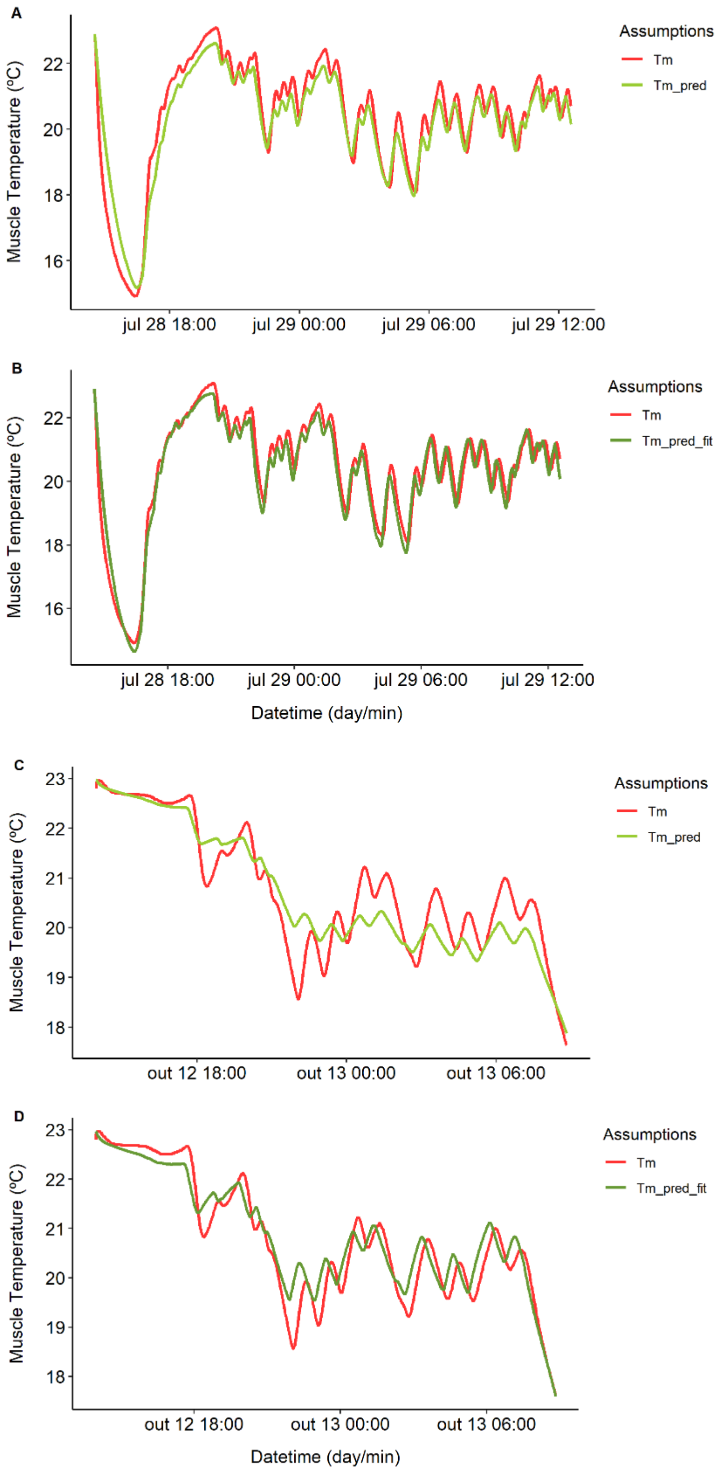

***Figure 2.14.* Blue shark muscle temperature flutuations, real prediction and fitted values**. Entire tracking period showing Tm, Tm_pred and Tm_pred_fit during descents, surface intervals and basking events. Simulated muscle temperature (Tm_pred) and improved simulated muscle temperature provided by the model (Tm_pred_fit), traces to the actual muscle temperature record (Tm). (A, B) Shark Blue15; (C, D) Shark Blue18.

