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Temperature and the ecophysiology of marine ectotherms

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Declaration

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Summary

Temperature influences the physiology, behaviour, and distribution of organisms and the field of thermal ecology has been stimulated in recent decades by the need for a greater understanding of how climate change will affect Earth's organisms. Although widely studied, a number of key knowledge gaps persist. I aim to contribute to these by investigating both fundamental and applied aspects of thermal ecology. The relationship between temperature and physiological rates is well studied and persistent patterns arise, such as that between temperature and metabolism. The thermal sensitivity of metabolism in ectotherms, consistently shows a Q_{10} value in the range of 2 – 3, indicating a doubling or tripling in metabolic rate with every 10°C increase in temperature. However, a small group of organisms have evolved specialised physiologies, allowing them to elevate their body temperature, thereby creating less of a connection between body temperature and ambient temperature. By studying the ecophysiology of these animals, we can explore how they break away from this metabolism-temperature constraint. But what are the ultimate drivers of these adaptations? In **Chapter 2**, I investigate two competing hypotheses generally proposed to explain the evolutionary drivers behind regional endothermy in fishes: thermal niche expansion and elevated cruising speeds. By compiling published biologging data and collecting precise speed measurements from free-swimming fishes in the wild, I directly tested whether endothermic fishes encounter broader temperature ranges, swim faster, or both. I found that regionally endothermic fishes do not encounter broader temperature ranges but that they swim at elevated cruising speeds, ≈ 1.6 times faster than their ectothermic counterparts, suggesting the significance of endothermy in fishes lies in the advantages it confers to swimming performance rather than facilitating occupation of broader thermal niches. Specialised physiology, such as this, is one way that animals have evolved to break the connection between body temperature and ambient temperature and break away from the constraints of the metabolic 'Q₁₀ effect' (as expected under the Metabolic Theory of Ecology). However, it is increasingly realised that the aforementioned metabolic scaling 'laws' in fact exhibit significant variation and can be context dependent. Research to date has primarily focused on static temperature experiences (i.e., estimating metabolic rate at a range of constant temperatures). However, temperature in nature is rarely static, so our existing understanding from experiments may not truly reflect how temperature influences metabolism in natural systems. Using closed chamber respirometry, I investigate if rate of temperature change influences the oxygen consumption (a widely accepted proxy of aerobic metabolism) of an aquatic ectotherm under varying thermal conditions (**Chapter 3**). I show the rate of temperature change has a systematic effect on the oxygen consumption of ectotherms and as temperature increases more rapidly, the rate of oxygen consumption increases. It is currently uncertain if large-bodied fishes exhibit rapid

temperature increases (such as those tested in **Chapter 3**), but we might expect this to occur during periods of physical exertion, such as during catch-and-release fishing interactions. When sharks are hooked, they often exhibit intensive swimming acceleration, as they attempt to escape. This can elevate the metabolic rate, resulting in the generation of heat. This excess heat may accumulate and manifest as an elevation of body temperature in these animals. In **Chapter 4** I investigate this using state of the art biologging technology, in combination with blood biochemistry. In doing so, I record a previously undocumented thermal stress response in captured sharks (**Chapter 4**): I find ectothermic sharks experience acute elevations in body temperature during catch-and-release events, with subcutaneous temperature elevated by as much as 2.7°C. Furthermore, these elevations occur at rates as fast as 0.8°C min⁻¹, significantly faster than any of the rates tested in **Chapter 3**, implying an even greater magnitude of metabolic increase, should this relationship extend to ectothermic sharks. Overall, I have addressed fundamental, unanswered questions in the field of thermal ecology and provided novel insights into the pathways by which temperature influences several key physiological parameters. I challenge long-held assumptions within the field, record previously undocumented thermal stress responses and identify key ecophysiological relationships which should be accounted for when predicting animals' responses to thermal change. These novel findings contribute to an ever-expanding field and aid in our ability to predict ectotherm responses to climate change.

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They say life is about the journey, not the destination (unless it's the Bahamas!).

Table of Contents

Declaration	ii
Summary.....	iii
Acknowledgements	v
Table of Contents	vi
List of Figures.....	viii
Additional published or submitted work.....	x
1. Introduction.....	1
1.1. Thesis structure & objectives	5
2. Chapter 2 Endothermy makes fishes faster but does not expand their thermal niche	6
2.1. Abstract	6
2.2. Introduction.....	7
2.3. Materials & Methods.....	9
2.3.1. Data collation: Thermal niche expansion dataset	9
2.3.2. Speed measurements: Elevated cruising speeds dataset	9
2.3.3. Data analyses.....	10
2.3.3.1. Phylogenies and MCMCglmm.....	11
2.4. Results	12
2.4.1. Thermal niche expansion.....	12
2.4.2. Elevated cruising speeds.....	14
2.5. Discussion	15
3. Chapter 3 Energetic costs increase with faster heating in an aquatic ectotherm.....	18
3.1. Abstract	18
3.2. Introduction.....	18
3.3. Materials & Methods.....	20
3.3.1. Data collection.....	21
3.3.1.1. Acclimation phase.....	21
3.3.1.2. Temperature trials	22
3.3.2. Data analyses.....	23
3.3.2.1. Modelling.....	23
3.4. Results	25
3.5. Discussion	27
4. Chapter 4 Capture heats up sharks	30

4.1.	Abstract	30
4.2.	Introduction	31
4.3.	Materials & Methods	32
4.3.1.	Data collection	32
4.3.1.1.	Biologging.....	32
4.3.1.2.	Additional body temperature measurements of blue sharks.....	33
4.3.1.3.	Caudal peduncle blood sampling	33
4.3.1.4.	Ethics	34
4.3.2.	Data analyses	34
4.4.	Results.....	34
4.5.	Discussion.....	39
5.	Discussion.....	43
5.1.	The role of endothermy in fishes.....	43
5.2.	Rate of temperature needs to be accounted for	44
5.3.	Capture heats up sharks.....	44
5.4.	Practical applications of this work	45
5.5.	Future research.....	46
5.6.	Conclusions	47
6.	Bibliography	49
	Appendix A Supplementary information for Chapter 2: Endothermy makes fishes faster but does not expand their thermal niche	A.1
	Appendix B Supplementary information for Chapter 3: Energetic costs increase with faster heating in an aquatic ectotherm.	B.11
	Appendix C Supplementary information for Chapter 4: Capture heats up sharks.....	C.16

