UNIVERSIDADE FEDERAL DE PERNAMBUCO
CENTRO DE TECNOLOGIA E GEOCIÊNCIAS
DEPARTAMENTO DE OCEANOGRAFIA
PROGRAMA DE PÓS-GRADUAÇÃO EM OCEANOGRAFIA

LEONARDO DE LIMA FIDELIS

EFEITO DA TEMPERATURA NA UTILIZAÇÃO DA ZONA MESOPELÁGICA OCEÂNICA POR UM PREDADOR ECTOTÉRMICO, O TUBARÃO TIGRE (*GALEOCERDO CUVIER*)

Recife

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Dissertação apresentada ao Programa de Pós Graduação em Oceanografia da Universidade Federal de Pernambuco (PPGO-UFPE), como requisito parcial para obtenção do título de Mestre em Oceanografia.

Área de concentração: Oceanografia Biológica

Orientador: Prof. Dr. Fábio Hissa Vieira Hazin

Coorientador: Dr. André Sucena Afonso

Recife

2019

Catalogação na fonte

Bibliotecária Valdicéa Alves, CRB-4 / 1260

F451e Fidelis, Leonardo de Lima.

Efeito da temperatura na utilização da zona mesopelágica oceânica por um predador ectotérmico, o tubarão tigre (*Galeocerdo cuvier*). / Leonardo de Lima Fidelis - 2019.

38 folhas.

Orientador: Prof. Dr. Fábio Hissa Vieira Hazin.
Coorientador: Prof. Dr. André Sucena Afonso.

Dissertação (Mestrado) – Universidade Federal de Pernambuco. CTG. Programa de Pós-Graduação em Oceanografia, 2019.
Inclui Referências.

1. Oceanografia. 2. Excursões mesopelágicas. 3. PSAT. 4. Termorregulação comportamental. 5. Temperatura ambiental. I. Hazin, Fábio Hissa Vieira(Orientador). II. Afonso, André Sucena (Coorientador). III. Título.

UFPE

551.46 CDD (22. ed.) BCTG/2019 - 174

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Aprovada em: 07/03/2019.

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AGRADECIMENTOS

Agradeço a Deus, por me amar tanto, por me dar a oportunidade de viver e por cuidar de mim como um pai cuida de um filho. Agradeço à CAPES por proporcionar o apoio financeiro da bolsa de estudos e de projetos de pesquisa em que tive a oportunidade de participar.

Agradeço grandemente a toda minha família e principalmente aos meus pais Jeremias e Marcia e minha irmã Laura por todo o apoio dado desde a minha existência e por sempre torcer para o meu sucesso.

Agradeço ao meu orientador Fábio Hazin que confiou que eu poderia realizar um bom trabalho e por sempre ter aberto as portas para mim. Agradeço também ao Fabinho, que me ajudou a enxergar o mundo de uma forma mais leve, livre e com menos sofrimento.

Agradeço ao meu coorientador e amigo André Afonso, por acompanhar o meu trabalho e pela sua participação na parte estatística, programação e revisão do trabalho, além da confiança na participação de grandes projetos de pesquisa, que me tornou um melhor cientista.

Agradeço ao meu xará Leo Veras, meu professor do mar, por todos os ensinamentos sobre a vida e sobre o mar.

Agradeço a Sophie e Arnaud Bertrand, que auxiliaram meu trabalho num momento de bastante dificuldade, quando eu pensava que não ia conseguir eles me apoiaram. Quero agradecer em especial a Sophie por lecionar a melhor disciplina que participei nessa pós-graduação.

Agradeço aos companheiros de laboratório do LATEP, LEP e LOP pela união e parceria ao longo da minha permanência nestes laboratórios e um abraço especial ao meu irmão do peito Bruno César pelas horas de conversa e descontração ao longo da rotina diária no laboratório.

Agradeço a minha gatinha Luisa, que vem me dando suporte desde que nos conhecemos, além de tornar minha vida mais doce.

Agradeço a todas as pessoas que oraram, rezaram ou mandaram energias positivas para mim durante um dos momentos mais difíceis da minha vida, que ocorreu durante essa pós-graduação, para eu continuar com a missão e procurar contentamento na vida. Agradeço a todas as pessoas que passaram na minha vida e que de alguma forma contribuíram para eu estar onde estou e a ser quem sou.

RESUMO

O tubarão tigre (*Galeocerdo cuvier*) é um predador marinho de topo que possui comportamento altamente migratório, com distribuição em todos os oceanos tropicais, fazendo parte de uma ampla teia trófica. É uma espécie capturada mundialmente por várias artes de pesca, tanto como espécie alvo como incidentalmente, havendo, portanto, o risco de sobrepesca dos seus estoques. Embora a espécie reconhecidamente costume realizar mergulhos profundos na região mesopelágica, as razões para este comportamento ainda não são bem conhecidas. O presente estudo tem como objetivo entender o comportamento de excursões mesopelágicas relacionado ao gradiente térmico da coluna d'água, bem como o efeito do tamanho dos indivíduos sobre tal comportamento. Para isso, PSATs (*pop-up satellite archival tags*) foram utilizadas para registrar parâmetros ambientais, profundidade e temperatura, em alta resolução temporal a fim de calcular variáveis com significância biológica e assim melhor compreender o comportamento de mergulho. Os mergulhos foram definidos a partir de uma temperatura de limiar (22ºC) e então Modelos Lineares Generalizados (GLM) foram utilizados para entender a relação do comportamento de mergulho com a camada de mistura (MSL). Os resultados evidenciaram que os tubarões tigre permaneceram majoritariamente acima de 50 m de profundidade e em águas com temperaturas acima de 25ºC, embora tenham realizado incursões a até 689,5 m, em temperaturas de 4,9ºC. Os resultados também mostraram que estes animais permanecem em maiores profundidades com temperaturas mais elevadas da MSL antes dos mergulhos profundos, os quais apresentam um movimento em formato de "V". De maneira oposta, em mergulhos mais rasos (<200 m) os tubarões tenderam a realizar mergulhos em formato de "U". Após mergulhos profundos, onde estiveram expostos a baixas temperaturas, estes animais tenderam a passar um tempo considerável em águas mais rasas com temperaturas elevadas, onde certamente são capazes de recuperar o calor perdido durante o mergulho. O presente trabalho fornece informações relevantes para um melhor entendimento da biologia e ecologia dos tubarões tigre, integrando um conhecimento para a espécie, bem como contribuindo para futuras medidas de manejo para a sua conservação.

Palavras-chave: Excursões mesopelágicas. PSAT. Termorregulação comportamental. Temperatura ambiental.

ABSTRACT

The tiger shark (*Galeocerdo cuvier*) is a marine top predator that presents highly migratory behavior with circum tropical distribution, forming part of a large trophic food web. It is a species captured worldwide by many fishing gear, as target species or by-catch, which may carry it to stock overfishing. Although the species is known to practice deep dives in the mesopelagic region, the reasons for this behavior are still not well known. The present study aims to understand the behavior of mesopelagic excursion related to thermal gradient of water column, as well as the effect of size of individuals on such behavior. For this purpose, PSATs (*pop-up satellite archival tags*) were utilized to record environmental parameters, depth and temperature, in high temporal resolution in order to calculate variables with biological significance and thus to define the diving behavior. The dives were defined from a threshold temperature (22ºC) and then Generalized Linear Models (GLM) were utilized to understand the relationship between the diving behavior and mixed surface layer (MSL). The results showed that the tiger sharks remained mostly above 50 m depth and in waters with temperatures above 25 ° C, although they did incursions up to 689.5 m, at temperatures of 4.9 ° C. The results also showed that these animals remain at greater depths with higher MSL temperatures before the deep dives, which have a V-shaped movement. Conversely, in shallower dives (<200 m) sharks tended to perform U-shaped dives. After deep dives where they were exposed to low temperatures, these animals tended to spend considerable time in shallower waters with elevated temperatures, where they are certainly able to recover the heat lost during the dive. The present work provides relevant information for a better understanding of the biology and ecology of tiger sharks, integrating knowledge for the species, as well as contributing to future management measures for its conservation.

Keywords: Mesopelagic excursions. PSAT. Behavioral thermoregulation. Environmental temperature.

SUMÁRIO

1 INTRODUÇÃO

A compreensão dos processos ecológicos na vida marinha requer informações sobre a dinâmica de uso de habitat, não apenas horizontalmente mas verticalmente, posto que muito predadores pelágicos, associados primariamente com o ambiente epipelágico, frequentemente mergulham além da camada mesopelágica, sendo ainda desconhecida a razão deste comportamento (HOWEY et al., 2016). Os animais ectotérmicos são caracterizados por não possuírem mecanismos internos controladores da temperatura corporal, de forma que a temperatura do seu corpo é igual ou muito próxima da temperatura do ambiente circundante. Por essa razão, os animais ectotérmicos possuem limitação temporal em mergulhos mesopelágicos, visto que a temperatura nesta zona é muito baixa, o que poderia comprometer suas atividades metabólicas.