In order to get a more generalized perspective on the profiles of diving depth, temperature and the accuracy of the muscle temperature prediction model based on heat transfer coefficients, graphical representations such as Figure 2.15 were made. The similarity between the profile of variation in depth and ambient temperature throughout the dive is evident, as is the slower variation in muscle temperature. In the case of the shark in Figure 2.15 (shark Blue15), the similarity between the measured and calculated temperatures is very marked. This shows that the model is very accurate.

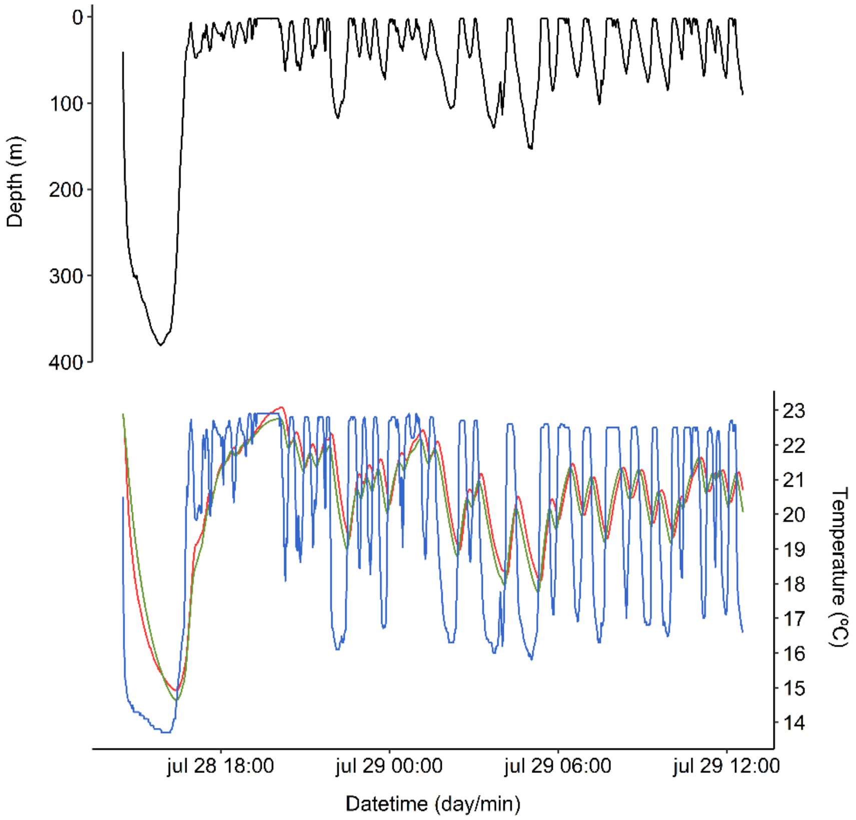

***Figure 2.45.* General perspective of blue sharks temperatures flutuations and heat exchange model performance**. (Top panel) Representative vertical movement patterns of shark Blue15. Time-depth profile during the entire period at 1 min intervals. (Bottom panel). Ambient temperature (blue line) is shown with muscle temperature (red line) and with its improved prediction (green dashed line) based on the ambient water temperature and heat exchange model.

As mentioned by Schmidt-Nielsen (1984), body mass can influence heat conservation and the rate of heat exchange to the environment. The difference between ambient and body temperature at the time did not vary greatly due to body mass, showing a very slight negative trend (Figure 2.16). The average difference between ambient water and muscle temperature never exceeded 1.5ºC and was not significantly influenced by increasing or decreasing body mass, showing almost a constant variation. As body mass increases there is a slight upward trend in the average difference between ambient and muscle temperature (Figure 2.16). As such, muscle temperature was higher than ambient temperature for most of the diving period recorded.