List of Figures

Figure 2.1: **2.1A:** Absolute thermal range (max. T_a – min. T_a) as a function of body mass (\log_{10} transformed; kg), taken from thermal niche expansion dataset: thermal range of fishes with regional endothermy (red triangles) and fishes without it (light blue circles); **2.1B:** The 80th percentile thermal range (90th – 10th percentile T_a) as a function of body mass (\log_{10} transformed; kg): thermal range of fishes with regional endothermy (red triangles) and fishes without it (light blue circles) recorded in the wild. Endothermy does not have an influence on the thermal range individuals spent 80% of their time in; **2.1C:** The 80th percentile depth range (90th – 10th percentile depth) as a function of body mass (\log_{10} transformed; kg): depth range of fishes with regional endothermy (red triangles) and fishes without it (light blue circles) recorded in the wild. Endothermy does not have an influence on the depth range individuals spent 80% of their time in. 13

Figure 2.2: Cruising speed (\log_{10} transformed; $m\ s^{-1}$) as a function of body mass (\log_{10} transformed; kg): cruising speed of fishes with regional endothermy (red triangles) and fishes without it (light blue circles) recorded in the wild. Fishes with regional endothermy have higher cruising speeds (pMCMC = 0.016)..... 14

Figure 3.1: Average MO_2 ($mg\ O_2\ min^{-1}\ kg^{-1}$), for the duration of the trial, against average temperature ($^{\circ}C$) for all stable temperature individuals, with thermal performance curve fitted, following the method of Rezende and Bozinovic (2019). 25

Figure 3.2: Log observed vs predicted O_2 consumption (mg) for each ramping individual, with points coloured by rate of temperature change ($\lambda\ ^{\circ}C\ min^{-1}$) and symbols indicating if the temperature was heating (triangle) or cooling (circle). The 1:1 (grey dashed) line indicates where we would expect the points to lie along if the stable treatments perfectly predicted the ramping trial O_2 consumption..... 26

Figure 3.3: Residuals (i.e., log of observed O_2 consumption minus log of predicted O_2 consumption) against rate of temperature change ($\lambda\ ^{\circ}C\ min^{-1}$). Breakpoint regression lines fitted; one for the heating data (red dashed line) and one for the cooling data (blue dashed line). Red points indicate heating trials and blue points indicate cooling trials. The residuals of the stable trials were calculated and overlaid (navy points). A 1:1 identity line is included (grey dashed line). 27

Figure 4.1: Body temperature elevation of tiger sharks and blue sharks recorded immediately upon capture (panels A & B), and average elevation of body temperature, during a 30-minute period under natural conditions several hours after release (panels C & D). Dashed black lines indicate a 1:1 identity line. [Blue shark image created by Ignacio Contreras and reproduced under the Creative Commons Attribution 3.0 Unported license: <https://creativecommons.org/licenses/by/3.0/legalcode>]..... 35

Figure 4.2: Average heating rate ($^{\circ}C\ min^{-1}$) for each blue shark during capture period (red circles; n = 15) and average heating rate every 30 sec for two biologged blue sharks (BSCC & BS09) during post-release phase (n=4205). Capture datapoints (red circles) are placed arbitrarily to left of x-axis to illustrate their collection before the beginning of the time series post-release. 36

Figure 4.3: Water temperature measurements (triangles) and body temperature measurements (circles) taken at 2cm and 4cm penetration into the dorsal musculature of 4 blue sharks. 37

Figure 4.4: Body temperature, water temperature and depth data for tiger sharks T1 (top panel) and T4 (bottom panel) from moment of release. A 500-point moving average smoother was applied to all data. 38

Figure 4.5 (A - C): (A) Temperature differential (ΔT) against hooking time for blue sharks with no significant relationship; (B) temperature differential (ΔT) against log (body mass) with no significant relationship; (C) temperature differential (ΔT) against lactate upon capture for blue sharks with no significant relationship. 39

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1. Introduction

Temperature influences and regulates almost all biological and ecological interactions and processes, and its significance extends from cellular up to ecosystem level. It controls reaction rates, regulates individuals' behaviour, and drives global patterns of species distributions. As atmospheric CO₂ levels continue to drive up global temperatures, disrupt weather patterns and increase the frequency of extreme weather events, understanding temperature's control on biological systems is paramount. Although thermal ecology is a well-established, continually expanding field of research, in recent decades it has been further stimulated by the threat of global warming, with policy makers looking to scientists to understand and predict how organisms will be impacted. To do this, we must further our understanding of the influence of temperature on species physiology, behaviour and distribution (Payne *et al.*, 2018, Payne *et al.*, 2016b, Pinsky *et al.*, 2019, Pörtner and Knust, 2007, Reynolds and Casterlin, 1980, Stevens *et al.*, 2010) which is key if we are to forecast their responses to climate change (Pörtner and Farrell, 2008). This thesis aims to contribute to this field of study by investigating both fundamental and applied aspects of thermal ecology, challenging long-held assumptions pervasive within the field, informing management practices, and identifying key ecophysiological relationships which must be accounted for when predicting animal's responses to thermal change.

Metabolism and its relationship with temperature is a wide field of research, with many branches in biology and ecology (Brown *et al.*, 2004). Many biologists and ecologists have dedicated their work to modelling temperature's influence on metabolism, and other biological rates, generating thermal performance curves for many of these relationships (Huey and Stevenson, 1979, Padfield *et al.*, 2021, Rezende and Bozinovic, 2019). Through these investigations into metabolic scaling, persistent patterns emerge, perhaps most notably the universal temperature dependence (UTD) model (Gillooly *et al.*, 2001), which underpins the metabolic theory of ecology (MTE) (Brown *et al.*, 2004). Although the UTD model and MTE are widely accepted concepts, controversy has arisen as to the UTD's ability to accurately capture the complexity of the thermal sensitivity of metabolism (Clarke, 2004, Clarke, 2006, O'Connor *et al.*, 2007). Numerous studies also support the consistent relationship between metabolism and temperature quantified as a Q₁₀ value (which is a measure of the temperature sensitivity of biological processes (Mundim *et al.*, 2020)) in the range of 2-3, indicating a doubling or tripling in metabolic rate with every 10°C change in temperature (Dell *et al.*, 2011). The thermal sensitivity of metabolism is particularly relevant for ectotherms because their metabolism more closely responds to temperature changes in their environment. Approximately 99% of Earth's organisms are ectothermic (Ohlberger, 2013) – lacking the ability to regulate their own body temperature – and so these organisms body temperatures,

and therefore their physiological rates, are governed by the environment they exist in and the associated metabolic scaling laws (i.e., the MTE and UTD). However, a small group of animals have evolved specialised physiologies, allowing them to elevate their body temperature and create less of a connection between their internal temperature and the ambient temperature; these are known as endotherms and regional endotherms. By investigating animals with these specialised physiologies, we can explore the potential advantages of breaking away from this connection.