Em animais marinhos que respiram ar, o comportamento de mergulho está relacionado com a taxa de recuperação de oxigênio na superfície e o tempo gasto em profundidades (COOK et al., 2008). Diferentemente, os animais marinhos que respiram por brânquias podem possuir diversos motivos, inclusive simultaneamente, para realizar um mergulho mesopelágico. Os possíveis motivos para utilização de camadas profundas por esses animais compreendem: variabilidade comportamental intraespecífica (VAUDO et al., 2014), orientação, navegação (HOLMES et al., 2014), termorregulação comportamental (HIGHT; LOWE, 2007), conservação de energia (KLIMLEY et al., 2002) e forrageio (NAKAMURA et al., 2011). A grande quantidade de hipóteses ainda não testadas ressalta a importância de se desenvolverem estudos específicos para elucidar as funções dos mergulhos profundos de peixes que estão geralmente associados ao ambiente epipelágico.

Observar padrões de movimento e uso de habitat de predadores de topo é importante para prover um melhor entendimento sobre a ecologia e adquirir informações para ações de manejo e conservação (BLOCK et al., 2011). O deslocamento dos animais depende de fatores internos e externos, porém, o grau de influência de cada fator na decisão do animal varia substancialmente por espécie e local (MARTIN et al., 2013). A temperatura é um fator de grande influência na dinâmica das espécies, modificando suas abundâncias e distribuições de suas populações, podendo alterar teias alimentares, além de mudar a estrutura e funcionamento do ecossistema em caso de espécies-chave (ASPILLAGA et al., 2017).

Mudanças bruscas de temperatura podem alterar drasticamente a taxa metabólica, i.e. a velocidade com que diversas funções fisiológicas se processam (BEITINGER; FITZPATRICK, 1979), razão pela qual a regulação da temperatura corporal está diretamente associada à ecologia dos animais ectotérmicos (BERMAN; QUINN, 1991). A capacidade de termorregulação, portanto, molda, em grande medida, o comportamento e a seleção de habitat dos grupos taxonômico ectotérmicos (DUBOIS et al., 2009). Os tubarões ectotérmicos necessitam de uma estratégia comportamental para a termorregulação, diferentemente dos animais endotérmicos que possuem dispositivos fisiológicos que lhes conferem uma maior estabilidade de temperatura corporal. O gradiente vertical de temperatura na coluna d'água, portanto, possivelmente influencia as atividades metabólicas dos tubarões tigre, moldando o seu comportamento de mergulho. A análise dos movimentos verticais realizados pelos tubarões tigre, particularmente em relação às variações de temperatura, é, assim, muito importante para o entendimento dos processos que regulam a sua utilização do habitat.

Nas últimas décadas, as capturas de elasmobrânquios vêm crescendo em escala global, com esses animais sendo capturados tanto como alvo da pesca como incidentalmente (CAMHI et al., 2009). Essa crescente pressão pesqueira tem causado uma rápida depleção de vários estoques de tubarões (CORTÉS, 2002), alterando estrutura e parâmetros populacionais (STEVENS et al., 2000). A grande escala do ambiente pelágico marinho, porém, limita a capacidade humana de monitorar as populações de tubarões adequadamente, de forma que o efeito da pesca sobre muitas espécies ainda é desconhecido (BAUM et al., 2003). Nesse contexto, estudos de telemetria revelaram-se extremamente úteis para a identificação dos efeitos da pesca sobre populações de tubarões, em determinadas regiões (QUEIROZ et al., 2016), além de fornecerem uma série de dados bioecológicos essenciais para o manejo e conservação desses recursos, particularmente no caso de espécies altamente migradoras, como no caso do tubarão tigre.

1.1 OBJETIVOS

Segue abaixo os objetivos referentes ao presente trabalho.

1.1.1 Objetivo Geral:

Averiguar o papel da temperatura no comportamento de incursões mesopelágicas de tubarões tigre.

1.1.2 Objetivos Específicos:

Avaliar a relação entre a utilização de águas da zona mesopelágica, caracterizadas por temperaturas mais frias, e a utilização de águas epipelágicas, com temperaturas mais quentes; e

Estudar a distribuição vertical dos tubarões tigre na coluna d’água em função do respectivo gradiente térmico.

1.2 ESTRUTURA DA DISSERTAÇÃO

A dissetação foi desenvolvida em formato de artigo, o qual todos os resultados, discussão e apêndices das análises estatísticas estão contidos dentro do artigo. Este artigo foi submetido à revista Journal of Experimental Marine Biology and Ecology com o título Environmental temperature effect on mesopelagic excursions by an ectotherm top predator, the tiger shark (*Galeocerdo cuvier*).

2 ENVIRONMENTAL TEMPERATURE EFFECT ON MESOPELAGIC EXCURSIONS BY AN ECTOTHERM TOP PREDATOR, THE TIGER SHARK (*GALEOCERDO CUVIER*).

Introduction

Understanding environmental conditions that drive the movements of top marine predators over large distances is important to predict how these animals will respond to the rapid changes in the marine environment prompted by human interference, in particular to climate change (PAPASTAMATIOU et al., 2013), including changes in spatial and temporal distribution (HUSSEY et al., 2015). To correctly manage these species, it is important to recognize the necessity to better know their distribution and vertical behavior and to examine their overlap with fishing gear and thus the species' vulnerability to fishing pressure. Accordingly, the analyses of vertical movements provide insights to link environmental parameters and the behavior of marine animals and adds understanding to the link between pelagic habitats below euphotic zone and the ocean surface. Telemetry studies provide high-resolution data about species behavior and distribution which were difficult to obtain before the development of this technology, enabling scientists to predict changes and to manage marine resources more effectively (HUSSEY et al., 2015). Despite involving complex and expensive techniques, telemetry provides a very detailed information on a small number of animals (POLLOCK; PINE, 2007) and provides information on environmental factors which facilitate the understanding of ecological processes in a specific habitat. Both telemetry and fishing records show that tiger sharks utilize pelagic habitats, although the function and importance of this habitat in their life cycle are not yet clear (MEYER; PAPASTAMATIOU; HOLLAND, 2010; POLOVINA; LAU, 1993).

Ectothermic animals are characterized by not having internal mechanisms controlling body temperature, so their temperature is equal or very close to the surrounding environment. As a result, marine ectothermic fishes have temporal constraints in mesopelagic incursions because of the low temperatures of this layer, which could compromise their metabolic activities. Ectothermic sharks rely thus on behavioral strategies for thermoregulation by moving to find suitable water temperatures (BEITINGER; FITZPATRICK, 1979), contrasting with marine endothermic animals, which have physiological features that confer greater stability to body temperature (EMERY, 1986) and higher aerobic and anaerobic capacity of white muscle

(DICKSON et al., 1993). However, ectothermic elasmobranchs can alter physiological processes by taking advantage of environmental temperature variability (DI SANTO; BENNETT, 2011), since during a single day pelagic species may cross wide temperature and oxygen gradients (MISLAN et al., 2017). Vertical movement shifts of sharks in relation to environmental conditions are important to understand their role on marine ecosystem, as well as to decipher their environmental preferences and physiological capabilities (COFFEY et al., 2017). The possible reasons for mesopelagic utilization by ectotherms comprise intraspecific behavioral variability (VAUDO et al., 2014), orientation and navigation (HOLMES et al., 2014), behavioral thermoregulation (HIGHT; LOWE, 2007), energy conservation (KLIMLEY et al., 2002), and foraging (NAKAMURA et al., 2011). Such a large number of reasons highlights the importance to develop studies aiming at elucidating the functions of mesopelagic incursions by ectothermic fishes that are usually associated with epipelagic environments.

Tiger sharks are generalist predators which feed on many taxa and present ontogenetic dietary shifts (LOWE et al., 1996). As such, they exhibit vertical ontogenetic niche expansion (AFONSO; HAZIN, 2015), added to the ontogeny in their morphology (FU et al., 2016). In addition, they display both resident and migratory behavior, mediated in general by water temperature and prey abundance (BLAISON et al., 2015; HEITHAUS, 2001). This species exhibits low habitat specialization (GALLAGHER; KYNE; HAMMERSCHLAG, 2012) and fast growth in the juvenile phase compared to other sharks (AFONSO et al., 2012). The population depletion of *Galeocerdo cuvier* may produce considerable biomass variation in other taxa, making the species a keystone in tropical environment (STEVENS et al., 2000). Considering horizontal movements, it is known that tiger sharks utilize specific areas seasonally within their large home ranges, where temperature is the driver of habitat use (HEITHAUS et al., 2007). However, little is yet known about vertical movements of tiger sharks and the underlying drivers of these movements.