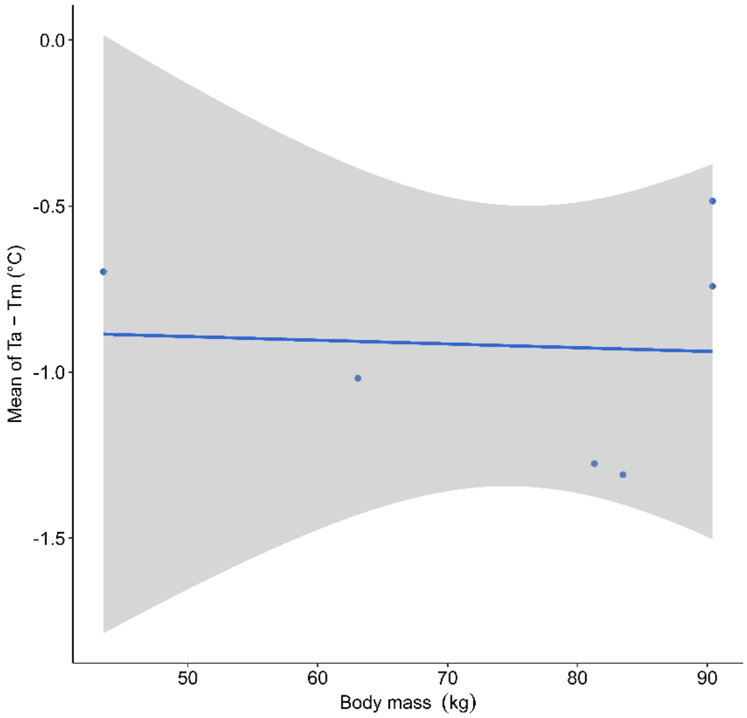

***Figure 56.* Correlation difference temperature between body and surrounding environment and body mass of each individual.** Mean difference of temperature between surrounding environment and muscle temperature of all six blue shark plotted against body mass with regression line (blue line).

For comparison, the body mass of the six blue sharks showed an inversely proportional correlation in both cooling and heating processes, with the whole-body heat transfer coefficient. The heat transfer coefficient decreases with increasing body mass (Figure 2.17). Shark Blue17 was the lightest shark recorded (43.5 kg) and the one recording the highest heat transfer coefficient values ($k_{cooling}$,0.0405; $k_{warming}$, 0.0991). Additionally, although the trend was negative, the lowest heat transfer coefficients recorded were not achieved by the heaviest sharks (90.4 kg, sharks Blue13 and Blue15), but for Blue16 (83.5 kg). However, it can be seen that the slope of the line for the warming process is steeper than for the cooling process (Figure 2.17). According to the figure, the linear regression for both processes tends towards the same point as muscle mass increases.