Approximately 0.1% of all described fishes (Wegner *et al.*, 2015) have evolved the ability to warm specific internal tissues, such as muscle, eyes, brain and viscera, by retaining metabolically derived heat through vascular countercurrent heat exchangers (Watanabe *et al.*, 2019b, Carey *et al.*, 1971, Harding *et al.*, 2021). These are referred to as regional endotherms. This thermoregulatory strategy has evolved independently in several lineages of marine fishes, including lamnid sharks, tunas, and billfishes. The convergent evolution of this trait across multiple lineages, coupled with the significant energetic cost of the strategy (Bernal *et al.*, 2001, Watanabe *et al.*, 2015, Payne *et al.*, 2015), implies strong ecological benefits and two popular hypotheses, with mixed support, for the evolutionary drivers of this trait persist: (i) thermal niche expansion (Block, 1991, Block *et al.*, 1993, Dickson *et al.*, 2000, Carey and Lawson, 1973, Dickson and Graham, 2004), and (ii) facilitation of elevated cruising speeds (Dickson and Graham, 2004, Watanabe *et al.*, 2015). The concept of 'thermal niche' was first introduced by Magnuson *et al.* (1979) and is widely used in ecology. Thermal niche expansion is a long-standing concept which predicts that regionally endothermic fishes can tolerate a broader range of environmental temperatures, owing to their thermoregulatory strategy, and in turn specialised physiology, and thus enabling them to expand their geographic range or niche (Block, 1991, Block *et al.*, 1993, Dickson *et al.*, 2000, Carey and Lawson, 1973, Dickson and Graham, 2004). Widespread acceptance of this concept led to the assumption that regionally endothermic fishes would be less susceptible to the deleterious impacts of global ocean warming. Alternatively, the elevated cruising speeds hypothesis focuses on how the power output of slow-twitch, oxidative myotomal muscle fibres within the centralised red muscle, increases with elevated temperature (Dickson and Graham, 2004, Watanabe *et al.*, 2015). These muscle fibres power sustained (aerobic) swimming and so the hypothesis arose that by elevating the temperature of these muscle fibres, it could facilitate increased cruising speed of the fish. Furthermore, temperature's influence on basal metabolic rate (which will increase under elevated temperature) increases the fish swimming speed at which the cost of transport is minimised (Iosilevskii and Papastamatiou, 2016), which may represent preferred speed for many fishes (i.e. COT_{min}). **Chapter 2** of this thesis aims to formally test these two hypotheses to decipher the evolutionary drivers of this specialised physiology.

Specialised physiologies are one way that animals have evolved to break the connection between body temperature and ambient temperature and break away from the constraints of the doubling-tripling of metabolic rate for every 10°C increase in environmental temperature (as expected under MTE). However, it is increasingly realised that metabolic scaling 'laws' in fact exhibit significant variation and can be context dependent. Although the thermal sensitivity of metabolism has been widely studied, research has primarily focused on static temperature experiences (i.e., estimating metabolic rate at a range of constant temperatures). However, temperature in nature is rarely static, so our existing understanding from experiments may not reflect how temperature influences the metabolism of organisms in natural systems. Therefore, we need to better understand how the thermal sensitivity of metabolism varies when temperature is undergoing change. I explore this knowledge gap in **Chapter 3**. Using closed chamber respirometry I measured the oxygen consumption rate (a widely accepted proxy of aerobic metabolic rate) of an aquatic ectotherm under varying thermal conditions to examine whether rate of temperature change affects the thermal sensitivity of aerobic metabolism. Improving understanding about the thermal sensitivity of metabolism will help inform predictions of high level ecosystem responses (Dillon *et al.*, 2010, Rubalcaba *et al.*, 2020) as well as individual level responses (Vajedsamiei *et al.*, 2021) to temperature change.

It is currently uncertain if large-bodied fishes exhibit rapid temperature increases (such as those tested in **Chapter 3**), but we might expect this to occur during periods of physical exertion, such as during catch-and-release interactions. Catch-and-release fishing is a popular practice in recreational fisheries (Brownscombe *et al.*, 2017, Danylchuk *et al.*, 2014, Cooke and Schramm, 2007). However, it is considered a multi-stressor interaction for individuals (Gale *et al.*, 2013). When sharks are hooked, they often exhibit intensive swimming acceleration (Gallagher *et al.*, 2017), and periods of exhaustive exercise (i.e., anaerobic exercise) (Schwieterman *et al.*, 2021), as they attempt to escape. This can elevate the metabolic rate (Mohan *et al.*, 2020, Kieffer, 2000) resulting in, among other things, the generation of heat. Moreover, sharks may be unable to swim freely when hooked and therefore, experience reduced capacity to dissipate heat across the gill surface during respiration (Stevens, 2011, Stevens and Fry, 1974, Nakamura *et al.*, 2020). This excess heat may accumulate and manifest as an elevation of body temperature in these animals. Thus, by measuring the body temperature and water temperature of captured sharks, through the use of novel biologging technology, I investigate the extent to which sharks heat up when captured (**Chapter 4**).

Studying thermal ecology is of great personal interest as temperature governs so much of the biological world, influencing global patterns at a macroecological scale whilst also playing a role in shaping individual level behaviour and physiology. Furthermore, focussing this research on the

aquatic realm has allowed me to employ a variety of new and old research approaches and methodologies, to explore the many interactions between the abiotic and the biotic world, an interface proliferating with curiosities. Traditionally this field of research has relied heavily on laboratory-based studies and although this has provided many mechanistic insights, there remains a need to bridge the gap between patterns observed in the laboratory and those observed in the field. This presents a unique opportunity to observe trends or relationships not yet recognised. Moreover, focusing on the individual level may allow us to observe relationships previously overlooked, as much of thermal ecology research so far has concentrated at the population level. This emergent field, although widely studied, still has lots of knowledge gaps, which are becoming increasingly important to address when taken in the context of climate change and ocean warming. This field of research will likely undergo exponential growth in the coming years as we seek to understand how our oceans will be affected by our warming planet.