Material and Methods

Tiger sharks were caught between August 2010 and August 2013 off Recife, northeast Brazil (8°10′S, 34°53′W), as part of a coastal shark survey (HAZIN; AFONSO, 2014). The sharks were caught with bottom longlines equipped with baited 17/0 circle hooks, which were set at dusk and retrieved in the following dawn, with soak time around 14-15 hours. The sharks were carefully brought on board and restrained in a seawater tank, where they had their eyes covered with a dark cloth and a hose with running seawater placed inside their mouths to keep them breathing. The sharks were then translocated offshore to deeper isobaths (25 – 30 m), with travel time spanning between 30 and 90 minutes, depending on oceanographic conditions. Shark translocation was conducted as a non-lethal shark hazard mitigation strategy which was implemented in this region since 2008 (HAZIN; AFONSO, 2014). Prior to release, all sharks were measured for total length (TL), fork length (FL), precaudal length (PCL) and interdorsal length (ID) to the nearest centimetre and were tagged with conventional dart tags (FH-69; Floytag, USA) and satellite transmitters. Pop-up satellite archival tags (PSAT), models mk-10PAT or miniPAT (Wildlife Computers, USA) were attached to the proximal middle portion of the shark's first dorsal fin.

This study focused on physically-recovered PSAT tags (Table 1), which rendered depth and temperature records of shark vertical movements with high temporal resolution (1-5 seconds). These tags operate mostly as dataloggers and they were programmed to record data in predetermined intervals. As the shark ID tags S130, S150, S170 and S184 recorded data in different intervals (i.e. 2, 1, 3 and 5 seconds, respectively), the collected data were resampled to uniformize the temporal resolution according to the least common multiple. Hence, a 5-second temporal resolution was used for tags S150 and S184, whereas a 6-second resolution was used for tags S130 and S170.

Table 1. Summary details of tiger sharks tagged

Shark ID	Deployment date	Total length (cm)	Sex	Nº of dives
S130	11-07-11	130	M	419
S150	07-08-10	150	M	52
S170	17-09-12	170	M	377
S184	31-08-13	184	F	304

The collected data were concatenated, and a depth-temperature profile was plotted to define the threshold temperature which sharks were considered to engage into dive mode (Figure 1). Primarily, the 60-m isobath was defined as a depth threshold because it corresponds to the depth of shelf break, but the dives were not very well defined because the temperature at this depth had great variability and did not differ much from the temperature at the sea surface. Then, temperature was chosen as a threshold, because the physiology of sharks is more altered by temperature than depth. Therefore, 22◦C was defined as the threshold, since this value is never attained at the surface, being recorded at depths ranging from 60m to 200m (Figure 1), with the beginning of this layer (60 m) coinciding, with the shelf break (60 m) and with the starting depth of the shallowest dives. Besides, according to PAYNE et al. (2018), this is a suitable temperature for tiger sharks. Therefore, dive mode corresponded to all data in which temperature was below 22◦C. In addition, two other modes were defined: the period prior to dive mode in which sharks moved in the mixed surface layer (MSL1) and the period posterior to dive mode in which sharks moved in the mixed surface layer (MSL2).

The main question of this paper is: Does environmental temperature have a regulatory effect on vertical behaviour of tiger sharks? From this query, we developed two main scientific questions that could be answered by the data:

1. Do the movement features in the MSL1 affect diving behaviour?
2. Do the dive characteristics affect movement behaviour in the MSL2?

For the first question, variables pertaining to the dive mode were regarded as response variables, whereas MSL1 variables were regarded as predictors. Based on this framework, four hypothesis were developed:

I) Warmer temperatures and shallower depths at MSL1 enable tiger sharks to be exposed to cooler temperatures when diving;

II) Warmer temperatures and shallower depths at MSL1 influence dive maximum depth;

III) Warmer temperatures at MSL1 promote “V”-shaped rather than “U-shaped” dives;

IV) Warmer temperatures at MSL1 proportionate increased accumulation of heat and, subsequently, allow tiger sharks to endure a greater amount of heat debit while diving.

For the second question, the MSL2 variables were regarded as response variables and dive variables were regarded as the predictors. Four hypothesis were tested in this framework:

V) Colder temperatures and deeper diving depths influence mean depth of movements at MSL2;

VI) Deeper dives influence the time spent in the MSL2;

VII) Deeper diving depths result in a greater amount of heat debits being acummulated by the sharks, thus leading to the need to accumulate a greater amount of heat at MSL2;

VIII) Deeper diving depths drive sharks to use shallower depths at MSL2.

Shark total length was also included in the models as a predictor variable.

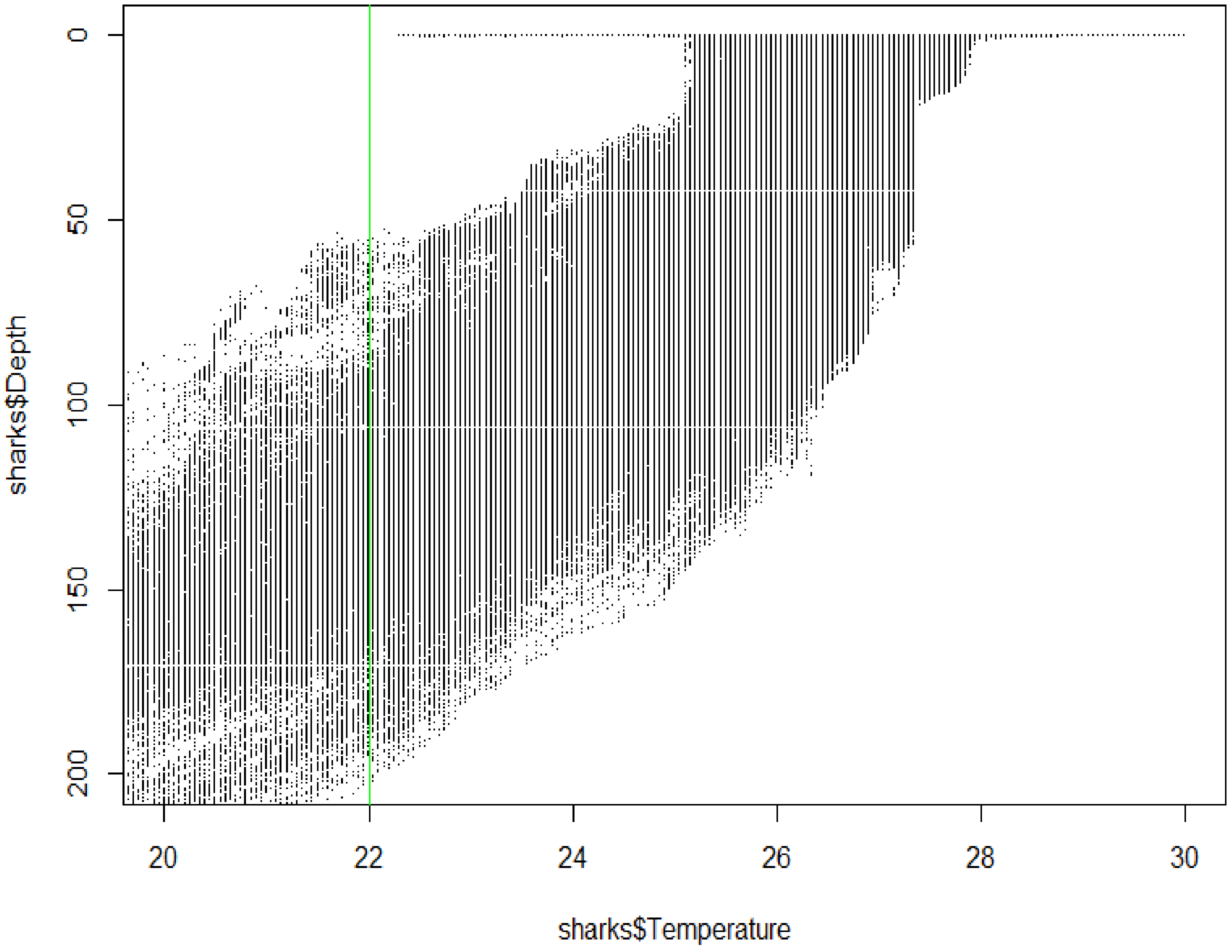

Figure 1. Depth and temperature of tiger shark movements. The green line represents the threshold temperature.

Only dives longer than 30 seconds were selected for analysis. Movement-related descriptors were derived from time, depth and temperature data and assessed for each movement mode (i.e. Dive, MSL1 and MSL2). These included mean depth, standard deviation of the mean depth, maximum depth, mean temperature, standard deviation of the mean temperature, minimum temperature, and dive duration. Additional variables were used to describe shark movements in greater detail. Thermal budget was defined as the sum of the differences between the temperature time-series of the movement mode and the 22ºC threshold temperature, and it linearly ascribed debits or credits of heat to shark movements. Bottom time was defined as the amount of time spent below the isobath placed at 90% of dive maximum depth. Lastly, dive shape ratio was defined as the ratio between bottom time and dive duration, yielding an index ranging from ~0.0

to 1.0 where small values represented “V”-shaped dives and high values represented “U”-shaped dives.