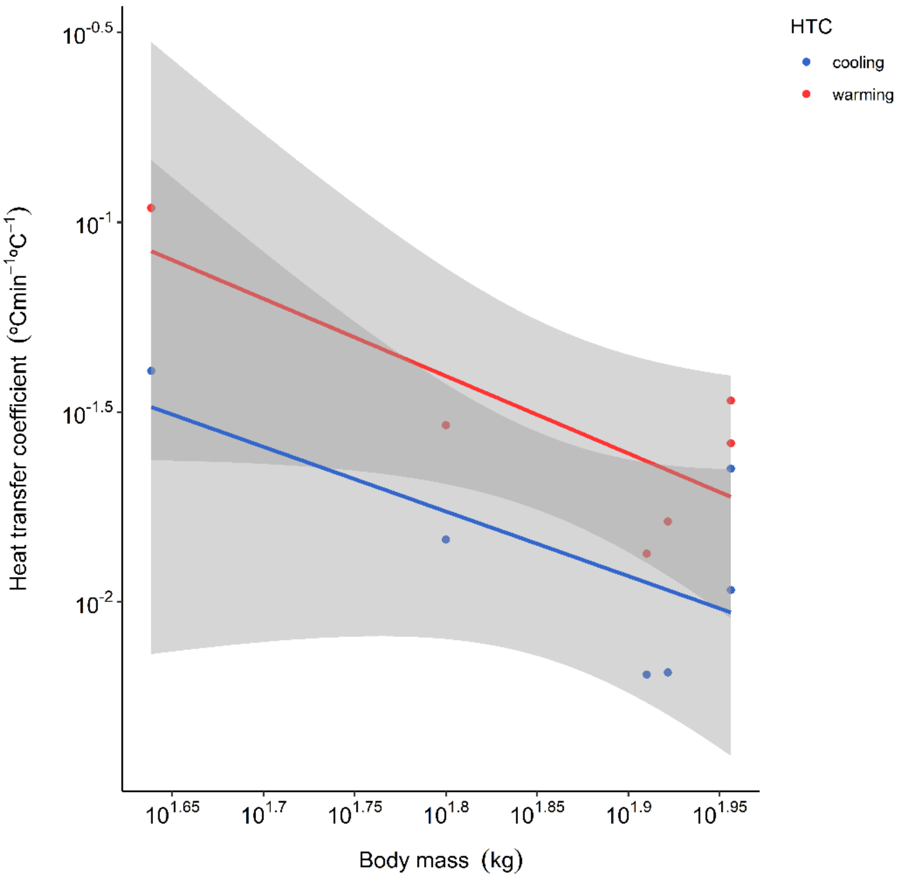

Figure 2.67. **Whole-body heat transfer coefficient and body mass correlation of blue sharks.** Heat transfer coefficients plotted against body mass for the warming process (orange points) and cooling process (blue points). Regression lines are also shown.

2.4. Discussion

Understanding how species' physiology, behavior, and ecology interact with environmental temperature is critical for predicting changes in their movement, distribution, and ecological function in response to climate change and can ultimately reveal the limiting constraints to their distribution (Kearney and Porter, 2009; Hazen et al., 2013; Payne et al., 2016; Kleisner et al., 2017; Morley et al., 2018; Payne et al., 2018). In order to achieve this, we analyzed data collected through biologging devices attached to six blue sharks in the Azores region. Our data provide a detailed insight into the swimming behavior and thermoregulatory capabilities of blue sharks during deep dives. The sharks described a regular dive profile across the water column thermal gradients, with their dives presumably mostly associated with thermoregulation or foraging behaviors. Ambient temperature presented a wide variation gradient through the water column and a positive correlation with fluctuations in muscle temperature, which is to be expected given that the blue shark is an ectothermic species. Muscle temperature had a more restricted range and a slower variation compared with water temperature. Blue sharks shift vertical swimming directions (descending or ascending) before their body temperature reaches the ambient water temperature, thereby supporting the thermoregulatory function of repeated deep dives. Behavioral and physiological thermoregulation strategies can be employed to manage the exchange of body heat with the surrounding environment. In this case, sharks in general show a great influence of body mass in heat transfer coefficient which could indicate a passive thermoregulation strategy.

2.4.1. Dive behavior

The movement of blue sharks off the Azores archipelago was tracked using archival tags. Six males were caught and tagged. The higher incidence of male catches in this region is in line with previous studies that point to their high prevalence further north in the Atlantic Ocean, off the Portuguese coast, compared to females (Litvinov, 2006; Vandeperre et al., 2014). The archival tags recorded daily data for a maximum period of 23 hours, varying between sharks due to technical errors in the equipment or handling by the team. The depth data collected by the accelerometer revealed a predominantly regular dive profile. The occasional deeper dives at an early stage may be associated with a post-capture stress reaction. Similar behavior has been reported before, not only in blue sharks (Landesman, 1984), but also in other species (Carey and Lawson, 1973; Carey and Robison, 1981).