In this thesis I draw on existing, well-established methodologies while also using novel approaches to study the thermal ecology of larger, threatened species. I aim to advance the field of thermal ecology in the marine realm as a large proportion of thermal ecology work to date focuses on terrestrial ectotherms (i.e., insects) with research less abundant on aquatic ectotherms. By collecting information at an individual level, for example using biologging technology, I aim to gather insight into the thermal niches of typically hard to study species, such as large sharks. Additionally, given the fine scale at which this data can be recorded, I hope to identify patterns, responses, and behaviours that might not be seen if solely focussing on the population level, such as fisheries data. Additionally, this work questions long-held assumptions that are pervasive in the field but often times have not been formally tested and yet are used as building blocks in other research.

This thesis has a number of implications, spanning applied practical applications to advancing scholarly understanding of the thermal niches of fishes. In terms of practical applications, this thesis aims to inform fishing management practices, such as catch-and-release protocols and guidelines with the view of improving post-release mortality for threatened fish species (**Chapter 4**). By examining the thermal niches of fishes and the thermal sensitivity of ectotherm metabolism, this thesis aims to contribute data that may be used to better our predictions of where animals may move or how they may alter their behaviour in response to climate change (**Chapter 2 & 3**). Additionally, data collected could feed into informing marine protected area (MPA) delineation as if we can better understand where animals will move, in response to temperature increase/decrease, we can better predict what areas animals will need under various climate warming scenarios. With regard to advancing scholarly understanding, this thesis will critically evaluate several concepts which have been persistent in this research field, such as the advantages

conferred by regionally endothermy, and the thermal sensitivity of aerobic metabolism. Furthermore, new concepts such as the potential influence of rate of temperature change on metabolic cost and oxygen consumption, and potential thermal stress responses in captured sharks will be introduced.

I use a combination of research approaches throughout this thesis. Firstly, I employ biologging technology to collect fine-scale individual level behavioural and physiological data from a range of wild fishes. Biologging is a rapidly advancing field and I aim to harness this technology to both explore long-held assumptions about the evolutionary advantages of endothermy (**Chapter 2**) and investigate if catch-and-release fishing causes thermal stress in captured sharks (**Chapter 4**). Secondly, I carry out an extensive literature review, and conduct comparative analyses of published data to harness publicly available, difficult to obtain data (**Chapter 2**). Thirdly, I use closed chamber respirometry, a classical method of measuring aerobic metabolic rate in small-bodied aquatic organisms (**Chapter 3**). By using a suite of complimentary approaches and combining novel and well-established methodologies, I take a holistic approach to understanding the thermal niches of fishes.

1.1. Thesis structure & objectives

This thesis has three main objectives:

1. To understand the role of regional endothermy in shaping the thermal niches of fishes and decipher the drivers behind the evolution of this trait (**Chapter 2**);
2. To determine if rate of temperature change has an effect on the aerobic metabolism of an aquatic ectotherm (**Chapter 3**); and
3. To investigate potential thermal stress of catch-and-release fishing on ectothermic fishes (**Chapter 4**).

2. Chapter 2 Endothermy makes fishes faster but does not expand their thermal niche

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2.1. Abstract

Regional endothermy has evolved several times in marine fishes, and two competing hypotheses are generally proposed to explain the evolutionary drivers behind this trait: thermal niche expansion and elevated cruising speeds. Evidence to support either hypothesis is equivocal, and the ecological advantages conferred by endothermy in fishes remain debated. By compiling published biologging data and collecting precise speed measurements from free-swimming fishes in the wild, we directly test whether endothermic fishes encounter broader temperature ranges, swim faster, or both. Our analyses avoid several complications associated with earlier tests of these hypotheses, as we use precise measurements of the thermal experience and speed of individual fish. Phylogenetically-informed analyses of 89 studies reporting temperature ranges encountered by tagged fishes reveal that endotherms do not encounter broader temperature ranges than their ectothermic counterparts. In contrast, speed measurements from 45 individuals (16 species, of which 4 were regional endotherms) show that endothermic fishes cruise ~ 1.6 times faster than ectotherms, after accounting for the influence of body temperature and body mass on speed. Our study shows that regionally endothermic fishes – those with the ability to conserve metabolically derived heat through vascular countercurrent heat exchangers and elevate the temperature of internal tissues – swim at elevated cruising speeds, although not as fast as previously thought. Contrary to previous studies of endothermy's role in thermal niche expansion, our results suggest the significance of endothermy in fishes lies in the advantages it confers to swimming performance rather than facilitating occupation of broader thermal niches. Given speed's major influence on

metabolic rate, our updated speed estimates imply endotherms have lower routine energy requirements than current estimates. Our findings shed light on the evolutionary drivers of regional endothermy in fishes and question the view that the trait confers resilience to climate change through broader thermal tolerance than that of ectotherms.