Shapiro-Wilk normality tests were conducted and they evidenced that the data did not conform with normality assumptions even after performing log, square-root, fourth-root and box-cox transformations. Therefore, generalized linear models (GLM) were selected as a non-parametric alternative. Spearman’s Rank Correlation tests were conducted to select poorly related variables (s < 0.4) which could be included simultaneously in the same model. The fittest models were selected using the Akaike Information Criterion (AIC) along with residual distribution. All statistical analyses had a significance level of 0.05 and were conducted in R software version 3.4.3.

Results

From 270 days of tracking data, 1152 dives were considered for analysis, which consisted in approximately 1.7% of the study period. During the majority of the track span, tiger sharks moved in shallow (<50 m) and warm waters (>25 ºC), corresponding to 83.2% and 93% of the time, respectively (Figure 2). Sharks were named after their total length of S130, S150, S170 and S184 and contributed with 419, 52, 377 and 304 dives, respectively. Dives were performed across a depth range from 55.0 to 689.5 m and a temperature range from 4.9 to 22.0ºC.

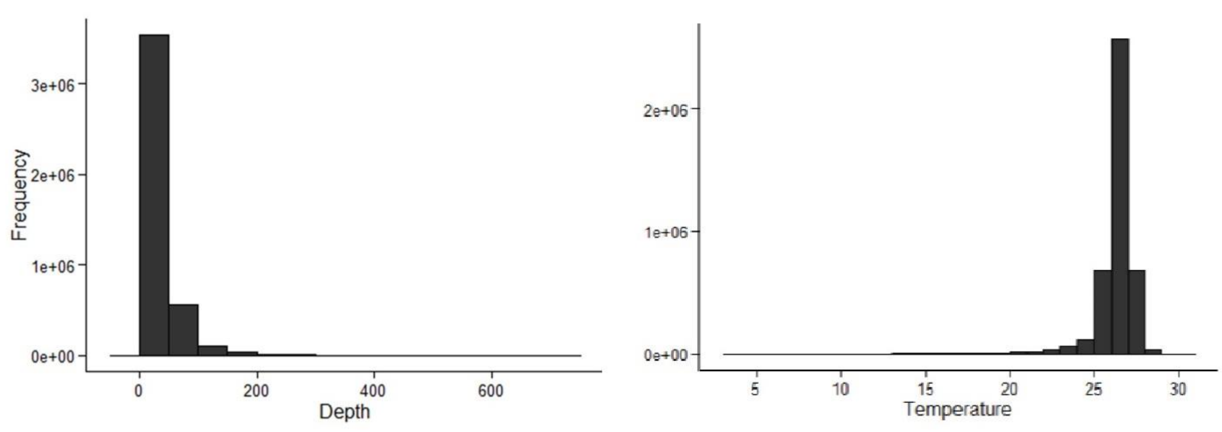

Figure 2. Depth and temperature frequency of the period of study

A positive relation between dive maximum depth and dive duration was observed, with deeper dives being associated with a longer duration (Figure 3). However, there were also some long shallow dives in the dataset, although these were performed in relatively warm waters and thus were of little interest to the scope of this study. On the other hand, shallow dives tended to be described as "U" shaped whereas dives deeper than ~250 m tended to assume "V" shaped profiles (Figure 4). Also, there was an inverse relation between minimum temperature and depth of dives (Figure 5), which evidenced that tiger sharks can experience a temperature decrease of up to 17.1°C while diving.

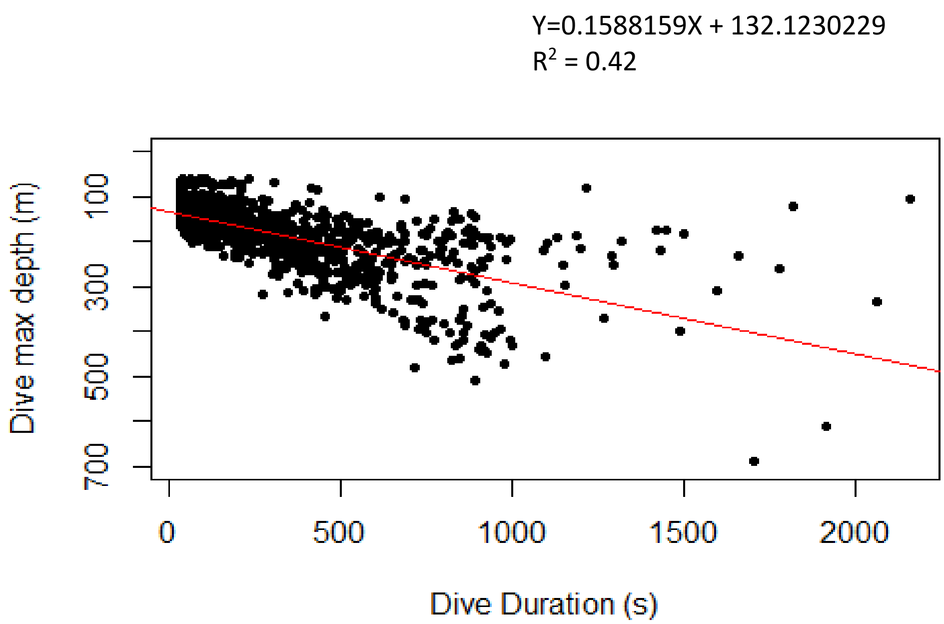

Figure 3. Linear relation between maximum depth and duration of dives.

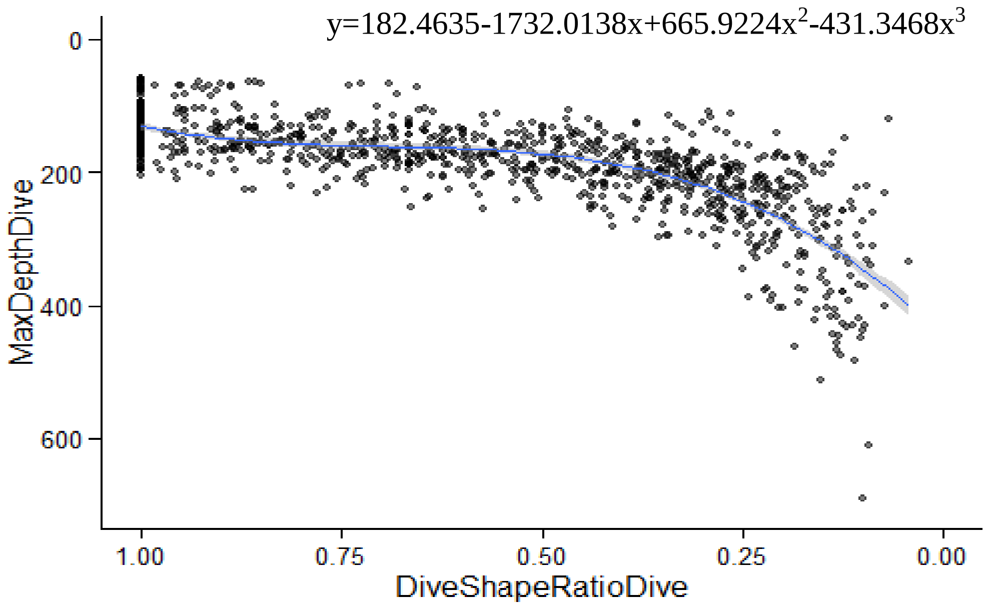

Figure 4. Relation between dive maximum depth and dive shape.

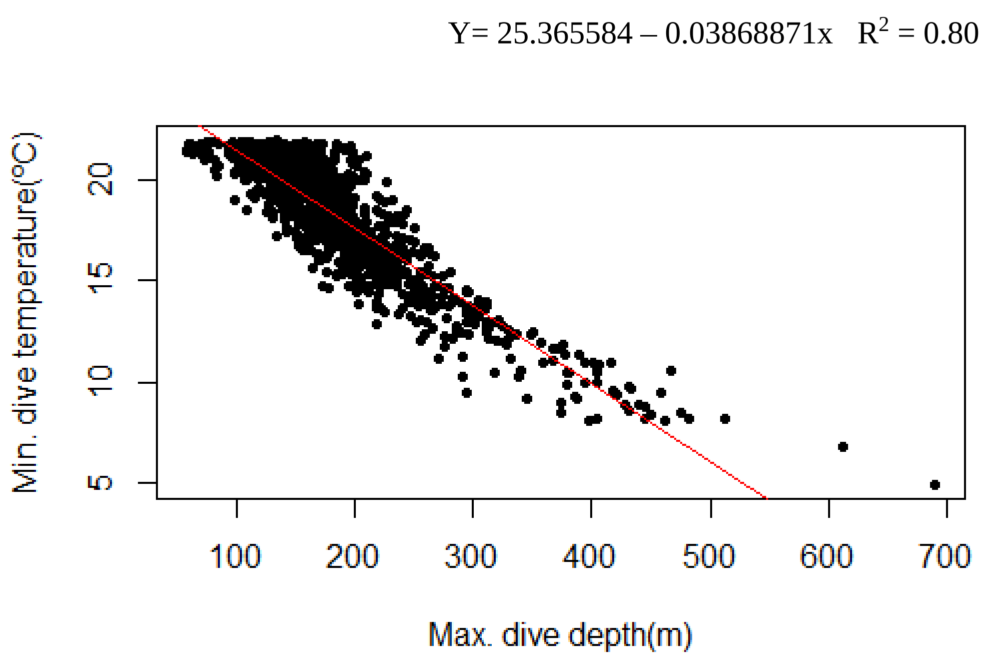

Figure 5. Relation between dive maximum depth and dive minimum temperature.