Diving depths were quite variable, with a maximum depth of 700 m being recorded. Despite this, the majority of dives are carried out mainly in the more superficial layers. In agreement, Queiroz et al., (2012), suggested the existence of prey patches in a limited depth layer considering the greater consistency of the diving depth of blue sharks between 200 - 400 m. Except for the Blue17 shark, all the others showed a greater frequency of dives at depths of less than 100 m, spending most of their time above the thermocline layer (av. 33.50 ± 7.01 m). The thermal gradient in the water column was very wide and proportional to the depths recorded. As the shark dived to the bottom, the ambient temperature decreased accordingly. Despite the wide range of variation, the ambient temperature recorded for the blue sharks analyzed was on average 17 - 20 ºC. The greatest oscillation in ambient temperature occurs in the thermocline zone, where in a few tens of meters the temperature can vary by up to 4 or 5 ºC. The physical properties of the water column can directly or indirectly affect the depth and spatial distribution of prey and consequently be responsible for the considerable variation in vertical habitat use described by the blue shark's diving behavior (Sims et al., 2005), as suggested by Queiroz et al., (2010, 2012). A similar behavior was described for blue sharks in the Pacific Ocean, where tagged individuals spent ~65% of their time above 50 m (Weng et al., 2005), and by blue sharks tracked by Queiroz et al., (2010) in the English Channel off southwest England, off south Portugal, and south of the Azores archipelago. This pattern was expected since thermocline, where the temperature drops rapidly with depth, acts as a barrier to contain prey (Sogard and Olla, 1993).

Blue sharks demonstrated a repetitive behavior of deeper dives during the day and an increased number of dives limited to the thermocline layer, especially during the night. Additionally, a similar pattern was described by Queiroz et al., (2012), also for blue sharks. A higher number of prey aggregations occur in warm surface waters during the night, justifying the higher foraging during this period (Sims et al., 2006; Papastamatiou et al., 2018). Unlike other species, such as bigeye tuna and the oceanic sunfish, *Mola mola*, which have more specialized diets and feed predominantly in deep waters, the blue shark feeds on a wide range of pelagic organisms (e.g., teleosts, cephalopods, pelagic crustaceans) in the water column (Markaida and Sosa-Nishizaki, 2010), which could explain its wide range of depths used. Thus, regular vertical movements may represent prey-seeking behavior, especially when prey densities at the surface are scarce. In terms of optimal foraging theory, predators should maximize the time spent in a prey area. In addition, crossing several layers of water may increase the likelihood of detecting olfactory trails of prey that move horizontally in layers of water with different physical properties, enhancing predator capture success and justifying the existence of occasional deeper dives (Carey and Scharold, 1990; Sims et al., 2003). Long-term diving records and given the global distribution of blue sharks in tropical and temperate waters have found that in blue sharks (Campana et al., 2011; Braun et al., 2019; Vedor et al., 2021) and other ectothermic pelagic sharks (Andrzejaczek et al., 2018) repeated deep-diving behavior is potentially associated with stratified water columns and higher surface temperatures (Carey and Scharold, 1990). The use of cameras and analysis of their videos would make it possible to infer with greater certainty the relationship between deeper dives and movements associated with the pursuit of prey, which was not possible in this study [as reported by Watanabe (2021)].

2.4.2. Thermoregulation

In the present study, muscle temperature showed a narrower variation in relation to water temperature for most of the individuals analyzed (an average of 20 ºC). Despite this, the sudden oscillation of water temperature in the thermocline zone showed no influence on muscle temperature. Carey and Gibson (1987) suggested that sharks did not hesitate to cross the thermocline, with a rapid and proportional response of muscle temperature to changes in water temperature. Despite this, a slower and smoother variation in muscle temperature compared to the surrounding environment was visible throughout the dive. The slower drop in muscle temperature can be explained by the high thermal inertia (i.e., low surface area/volume ratio). Their high thermal inertia allows blue sharks to make short foraging trips to deep cold waters without significantly reducing their body temperature, as they warm up again at shallow depths (Watanabe et al., 2019). In this study, a pattern of deeper dives followed by shallower dives is visible, which responds to the theory of Thums et al. (2013) which suggests that blue sharks would show thermoregulatory behaviors if the relationship between daytime temperatures and consecutive nighttime temperatures were negative. This can be seen from the fact that, in general, the colder the ambient temperature recorded on a dive, the warmer the water temperature on the following dive, in response to the need to reheat (Carey and Scharold, 1990; Nakamura et al., 2015). In addition, although there is a greater prevalence of sharks in the surface layers at night, occasional deeper dives have been recorded throughout the day, presumably associated with the need to reduce internal temperature (Campana et al., 2011). Previously, Carey and Scharold (1990) showed that blue sharks shift vertical swimming directions (descending or ascending) before their body temperature reaches the ambient water temperature. Thus, shark body temperature falls within a narrow range, thereby supporting the thermoregulatory function of repeated deep dives. Blue sharks perform their dives between the surface and the bottom without ever allowing their muscle temperature to equilibrate with the water temperature which reveals a mechanism for thermoregulating and maintaining body temperature in an optimal range. Previous studies assume that the DVMs observed on a global scale, from plankton to top predators