2.2. Introduction

Temperature has pervasive impacts on the physiology, behaviour, and distribution of organisms (Payne *et al.*, 2018, Payne *et al.*, 2016b, Pinsky *et al.*, 2019, Pörtner and Knust, 2007, Reynolds and Casterlin, 1980, Stevens *et al.*, 2010). Ocean temperature strongly regulates the movement and distributions of marine fish (Hazen *et al.*, 2013, Kleisner *et al.*, 2017, Hiddink and ter Hofstede, 2008) and is a key consideration for forecasting their responses to climate change (Pörtner and Farrell, 2008). However, the influence of temperature on fish behaviour and distribution varies across species. One major factor influencing this is the role of endothermy. Most fishes are ectothermic (Wegner *et al.*, 2015), however, regional endothermy has evolved independently in several lineages of marine fishes, including lamnid sharks, tunas and billfishes. Regional endothermy is the ability to conserve metabolically derived heat through vascular countercurrent heat exchangers, and elevate the temperature of specific internal tissues, such as muscle, eyes, brain and viscera, the term ‘regional’ referring to this localised warming. About 35 species of marine fishes are known to exhibit regional endothermy (Dickson and Graham, 2004), accounting for less than 0.1% of all described fishes (Wegner *et al.*, 2015). Currently, regional endothermy in fishes has been identified in marine species only (Bernal *et al.*, 2001, Block *et al.*, 1993, Carey *et al.*, 1971, Dickson and Graham, 2004) with no evidence for this trait in freshwater fishes. The convergent evolution of regional endothermy across multiple lineages, coupled with the significant energetic cost of the strategy (Bernal *et al.*, 2001, Watanabe *et al.*, 2015, Payne *et al.*, 2015), implies strong ecological benefits. Various hypotheses have been put forward to explain the ultimate driver of endothermy in fishes. These include that endothermy (i) enables thermal niche expansion (Block, 1991, Block *et al.*, 1993, Dickson *et al.*, 2000, Carey and Lawson, 1973, Dickson and Graham, 2004), (ii) facilitates elevated cruising speeds (Dickson and Graham, 2004, Watanabe *et al.*, 2015), (iii) allows for more effective perception of thermal gradients (Neill *et al.*, 1976), (iv) increases metabolic rates (Stevens and Neill, 1978, Brill, 1996), (v) facilitates increased rates of somatic and gonadal growth (Brill, 1996) and (vi) that it is simply an evolutionary by-product (Seebacher, 2020). The ‘thermal niche expansion’ and ‘elevated cruising speeds’ hypotheses are arguably the most widely discussed hypotheses at present, so we focused on them in this study.

The thermal niche expansion hypothesis predicts that regionally endothermic fishes can tolerate a broader range of environmental temperatures, enabling them to expand their geographic range or niche. Although it remains formally untested, this hypothesis is widely accepted and

underpins several long-standing hypotheses about the thermal niches of fishes, such as the latitudinal diversity gradient (Stevens, 1989). The ideas underlying the thermal niche expansion hypothesis were first formed during work undertaken in the 1970s by Carey and Lawson (1973) on Atlantic bluefin tuna *Thunnus thynnus* when it was postulated that by warming their red muscle the species could “greatly expand [its] range”. This idea was then formalised by Block (Block, 1991, Block *et al.*, 1993), supported further by Dickson *et al.* (2000), and remains one of the most widely accepted hypotheses (Weng *et al.*, 2005, Madigan *et al.*, 2015). Alternatively, the elevated cruising speeds hypothesis focuses on how slow-twitch, oxidative myotomal muscle fibres, within the centralised red muscle, power sustained (aerobic) swimming and how the output of these muscle fibres increases with elevated temperature (Dickson and Graham, 2004, Watanabe *et al.*, 2015), thereby allowing increased cruising speed of the fish. Furthermore, temperature’s influence on basal metabolic rate (which will increase under elevated temperature) increases the fish swimming speed at which the cost of transport is minimised (Iosilevskii and Papastamatiou, 2016), which may represent preferred speed for many fishes (i.e. COT_{min}).

Here, we simultaneously test the ‘thermal niche expansion’ and ‘elevated cruising speeds’ hypotheses using both collated and published animal-borne sensor data (i.e., biologging data) and by measuring speed and temperature experiences of individual fish of multiple species swimming in the wild. Specifically, we test whether regionally endothermic fishes encounter broader temperature ranges than ectothermic fishes and/or whether they swim at elevated cruising speeds. By using individual level data, we can better examine the factors influencing thermal niche formation and adaptation, as well as intra-specific individual variation in thermal ranges, and gain a more detailed measure of the extent and variability of thermal ranges of fishes.

Evidence supporting either hypothesis is rare, however, past studies have attempted to decipher the driving cause of endothermy in fishes and found mixed results; (Dickson and Graham, 2004) found evidence to support the thermal niche expansion hypothesis but could not provide direct support for the elevated cruising speeds hypothesis. Although Watanabe *et al.* (2015) showed support for the elevated cruising speeds hypothesis, some of the early endothermic speed values have since been shown to be overestimates (Watanabe *et al.*, 2019b). By improving consistency within our speed dataset, we avoid several complications associated with these earlier tests. We accomplished this by exclusively using propeller style speed loggers (from one manufacturer: Little Leonardo) for all speed measurements. This increases consistency in measurements and reduces likelihood of overestimates. Furthermore, our dataset includes more endothermic species, tagged with speed propellers, ($n = 4$) than Watanabe *et al.* (2015) ($n = 1$; Salmon shark *Lamna ditropis*) thereby reducing the impact of overestimates on the data as a whole.

This novel approach allows us to directly test the elevated cruising speeds hypothesis without complications seen in previous studies.

2.3. Materials & Methods

2.3.1. Data collation: Thermal niche expansion dataset

Data collection for this study consisted of an extensive literature review of peer-reviewed published sources. Library and electronic database searches were carried out across multiple platforms, such as JSTOR, Web of Science, ScienceDirect, Research Gate, among others. Title searchers and keywords included 'biologging', 'thermoregulation', 'endothemy', 'regional endothemy' 'tagging', 'shark(s)', 'teleost(s)', 'ectothermic', 'internal temperature', 'body temperature', 'thermal ecology', 'thermal niche expansion', 'elevated cruising speeds' and/or 'shark tagging'. In addition, studies cited in papers found during these searches, but not identified directly by the search, were also included. Papers for this study were chosen based on a number of selection criteria: (1) species tagged (e.g. marine species only), (2) tag type (e.g. Pop-up Archival Tag; PAT), (3) location of animal at time of tagging (e.g. only wild fishes in their natural habitat were utilised), (4) frequency of data collection/recording, (5) duration of recording, (6) type of publication (e.g. peer-reviewed journal articles only), (7) recorded parameters (e.g. depth, ambient temperature, internal temperature), and (8) availability and reliability of the data (e.g. robustness of methodologies and technologies used). We chose several data parameters to extract during this review: species common name, species scientific name, thermoregulatory ability, tag type, body size, number of individuals, ambient and body temperature (min., max., mean, 10% upper and lower percentiles), recording duration, depth (min., max., mean, 10% upper and lower percentiles) and latitude (if available).