GLMs developed for each shark with dive minimum temperature as the response variable revealed an inverse relationship between mean temperature of shark movements at MSL1 and minimum temperature of the dive (Figure 6). In addition, for the same MSL1 mean temperature, larger sharks tended to move into cooler waters in comparison with smaller sharks. For example, a 22◦C mean temperature in MSL1 for shark S150 resulted in this individual being exposed to temperatures higher than 21◦C while diving, whereas when MSL1 mean temperature was at 27◦C the shark tended to dive into cooler, 18ºC waters (Figure 6). Therefore, a mean temperature increase of 5◦C at the MSL can lead to 3◦C decrease in the mesopelagic realm. In addition, an inverse relation between maximum depth at MSL1 and minimum dive temperature was observed (Figure 6). Regarding the effect of shark length, shark S130 differentiated significantly only from shark S150 (Appendix, table2).

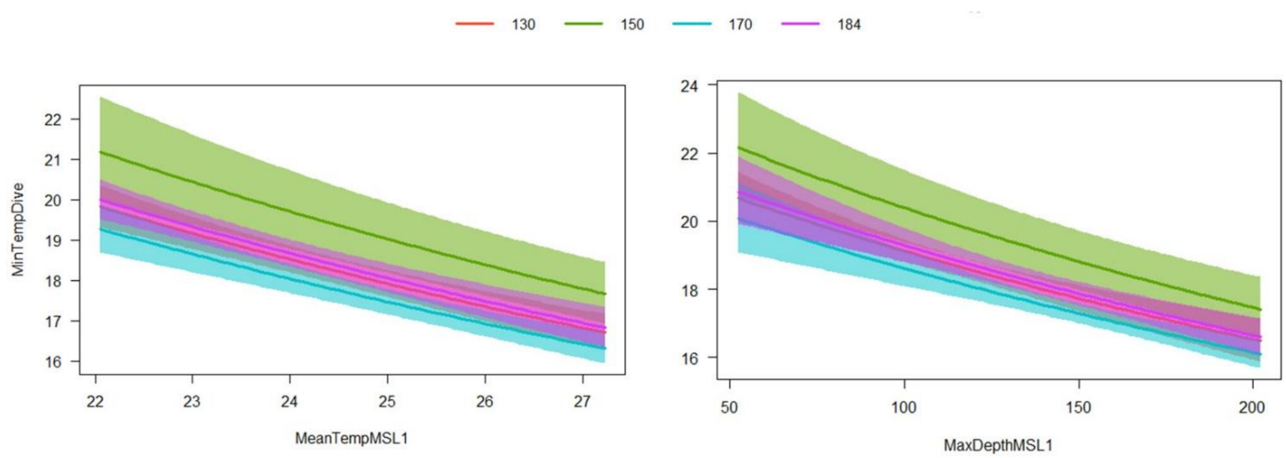

Figure 6. Relation between minimum temperature of dives and mean temperature and maximum depth at MSL1.

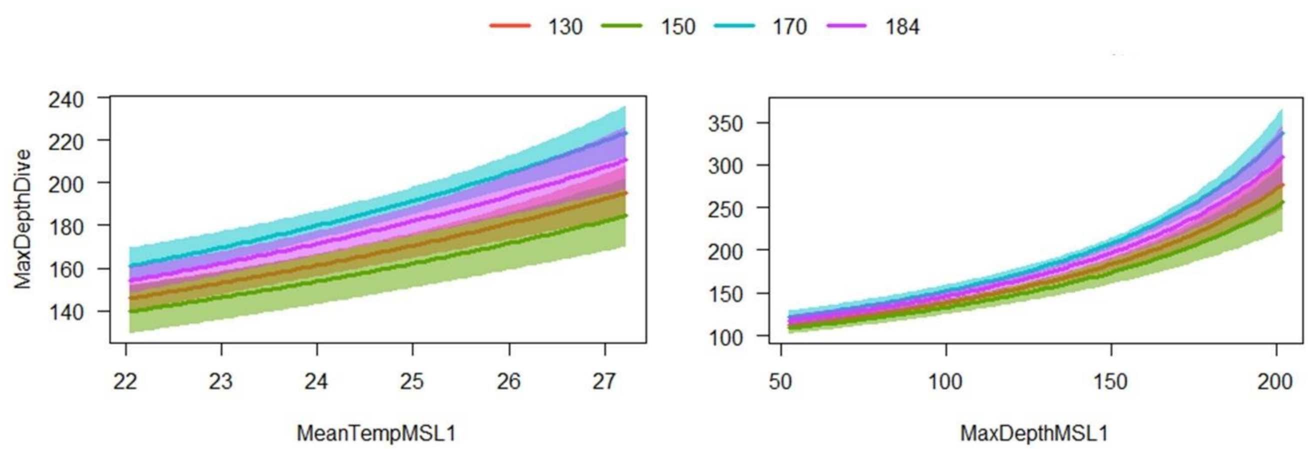

Figure 7. Relation between maximum depth of dives and mean temperature and maximum depth at MSL1.

Concerning dive maximum depth, the higher the mean temperature and maximum depth at MSL1 were, the deeper the dives were (Figure 7). Shark S130 had differences from S170 and S184 but did not differentiate from S150. Dive shape (U or V style) was influenced by mean temperature (Figure 8). Higher mean temperatures at MSL1 seem to promote "V" shaped dives, whereas mean temperature < 24◦C tended to promote "U" shaped dives. Moreover, the mean temperature at MSL1 positively influenced the diving thermal budget (Figure 9), i.e. higher mean temperature at MSL1 resulted in greater heat debit while diving. Shark S130 differentiated statistically only from S170 in both dive shape ratio and thermal budget dive models.

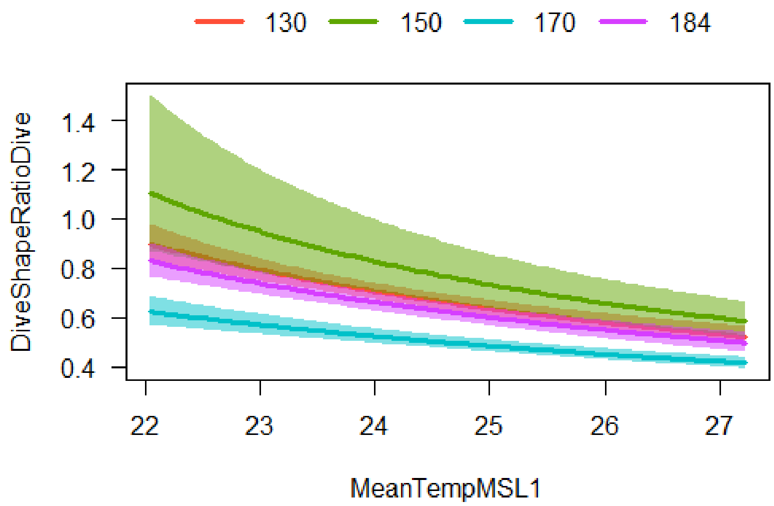

Figure 8. Relation between dive shape ratio and mean temperature at MSL1.

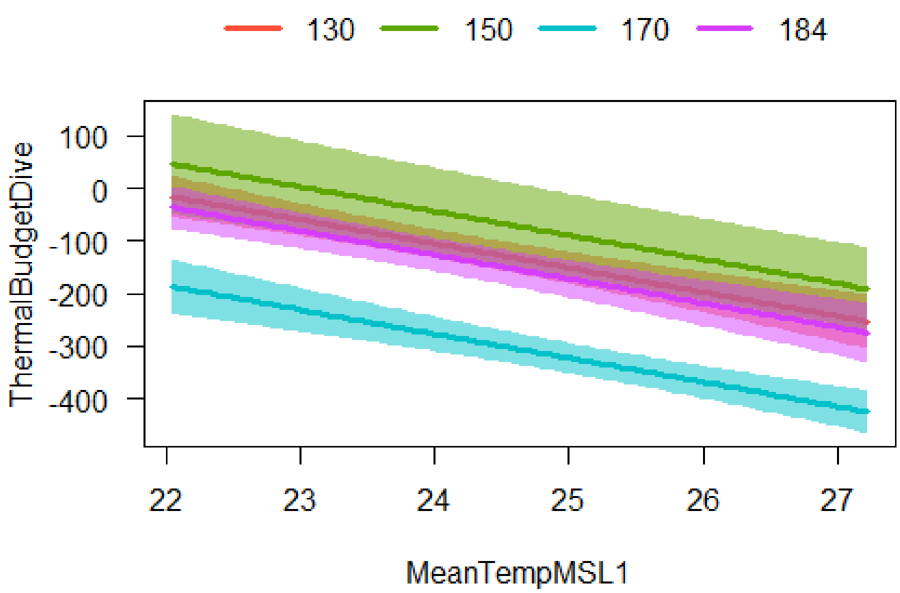

Figure 9. Relation between thermal budget of dives and mean temperature at MSL1 and shark total length.