(Longhurst and Harrison, 1989; Zhang and Dam, 1997), may be associated with thermoregulatory movements or optimization of predation strategies (e.g., Sims et al., 2006; Last et al., 2016; Hafker et al., 2017). Watanabe et al. (2021) also recently suggested that behavioral thermoregulation associated with foraging is fundamental to the vertically and geographically expanded thermal niches of blue sharks.

Ectothermic species, such as the blue shark, are expected to seek out suitable thermal conditions within their available habitat in the absence of additional restrictions. However, if such behavioral thermoregulation deprives the species of essential resources, it may be difficult to exploit thermal refugia during unfavorable temperature circumstances. Anthropogenic climate change is causing significant changes in the ranges of marine creatures throughout the world's oceans (Poloczanska et al., 2013). This is consistent with other regions' expected habitat changes for blue sharks and other species (Cheung et al., 2015; Lezama-Ochoa et al., 2016). Pelagic sharks are vulnerable to the effects of climate change (Jones and Cheung, 2018), and life cycle choices may determine the final patterns of species distribution, despite the fact that relatively little is known about how rising temperatures may affect sharks (Pistevos et al., 2015). Moving to deeper areas, for example, would help marine species avoid rising surface temperatures, but could also restrict their access to ideal feeding grounds (Freitas et al., 2016). As could also expose species to hypoxia, since oxygen supply generally decreases with depth (Deutsch et al., 2015). Thus, species with strong behavioral preferences for specific habitat types are predicted to be more vulnerable to changes in ocean temperature, while generalist species are less vulnerable (Matis et al., 2018).

2.4.3. Thermal modeling – heat exchange model

An individual's capacity to occupy habitats beyond their thermal optimum depends on the rate of heat exchange between the body and its surroundings. Ectothermic fish, such as the blue shark, do not have counter-current heat exchangers (Watanabe et al., 2021) and most of the metabolic heat is lost to the water via their gills (Stevens, 2011), therefore $\dot{T}_0$ is considered zero in this study. In addition, there are still no published studies on the metabolic potential of the blue shark, presumably due to the difficulty of measuring physiological parameters or controlling them in captivity. The heat transfer coefficient is calculated for data collected every minute. In order to apply the model to the data collected, it was necessary to group the data (which we collected every second). The method chosen was based on averages of values every minute rather than the last values recorded every minute, assuming that there would be a greater representation of the fluctuation in temperature values as well as greater precision with the use of the average.