2.3.2. Speed measurements: Elevated cruising speeds dataset

The elevated cruising speeds hypothesis has been tested previously primarily using data from accelerometers, time depth recorder's and pop-off satellite archival tag data, none of which directly record the swimming speed of free-swimming fish in the wild, and could therefore provide inaccurate speed estimates (Cade *et al.*, 2018, Bidder *et al.*, 2012). Furthermore, studies that did use speed propeller sensors (Watanabe *et al.*, 2015) combined multiple sensor manufacturers, several logger types and other speed estimation methods. This resulted in inconsistent estimates with large variation among individuals and may introduce methodological biases. Therefore, we confined our data collection to speed propellers of the same type, from the same manufacturer, to directly collect precise speed measurements of fishes free-swimming in the wild, whilst simultaneously recording the ambient temperature, along with several other parameters.

We captured fish by drum lines, long lines, or by angling. Biologging packages were fitted to dorsal or pectoral fins of each animal, which was then immediately released; associated methods detailed further in published sources (Watanabe *et al.*, 2019a, Watanabe *et al.*, 2019b, Huvneers *et al.*, 2018, Papastamatiou *et al.*, 2018, Watanabe *et al.*, 2015, Nakamura *et al.*, 2011). Biologging packages varied slightly among species but all packages included accelerometers (recording tri-axial acceleration at 25Hz and depth at 1Hz; Techno-Smart AGM-1), temperature loggers (recording ambient temperature at 1Hz) and propeller-based speed sensors (all manufactured by Little Leonardo Corp.) of similar models (PD3GT logger, maximum dimensions 115 x 21mm, 60g in air; W1000-PD3GT logger, 22 x 123 mm, 90 g in air; and ORI400/1300-PD3GT logger, 16 mm x 74 mm, 37 g in air), measuring speed in m s^{-1} (accuracy of 0.03 – 0.05 m s^{-1}), recording at 1Hz (Payne *et al.*, 2016a, Nakamura *et al.*, 2011, Watanabe *et al.*, 2015). To enable retrieval, tag packages also included a VHF transmitter (Advanced Telemetry Systems, MM100), satellite position only tag (Wildlife Computers Model 258; ARGOS enabled) and a time-release mechanism. Once detached from the animal, packages floated to the surface as they were constructed of a positively buoyant material (Diab Syntactic © non-compressible foam). Packages were then located using the ARGOS system and a VHF receiver and retrieved from the ocean surface by boat. A total of 16 species (4 regional endotherms and 12 ectotherms) were tagged, ranging between 8.2 and 807.5 kg body mass and having encountered a range of water temperatures (12 – 28.2 °C).

2.3.3. Data analyses

Data handling and statistical analyses were carried out in R Version 4.0.2 (R Core Team, 2020), with similar methodologies implemented for analyses of both collated (thermal niche expansion hypothesis) and measured (elevated cruising speeds hypothesis) data. Several parameters had to be estimated using source data (e.g., total length, body mass) and published conversion factors or equations (**Table A.1** and **Table A.2**) when not reported or directly recorded. Additionally, several studies compiled as part of the thermal niche expansion dataset reported data in the form of figures but did not provide the raw dataset. In this instance, we used plot digitizer software (Rohatgi, 2019) to extract data for analysis. For the elevated cruising speeds dataset, as each individual displayed strongly unimodal ambient temperature experiences and spent most time in a small range (2 – 3 °C) of temperatures throughout sensor deployment, we used mean ambient temperature for each individual (to the nearest °C) in subsequent analyses. As body temperature was not directly recorded, for ectotherms it was set at the same value as the mean ambient temperature (Watanabe *et al.*, 2015). For endotherms, body temperature (T_b) was estimated from published relationships with ambient temperature (T_a); for Atlantic bluefin tuna *T. thynnus* Addis *et al.* (2009) used $T_b = 0.5531T_a + 17.2365$, for salmon sharks *L. ditropis* Goldman *et al.* (2004) used $T_b = 0.2047T_a + 23.156$ and for white sharks *Carcharodon carcharias* and striped marlin *Kajikia*

audax, T_b was extrapolated from figures in Goldman (1997) and Morrow and Mauro (1950), respectively. As our speed measurements were strongly unimodal and right-skewed, the modal speed was used in the models to represent the cruising speed of the animal, as opposed to burst events. Cruising speed was chosen specifically for analysis as it is aerobically powered, can be sustained for prolonged periods of time (Ryan *et al.*, 2015, Watanabe *et al.*, 2012, Ware, 1978, Gioanni, 1988) and is the most common speed at which the animals travel as we have defined it (i.e. modal swimming speed).

2.3.3.1. Phylogenies and MCMCglmm

We first used nonphylogenetic regression analyses to determine the appropriate fixed effects and explanatory variables, with model selection based on AIC scores. Phylogenetically informed allometry, to account for phylogenetic non-independence, was then performed with the best model, to test whether regionally endothermic fishes encounter a broader range of temperatures than ectothermic fishes and/or whether they swim at elevated cruising speeds. Phylogenetic trees were created using the Tree of Life package (Hinchliff *et al.*, 2015, Michonneau *et al.*, 2016) (**Figure A.2** and **Figure A.3**). The tree was then used to inform the modelling analyses using the R-package 'MCMCglmm' (Hadfield, 2009). Continuous variables (i.e., 'days at liberty', body mass, speed, depth, body temperature, and ambient temperature) were \log_{10} transformed to improve linearity of relationships among variables. 'Days at liberty' and number of individuals were included in models to account for the influence of sample size on thermal range. Body mass and body temperature were included to account for the influence of thermal inertia and elevated spatial range of large-bodied animals. Depth range was also included to account for potential vertical niche expansion (Madigan *et al.*, 2015). Fish thermoregulatory ability was included as a categorical variable (i.e., regional endotherm, ectotherm) and species name was included as a random factor. Thermal niche was represented by two separate measures of the individuals' thermal experience: absolute thermal range ($\max. T_a - \min. T_a$) and the 80th percentile thermal range (90th– 10th percentile T_a). The latter measure indexes a range of water temperatures that each individual spends ~ 5 hours per day (or 12 min h^{-1}) outside. These individual measures were used concurrently to account for the absolute maximum and minimum temperature each individual experienced, whilst also accounting for the thermal range they spent most time in (i.e., 80% of their time). This allows us to more accurately represent the realised thermal niche of these animals and mitigates issues presented by thermal inertia effects. The measure chosen to evaluate depth range was the 80th percentile depth range (i.e., 90th - 10th percentile depth). This measure indexes a range of depths that each individual spends ~ 5 hours per day (or 12 min h^{-1}) outside of. This represents the depth range the individuals spend most time in (i.e., 80% of their time). Alternate models were constructed to test the opposing hypotheses (**Table A.3** and **Table A.4**).