After tiger sharks diving into cooler and deeper waters (approximately < 15°C and > 200 m, respectively) they tended to use warmer waters (> 25°C) from the mixed surface layer. All individuals showed different behaviors but, interestingly, sharks S130 and S184 showed similar trends (Figure 10). Dive depth was directly related with time spent at MSL2 and the corresponding heat credit, so that deeper dives result in sharks requiring a longer time to recover and, thus, a greater amount of heat credits to be collected after the dive except for S130. As shark increases body size, less time it needs to recover at MSL2 (Figure 11). Moreover, shallow dives (< 200 m), usually above the thermocline, enabled sharks to stay in deeper layers of MSL2. In contrast, when tiger sharks dove into waters deeper than 250 m, they tended to stay around the 100-m isobath or shallower after completing the dive. Yet, the effect of total length on behavior was considerably distinct, with larger sharks tending to stay in deeper layer at MSL2, whereas smaller sharks tended to stay in shallower depths at MSL2, except for S130, which had a behavior closest to S184 (Figure 12).

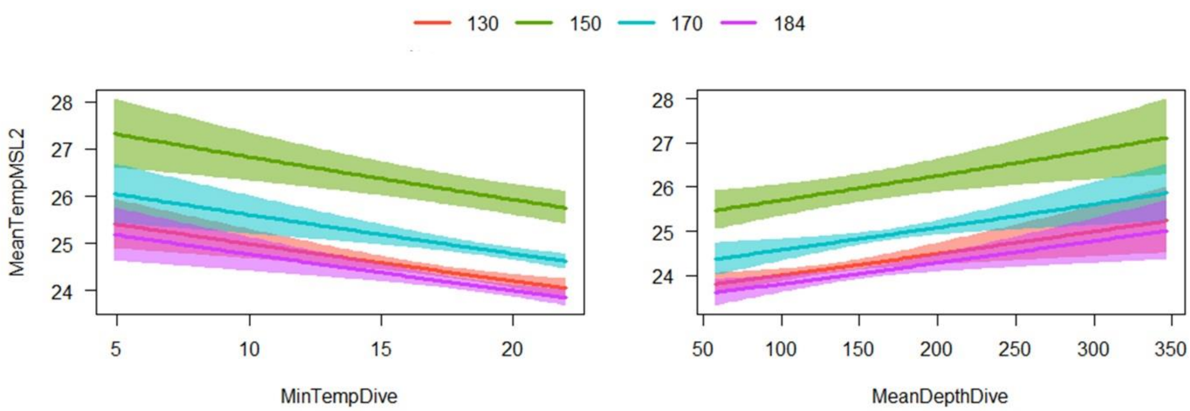

Figure 10. Relation between mean temperature at MSL2 and minimum temperature and mean depth during dives.

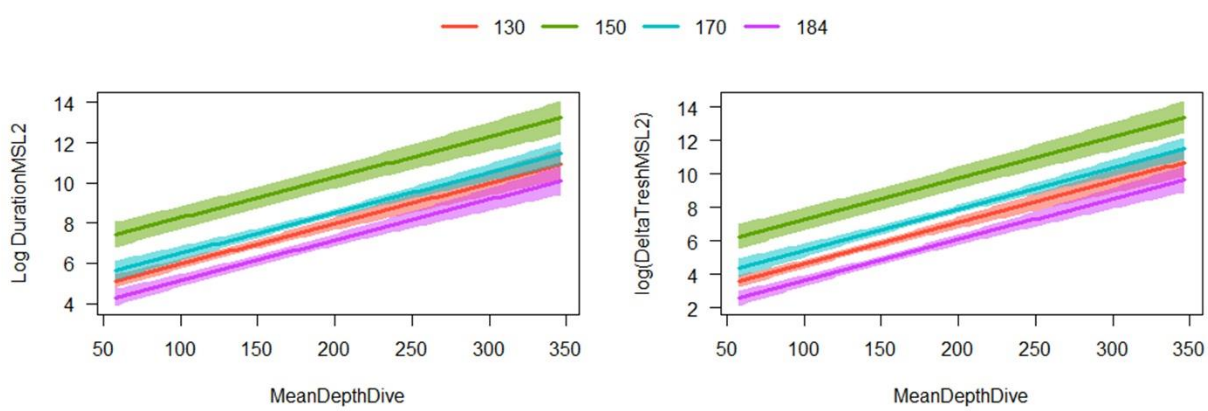

Figure 11. Relation between duration and heat credit at MSL2 with maximum dive depths.

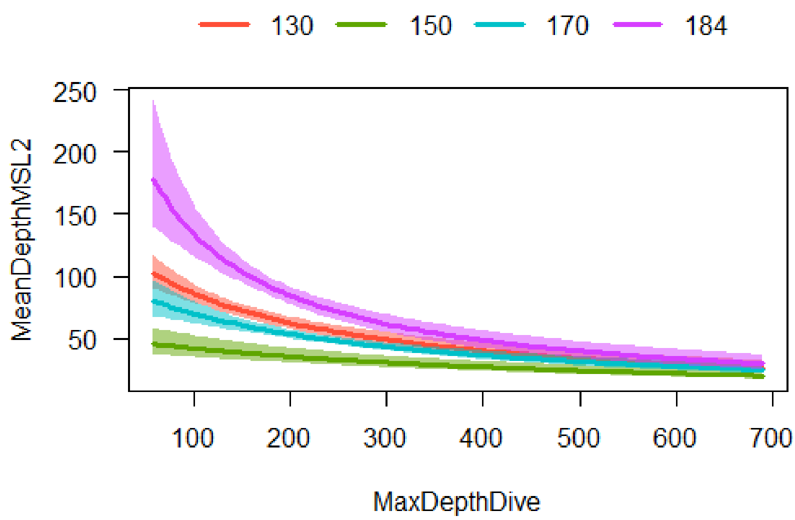

Figure 12. Relation between mean depth at MSL2 and dive maximum depth.

Discussion

In deep dives, when the tiger sharks reached low temperatures (4.9ºC), they performed “V”-shaped movements, differently from the “U”-shaped dives done in shallower and warmer waters, suggesting that the time tiger sharks can spend in cold waters is limited by thermal tolerance. As ectothermic animals, they have a preferable temperature range, where their physiologic performance is maximized (ASPILLAGA et al., 2017). As the body temperature decreases, shark physiology and behavior are increasingly affected (HUEY, R B & STEVENSON, 1976). Moreover, tiger sharks naturally spent longer times to reach deeper depths, due to a longer displacement time, as some sharks optimize dive energy through swimming at constant speed (PAPASTAMATIOU et al., 2018).

Since temperature is an environmental factor that can profoundly alter the physiology of fishes, it surely influences the fitness and survival of ectothermic organisms (BROWN et al., 2004). Large ectothermic marine animals have been studied in regard to their thermoregulatory behavior, for quite a while (CAMPANA et al., 2011; CASEY; JAMES; WILLIARD, 2014; NAKAMURA; GOTO; SATO, 2015; SIMS et al., 2006). Temperature is a crucial factor in shark life history because thermal conductance and the specific heat of water provides a challenging environment, as gills works as countercurrent heat exchangers (BEITINGER; FITZPATRICK, 1979). Besides physiological mechanisms to endure more time in cooler waters during foraging, large endothermic fishes also present behavioral thermoregulation (HOLLAND et al., 1992; KITAGAWA et al., 2001; REYNOLDS; CASTERLIN, 1979). Additionally, according to THORROLD et al., (2014) just a few species have been documented diving over the mesopelagic zone due to physiological or energetic constraints caused by low temperature, high pressure and low dissolved oxygen environment. Tiger sharks are one of these species, together with whale sharks (TYMINSKI et al., 2015), mobula rays (FRANCIS; JONES, 2017) and blue sharks (CAREY; SCHAROLD; KALMIJN, 1990).