In this study, we analyzed the rates of heat transfer between the body and the environment in order to understand the mechanics of thermoregulation. Very few studies have measured the rate of heat transfer per se (e.g., Brill et al., 1978). As in this study, most infer the pathways and rates of heat exchange with the environment by measuring temperature or rates of temperature change (e.g., Stevens and Fry, 1974; Stevens and Sutterlin, 1976). The cooling and heating rates of blue sharks were suggested by Carey and Scharold (1990). The whole-body heat transfer coefficients, or k-values, of large pelagic fish can be higher during the ascending (i.e., warming) phase of dives than during the descending (i.e. cooling) phase (Holland et al., 1992; Nakamura et al., 2015, 2020). In the case of the blue sharks analyzed, the $k_{warming}$ values were always about two orders of magnitude higher than the $k_{cooling}$ values. A $k_{warming}$ value four times higher than the $k_{cooling}$ value was discovered in a previous study that reanalyzed Carey and Scharold's (1990) data on a single blue shark (Bernal et al., 2001). The shark's muscle warms up faster than it cools down (Carey and Gibson, 1987). This may allow them to achieve a faster rate of warming than cooling, as previously demonstrated by the ectothermic blue shark (Carey and Gibson, 1987; Carey and Sharold, 1990). These results suggest that blue sharks change heat exchange rates depending on the phase of their dives, similar to bigeye tuna (Holland et al., 1992) and oceanic sunfish (Nakamura et al., 2015). This observation suggests that they have the ability to physiologically improve the body heating process, which results in shorter post-dive times and greater foraging efficiency during a dive cycle (Nakamura et al., 2015).

Kitagawa and Kimura (2006) quantified the heat transfer coefficients of blue sharks and found that the variables could be linearly separated based on the thermal conductivity of the tissue outside the isothermal core and the amount of heat transported to the gills from the isothermal core. This indicates that the blood regulates heat flow and not metabolic heat production as the cause of the body's ability to increase its temperature. The amount of heat exchange in the gills increased with the increase in perfusion flow, and the gills were responsible for 60% of all heat exchange (Sorenson and Fromm, 1976). However, without their high thermal inertia, blue sharks are unable to control the temperature of their muscles. Their large volume is an important factor in minimizing heat transfer, especially heat conduction (Schmidt-Nielsen, 1984). The values of the heat transfer coefficients for the smallest fish (e.g., 40 kg) are about three orders of magnitude higher than for fish weighing 80-90 kg. As with the sixgill shark (Royer, 2020), analysis of the heat transfer coefficient revealed a constant rate of heat exchange between the muscle and the ambient water temperature, which predicts that blue sharks rely on passive thermoregulation when moving between different thermal environments. The large body masses provide sufficient thermal inertia to slow down the rate of heat exchange with the environment. Thermal inertia allows the core muscle temperatures of adult hammerhead sharks to remain warmer than the deep ambient water during the daytime phases when the sharks are most active, and cooler than the ambient water during the nighttime phases when the shallower depths approach critical ambient temperatures (Royer, 2020). According to the surface area law (Schmidt-Nielsen, 1984), larger fish also have a lower ratio between the surface area and the mass of their bodies. Due to their high thermal inertia and limited thermal conductivity, which allow for greater insulation of their bodies, they are able to physiologically control the temperature of their muscles (Neill and Stevens, 1974; Paladino et al., 1992).

2.5. Conclusion

Despite the small sample size, we were able to demonstrate that blue sharks thermoregulate their behavior and forage during repeated deep dives. During these repeated dives, they pursue prey that is widely dispersed throughout the water column. By starting ascents before their bodies cool down excessively and starting descents before their bodies heat up excessively, they maintain their body temperatures within a small range. They are able to regulate heat transfer rates thanks to the increased thermal inertia of their huge bodies, which is measured by whole-body heat transfer coefficients. Studies using tags to track blue sharks have been successful in collecting data on their short- and long-term movements and migrations. In addition, it is essential to understand the horizontal and vertical habitat use patterns of marine predators in relation to the physical characteristics of the environment, as these have a significant impact on the movements and distribution of predators and help us to predict the behavior of animals in the face of changing environmental conditions. However, in future studies, temperature measurements combined with oxygen level measurements would also be useful to understand whether movements in the water column are influenced not only by thermal gradients, but also by the existence of hypoxia zones. Additional analyses of physiological parameters, such as heart rate or calculations of metabolic heat values, would be essential to elucidate how blue sharks and other ectothermic fish alter the rate of heat exchange during diving. Knowledge about the distribution, thermoregulation and life behavior of the blue shark is fundamental to improving conservation measures, given the threats they face not only due to high fishing pressure, but above all due to climate change.

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