2.4. Results

2.4.1. Thermal niche expansion

To test if regionally endothermic fishes encounter broader temperature ranges than their ectothermic counterparts, we compiled 89 published studies reporting temperature ranges encountered by tagged fishes of 41 species, 14 of which were regional endotherms. Nonphylogenetic regression analyses (**Table A.3**), followed by phylogenetically informed generalised linear mixed models, MCMCglmm (Hadfield, 2009), show that endothermy does not have an influence on absolute thermal range (posterior mean = 3.5, pMCMC = 0.08, $\lambda_{\text{mode}} = 0.002$). Endothermy does not affect the 80th percentile thermal range (posterior mean = 1.4, pMCMC = 0.4, $\lambda_{\text{mode}} = 0.00068$).

In addition to thermal range, we investigated the significance of endothermy on depth range in order to address vertical niche expansion (Madigan *et al.*, 2015). Phylogenetically informed generalised linear mixed models, MCMCglmm (Hadfield, 2009), show that endothermy does not have an influence on 80th percentile depth range (posterior mean = 33.3, pMCMC = 0.6, $\lambda_{\text{mode}} = -0.0001$).

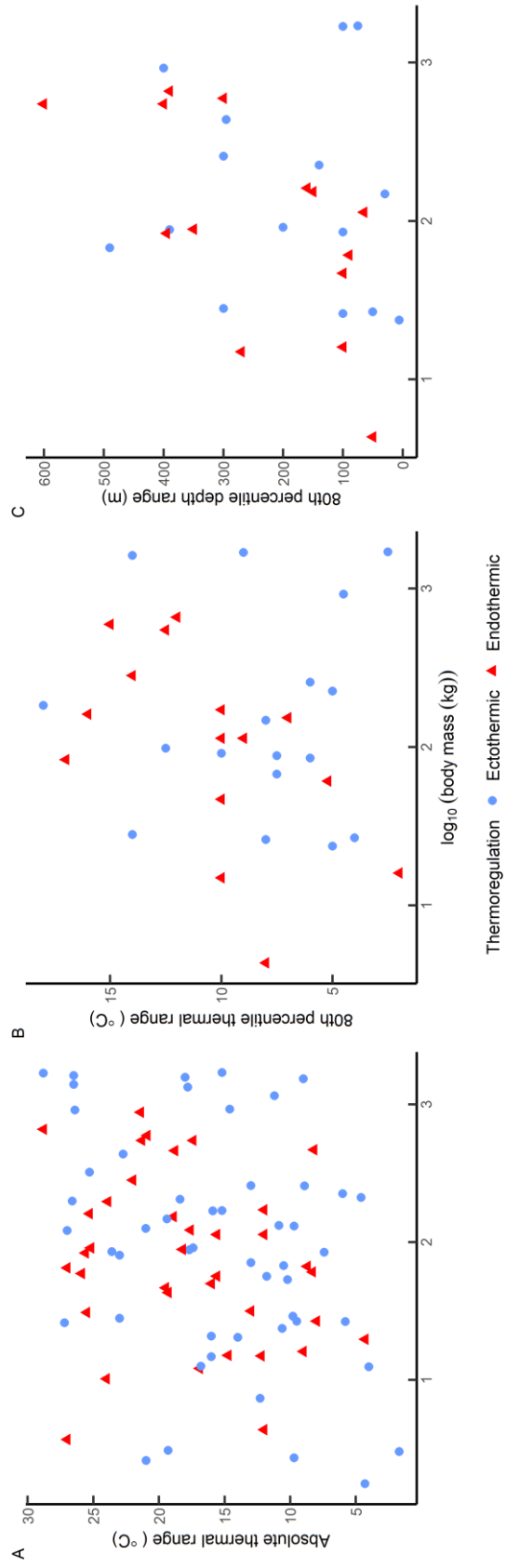


Figure 2.1: **2.1A:** Absolute thermal range (max. $T_a - \min. T_a$) as a function of body mass (\log_{10} transformed; kg), taken from thermal niche expansion dataset: thermal range of fishes with regional endothermy (red triangles) and fishes without it (light blue circles); **2.1B:** The 80th percentile thermal range (90th – 10th percentile T_a) as a function of body mass (\log_{10} transformed; kg); thermal range of fishes with regional endothermy (red triangles) and fishes without it (light blue circles) recorded in the wild. Endothermy does not have an influence on the thermal range individuals spent 80% of their time in; **2.1C:** The 80th percentile depth range (90th – 10th percentile depth) as a function of body mass (\log_{10} transformed; kg); depth range of fishes with regional endothermy (red triangles) and fishes without it (light blue circles) recorded in the wild. Endothermy does not have an influence on the depth range individuals spent 80% of their time in.

These results indicate that endothermic fishes do not encounter broader temperature ranges than their ectothermic counterparts. Larger bodied animals have greater absolute thermal ranges (**Figure 2.1A**; posterior mean = 3.2, pMCMC = 0.003) but no such relationship was found for the 80th percentile thermal range (**Figure 2.1B**; posterior mean = 1.1, pMCMC = 0.374). Furthermore, larger bodied animals do not encounter broader depth ranges (**Figure 2.1C**; posterior mean = 67.1, pMCMC = 0.2).

2.4.2. Elevated cruising speeds

To test if endothermy facilitates elevated cruising speeds in fishes we directly collected biologging data for 45 individual fish in the wild, from 16 species including 4 regionally endothermic species, ranging 8.2 – 807.5 kg body mass and a mean recording duration of 49.34 h (**Table A.5**). Nonphylogenetic regression analyses (**Table A.4**), followed by phylogenetically informed generalised linear mixed models, MCMCgImm (Hadfield, 2009) show that endothermy has a significant influence on speed (posterior mean = 0.20, pMCMC = 0.016, $\lambda_{\text{mode}} = 0.10$). Even after accounting for the influence of body temperature on speed, regional endotherms of given mass cruise faster than ectotherms (pMCMC = 0.016; **Figure 2.2**). A significant effect of endothermy, after also accounting for body temperature, suggests other traits of endotherms are involved with faster swimming in addition to temperature effects. Further, on average, for a given body mass across the range given here, regional endotherms swim ~ 1.6 times faster than ectotherms. Although body mass has a positive slope (posterior mean = 0.019) with speed, it is not significant (pMCMC = 0.7; **Figure 2.2**).