Higher temperatures in MSL1 allowed tiger sharks to reach lower temperatures, to swim in greater depths, in “V” shaped dives, and to increase heat debits during dives. This suggests that tiger sharks might raise their body heat before performing deep dives. As deep dives are associated with thermoregulatory capabilities to generate or retain heat in vital body parts in marine fishes, and this depends on their physiology (THORROLD et al., 2014), tiger sharks capability to dive deeper may increase with body size, as they present ontogenetic niche expansion (AFONSO; HAZIN, 2015). A larger body size will also mean a larger volume/ surface ratio, allowing them to lose heat more slowly. Furthermore, higher depths at MSL1 seems to enable tiger sharks to reach lower temperatures and higher depths, as well. Dives started at 22ºC, but the MSL depth extended up to ~200 m, so with a deeper MSL sharks would start their dives at similar temperatures but much greater depths, spending less energy to reach cooler temperatures compared with dives starting at ~60 m. For example, *C. longimanus* in the North Atlantic, during summer, tended to dive down to 200 m depths more frequently than during the winter, when they tended to stay mostly in the upper 50 m (ANDRZEJACZEK et al., 2018).

Greater depths and cooler temperatures in the course of diving led tiger sharks to move into shallower and warmer waters, spending longer time there, to collect greater amounts of heat credit at MSL2, suggesting they needed that to recover from the heat loss. Comparatively, bigeye tuna (*Thunnus obesus*) combine behavioral and physiological thermoregulation to forage in deep and cold waters where prey is more abundant, and then come to warm surface waters to recover from heat loss (HOLLAND et al., 1992). Endothermy in fishes confers advantages in cruising speed and thermal niche expansion, however the cost of transport is two to three times greater than that of ectothermic fishes. Analogously, behavioral thermoregulation of tiger sharks allowed them to have similar maximum annual migration to porbeagle sharks and yellowfin tuna, both endothermic fishes (WATANABE et al., 2015). Therefore, this behavioral thermoregulation is also important to migration and niche expansion of tiger sharks.

Although shark size influences their behavior, it is probably also affected by intraspecific variability (VAUDO et al., 2014), as the smallest shark showed a behavior closer to the largest one. The sizes of the sharks analyzed, however, were not so much different, ranging from 130 cm to 184 cm TL, thus their body volume/ surface ratios did not differ much either, neither their heat exchange with the surrounding environment. Yet, the fat contents were not measured and could influence shark movement, since more fat would mean a better body insulation. Small tiger sharks seem to prey mainly upon coastal and shallow habitat, contrasting with larger sharks that frequently feed on deep-water teleosts and squids found in more than 200 m deep (DICKEN et al., 2017). This suggests that larger predators use much more deeper waters, than small sharks, probably due to temperature. As tiger sharks present ontogenetic morphological shifts (FU et al., 2016), the body volume increases with increasing length, which may allow them to loose heat more slowly when they are large and thus to reach deeper and cooler waters.

Some studies have been conducted to understand diel vertical migration of pelagic sharks and their movements in relation with at least part of behavioural thermoregulation. However, it is difficult to identify which factors are responsible for this behavior (SIMS et al., 2006). This study suggests temperature as one of the main drivers, coupled with a foraging strategy (NAKAMURA et al., 2011), which enable sharks to increase the diversity of prey resource and abundance, particularly in more oceanic, and oligotrophic areas, by allowing them to efficiently forage much deeper in the water column (AFONSO; HAZIN, 2015). The dogfish S*cyliorhinus canicular*, for instance, can perform trade-offs between suitable thermal habitats and foraging grounds, exerting a fine control of their thermal niche to optimize metabolic rates (SIMS et al., 2006). Furthermore, laboratory studies show that the horn shark (*Heterodontus franscisi*) can select preferred temperatures in a thermal gradient, as a behavioural response (REYNOLDS; CASTERLIN, 1979).

Many marine predators perform deep dives regularly to forage on deep-water fish and squid, which high biomasses are very important for pelagic food webs, even though their ecological importance are yet poorly understood (THORROLD et al., 2014). Deep-water cephalopods, found in more than 200 m deep, are an important functional prey group in many different size classes of tiger sharks (DICKEN et al., 2017), and may very well be one of the trophic reasons for tiger shark deep diving. In addition, the water strata utilized by tiger sharks overlap with longlines for tunas and swordfish (BEZERRA; TRAVASSOS; HAZIN, 2016; TOLOTTI et al., 2015), which may lead tiger sharks to be caught as by-catch.

The management and conservation of highly migratory marine predators depend on the understanding of their movements in relation with oceanic processes, behavior, and physiology, through a defined space and time scale, which is still unclear (BLOCK et al., 2011). Therefore, this study has provided relevant information about tiger shark behavior, concerning thermoregulation strategies and importance of vertical habitat use. However, this research is limited due to the small sampling size and due to individuals exhibiting similar sizes, since this species has a range size of approximately 4.5 m. Additionally, further research measuring internal temperatures would give more accurate results and would allow to calculate the exact body heat loss and heat gain rates, which would provide a better understanding of heat loss process towards decrease in environmental temperature. Furthermore, the study of body condition is also important, because it would provide a better understanding of the relation between shark size, energy storage, migration and other energetic challenges (GALLAGHER et al., 2014).

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Appendix

Table 1. Summary of model selection procedure for diving behavior. DF: Degrees of freedom, AIC: Akaike information criterion. MinTempDive: Minimum diving temperature, MaxDepthMSL1: Maximum depth at MSL1, MeanTempMSL1: Mean temperature at MSL1, SDTempMSL1: Standard deviation of temperature at MSL1, sharkTL: Shark total length, MaxDepthDive: Maximum diving depth, SDDepthMSL1: Standard deviation of depth at MSL1, MeanDepthMSL2: Mean depth at MSL2, MeanDepthDive: Mean diving depth, MeanTempMSL2: Mean temperature at MSL2. * means that the model is not significant.

Response variable	Candidate explanatory variable	DF	AIC
MinTempDive	MaxDepthMSL1	1150	5973.1
MinTempDive	MeanTempMSL1	1150	5969.2
MinTempDive	DurationMSL1	1150	6079.5
MinTempDive	SDTempMSL1	1150	6084.1
MinTempDive	sharkTL	1148	6001.6
MinTempDive	MeanTempMSL1+MaxDepthMSL1	1149	5905.3
MinTempDive	MeanTempMSL1+DurationMSL1	1149	5970.8
MinTempDive	MeanTempMSL1+SDTempMSL1	1149	5966.3
MinTempDive	MeanTempMSL1+sharkTL	1147	5932.6
MinTempDive	MeanTempMSL1+MaxDepthMSL1+DurationMSL1	1148	5906.7
MinTempDive	MeanTempMSL1+MaxDepthMSL1+SDTempMSL1	1148	5905.3
MinTempDive	**MeanTempMSL1+MaxDepthMSL1+sharkTL**	**1146**	**5898.2**
MinTempDive	MeanTempMSL1+MaxDepthMSL1+sharkTL+SDTempMSL1	1145	5897.8
MinTempDive	MeanTempMSL1+MaxDepthMSL1+sharkTL+DurationMSL1	1145	5898.9
MaxDepthDive	MaxDepthMSL1	1150	12217
MaxDepthDive	MeanTempMSL1	1150	12582
MaxDepthDive	DurationMSL1	1150	12813
MaxDepthDive	SDTempMSL1	1150	12811
MaxDepthDive	sharkTL	1148	12460
MaxDepthDive	MaxDepthMSL1+MeanTempMSL1	1149	12124
MaxDepthDive	MaxDepthMSL1+DurationMSL1*	1149	12215
MaxDepthDive	MaxDepthMSL1+SDTempMSL1	1149	12206
MaxDepthDive	MaxDepthMSL1+sharkTL	1147	12172
MaxDepthDive	MaxDepthMSL1+MeanTempMSL1+SDTempMSL1*	1148	12124
MaxDepthDive	**MaxDepthMSL1+MeanTempMSL1+SharkTL**	**1146**	**12097**
DiveShapeRatioDive	MeanDepthMSL1	1150	562.24
DiveShapeRatioDive	MaxDepthMSL1	1150	596.68
DiveShapeRatioDive	SDDepthMSL1	1150	551.93
DiveShapeRatioDive	MeanTempMSL1	1150	540.21
DiveShapeRatioDive	SDTempMSL1	1150	629.48
DiveShapeRatioDive	DurationMSL1	1150	632.11
DiveShapeRatioDive	sharkTL	1148	536.91
DiveShapeRatioDive	sharkTL+MeanDepthMSL1	1147	496.48

DiveShapeRatioDive	sharkTL+SDDepthMSL1	1147	504.42
DiveShapeRatioDive	**sharkTL+MeanTempMSL1**	**1147**	**484.76**
DiveShapeRatioDive	sharkTL+SDTempMSL1	1147	533.95
DiveShapeRatioDive	sharkTL+DurationMSL1	1147	531.94
DiveShapeRatioDive	sharkTL+MeanTempMSL1+MeanDepthMSL1*	1146	485.96
DiveShapeRatioDive	sharkTL+MeanTempMSL1+SDTempMSL1*	1146	485.95
DiveShapeRatioDive	sharkTL+MeanTempMSL1+SDDepthMSL1*	1146	485.82
DiveShapeRatioDive	sharkTL+MeanTempMSL1+DurationMSL1*	1146	485.48
ThermalBudgetDive	MeanTempMSL1	1150	13731
ThermalBudgetDive	SDTempMSL1	1150	13860
ThermalBudgetDive	sharkTL	1148	13711
ThermalBudgetDive	DurationMSL1*	1150	13870
ThermalBudgetDive	MaxDepthMSL1	1150	13771
ThermalBudgetDive	**sharkTL+MeanTempMSL1**	**1147**	**13655**
ThermalBudgetDive	sharkTL+SDTempMSL1	1147	13709
ThermalBudgetDive	sharkTL+MaxDepthMSL1	1147	13701
ThermalBudgetDive	sharkTL+MeanTempMSL1+SDTempMSL1*	1146	13653
ThermalBudgetDive	sharkTL+MeanTempMSL1+MaxDepthMSL1*	1146	13655
MeanTempMSL2	MinTempDive	1150	3753.6
MeanTempMSL2	MeanDepthDive	1150	3712.6
MeanTempMSL2	DiveShapeRatioDive	1150	3775.7
MeanTempMSL2	sharkTL	1148	3684
MeanTempMSL2	sharkTL+MinTempDive	1147	3561.7
MeanTempMSL2	sharkTL+MeanDepthDive	1147	3569
MeanTempMSL2	sharkTL+DiveShapeRatioDive	1147	3583.8
MeanTempMSL2	**sharkTL+MinTempDive+MeanDepthDive**	**1146**	**3554.7**
MeanTempMSL2	sharkTL+MinTempDive+DiveShapeRatioDive	1146	3558.3
MeanTempMSL2	sharkTL+MinTempDive+MeanDepthDive+DiveShapeRatioDive*	1147	3547.4
Log DurationMSL2	MinTempDive	856	3711.7
Log DurationMSL2	MeanDepthDive	856	3625.7
Log DurationMSL2	sharkTL	854	3632.2
Log DurationMSL2	DiveShapeRatioDive	856	3732.1
Log DurationMSL2	MeanDepthDive+MinTempDive*	855	3626.7
Log DurationMSL2	**MeanDepthDive+sharkTL**	**853**	**3513.1**
Log DurationMSL2	MeanDepthDive+DiveShapeRatioDive*	855	3625.6
Log ThermalBudgetMSL2	DeltaTreshDive	1150	5568.9
Log ThermalBudgetMSL2	sharkTL	1148	5390.2
Log ThermalBudgetMSL2	MinTempDive	1150	5478.1
Log ThermalBudgetMSL2	MeanDepthDive	1150	5388.9
Log ThermalBudgetMSL2	**MeanDepthDive+sharkTL**	**1147**	**5247**
Log ThermalBudgetMSL2	MeanDepthDive+MinTempDive*	1149	5390.6
MeanDepthMSL2	MinTempDive	856	8700
MeanDepthMSL2	MaxDepthDive	856	8680.8

MeanDepthMSL2	sharkTL	854	8631.6
MeanDepthMSL2	sharkTL+MinTempDive	853	8582.1
MeanDepthMSL2	**sharkTL+MaxDepthDive**	**853**	**8580.6**
MeanDepthMSL2	sharkTL+MaxDepthDive+MinTempDive*	852	8580

Table 2. Summary of model coefficients

Model	Intercept	Variable	Estimate	Std. Error	t value	p-value
MinTempDive~MeanTempMSL1+MaxDepthMSL1+sharkTL						
	-7.01E-04	MeanTempMSL1	1.82E-03	2.18E-04	8.349	< 2e-16
		MaxDepthMSL1	8.22E-05	1.25E-05	6.581	7.10E-11
		sharkTL150	-3.24E-03	1.36E-03	-2.393	0.0169
		sharkTL170	1.44E-03	8.02E-04	1.794	0.073
		sharkTL184	-4.43E-04	6.90E-04	-0.642	0.5208
MaxDepthDive~MaxDepthMSL1+MeanTempMSL1+SharkTL						
	1.90E-02	MaxDepthMSL1	-3.54E-05	2.33E-06	-15.171	< 2e-16
		MeanTempMSL1	-3.37E-04	4.26E-05	-7.901	6.46E-15
		sharkTL150	3.02E-04	2.66E-04	1.133	0.2573
		sharkTL170	-6.41E-04	1.53E-04	-4.193	2.97E-05
		sharkTL184	-3.69E-04	1.44E-04	-2.569	0.0103
DiveShapeRatio~sharkTL+MeanTempMSL1						
	-2.31577	sharkTL150	-0.20725	0.11289	-1.836	0.0666
		sharkTL170	0.49424	0.06603	7.485	1.42E-13
		sharkTL184	0.0943	0.05334	1.768	0.0774
		MeanTempMSL1	0.15549	0.01908	8.15	9.46E-16
ThermalBudgetDive~sharkTL+MeanTempMSL1						
	0.0466496	sharkTL150	0.0010729	0.0017005	0.631	0.528
		sharkTL170	-0.004203	0.0007586	-5.54	3.75E-08
		sharkTL184	-0.001137	0.0009463	-1.202	0.23
		MeanTempMSL1	-0.001541	0.0002475	-6.224	6.78E-10
MeanTempMSL2~sharkTL+MinTempDive+MeanDepthDive						
	4.00E-02	sharkTL150	-2.75E-03	2.65E-04	-10.399	< 2e-16
		sharkTL170	-9.67E-04	1.70E-04	-5.704	1.49E-08
		sharkTL184	3.50E-04	1.52E-04	2.297	0.0218
		MinTempDive	1.30E-04	3.21E-05	4.058	5.28E-05
		MeanDepthDive	-8.22E-06	2.74E-06	-3.006	0.0027

Log DurationMSL2~MeanDepthDive+sharkTL						
	3.948343	MeanDepthDive	0.020111	0.001768	11.372	< 2e-16
		sharkTL150	2.306706	0.298251	7.734	2.93E-14
		sharkTL170	0.529968	0.182861	2.898	0.00385
		sharkTL184	-0.814245	0.178822	-4.553	6.05E-06
Log ThermalBudgetMSL2~MeanDepthDive+sharkTL						
	2.148468	MeanDepthDive	0.024661	0.001987	12.413	< 2e-16
		sharkTL150	2.694864	0.349265	7.716	2.60E-14
		sharkTL170	0.822875	0.201806	4.078	4.87E-05
		sharkTL184	-1.00683	0.182842	-5.507	4.51E-08
MeanDepthMSL2~sharkTL+MaxDepthDive						
	7.20E-03	sharkTL150	1.21E-02	2.44E-03	4.966	8.24E-07
		sharkTL170	2.67E-03	9.35E-04	2.857	0.00438
		sharkTL184	-4.17E-03	6.81E-04	-6.118	1.44E-09
		MaxDepthDive	4.39E-05	6.03E-06	7.285	7.33E-13

3 CONSIDERAÇÕES FINAIS

O presente trabalho demonstra que a temperatura é um fator regulador do comportamento dos tubarões tigres, em relação às suas incursões mesopelágicas, com esses animais permanecendo em temperaturas elevadas e baixas profundidades no período antecedente ao mergulho para assim poder efetuar mergulhos mais longos e profundos, onde estarão expostos a temperaturas mais frias. Quando estão expostos a temperaturas mais quentes na MSL1, esses tubarões tendem a realizar mergulhos em formato "V", enquanto que em temperaturas mais frias na MSL1 eles tendem a realizar um mergulho em forma de "U". Apesar de passarem a maioria do tempo em águas rasas, acima de 50 m, e quentes, acima de 25ºC, esses animais atingiram profundidades de 689,5 m e temperaturas de 4,9ºC. Após atingirem grandes profundidades durante o mergulho, porém, os tubarões tigre permaneceram considerável período de tempo em águas rasas e quentes na camada de mistura, certamente recuperando o calor perdido durante o mesmo, de forma a restabelecer uma temperatura corporal adequada a uma maior atividade metabólica. De uma maneira geral, indivíduos de maior porte tendem a se expor a temperaturas mais frias e profundas, apesar de uma importante variabilidade intraespecífica. As pesquisas sobre comportamento dos animais através de telemetria vêm se aprimorando em todo o globo, com a finalidade de se entender melhor a resposta dos animais em frente às mudanças climáticas, bem como com a relação de sobreposição a aparelhos de pesca. Grande esforço está sendo realizado para compreender os padrões de movimentação, tanto horizontal quanto vertical, em relação às variáveis ambientais, afim de se poder prever a distribuição das populações frente à intercorrências sazonais e/ou temporais, já que a qualidade do habitat muda ao longo do tempo (HUSSEY et al., 2015).

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