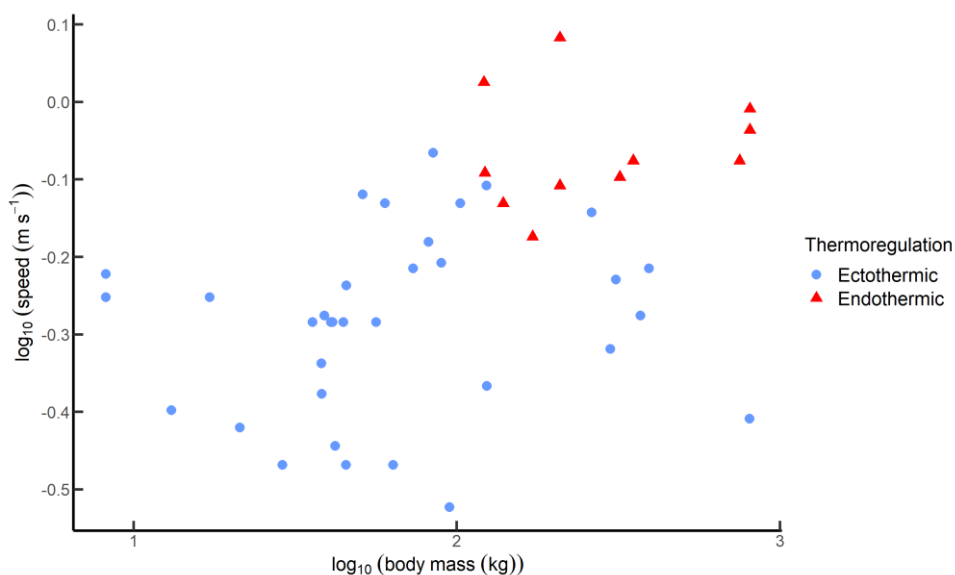


Figure 2.2: Cruising speed (\log_{10} transformed; m s^{-1}) as a function of body mass (\log_{10} transformed; kg): cruising speed of fishes with regional endothermy (red triangles) and fishes without it (light blue circles) recorded in the wild. Fishes with regional endothermy have higher cruising speeds (pMCMC = 0.016).

2.5. Discussion

Our study shows that regionally endothermic fishes do not encounter broader temperature ranges than their ectothermic counterparts, but that they swim at elevated cruising speeds. Contrary to previous studies of endothermy's role in thermal niche expansion (Weng *et al.*, 2005, Block *et al.*, 2001, Dickson and Graham, 2004, Carey and Lawson, 1973), our results therefore suggest that the significance of endothermy lies in the competitive advantages it confers to swimming performance rather than facilitating occupation of broader thermal niches.

It has been shown previously that elevated body temperature positively influences swimming speed in many fish species (Whitney *et al.*, 2016, Sisson and Sidell, 1987, Kieffer *et al.*, 1998, Rome *et al.*, 1984, Dickson and Graham, 2004), primarily through the mechanism of increased aerobic capacity of red muscle. Building upon this understanding, our study accounted for the effect of body temperature on speed and showed evidence for an additional influence of endothermy on cruising speed. Interestingly, while the eyes and brain of striped marlin are maintained at elevated temperatures their medially positioned red muscle is not (Dickson and Graham, 2004), yet they swim at relatively high speeds. Medial red muscle and regional endothermy are often conflated with one another because the traits are highly correlated. However, it is possible mechanical advantages of medial red muscle alone, such as restriction of body undulations toward the tail and associated drag reductions (Donley *et al.*, 2004), are largely responsible for higher speeds in species with that trait, most of which also maintain the red muscle at higher temperatures. More swimming speed data from species with medial and unheated red muscle would help address this question.

Taken together, our data remain in support of the general conclusions of Watanabe *et al.* (2015) that regional endotherms swim faster than ectotherms. However, we found a far smaller difference – 1.6 times faster than ectotherms, compared to 2.7 times faster in Watanabe *et al.* (2015) – likely attributable to our use of consistent measurement methodology (speed propellers), increased sample size and lack of extrapolated speed measurements culminating in a more accurate estimate of speed. This finding has important consequences for our understanding of fish energetics, particularly given speed's strong influence on rates of energy expenditure: as energy expenditure increases approximately to the cube of speed (Bernal *et al.*, 2012, Carlson *et al.*, 2004), routine metabolic rates (and therefore daily energy budgets) of regionally endothermic fishes would therefore be considerably lower than currently thought (e.g., Semmens *et al.* (2013) and Watanabe *et al.* (2019b)). Overestimation of energy requirements for regionally endothermic fishes, most of which are high level predators (e.g., white sharks, mako sharks, Atlantic bluefin tuna), is problematic for accurately predicting changes throughout lower trophic levels following changing abundances of such predators. These results highlight the significant uncertainties that

remain in our understanding of energetics of large marine fishes, many of which are too difficult to study in metabolic chambers (Bernal *et al.*, 2012, Payne *et al.*, 2015).

The potential advantages conferred by elevated cruising speeds include the ability to perform further annual migrations than ectothermic species (Watanabe *et al.*, 2015), increased predator-prey encounter rates (Jacoby *et al.*, 2015) and enhanced ability to identify and capture prey (Ryan *et al.*, 2015, Fritsches *et al.*, 2005, Schieber *et al.*, 2012) due to the higher temporal resolution in the visual system achieved under faster locomotion speeds; speed of locomotion determines the rate at which sensory information is encountered and processed by an animal as it moves through its natural environment (Ryan *et al.*, 2015). Taken in the context of the visual system, the higher the swimming speed, the faster the rate at which an image moves across the animal's eye (Eckert and Zeil, 2001), such that animals exhibiting higher swimming speeds tend to have higher temporal resolution and therefore process visual information faster (Ryan *et al.*, 2015, Autrum, 1958, Lisney *et al.*, 2011, McFarland and Loew, 1983). Although studies like ours have been conducted in the past, the novelty of our study lies in our methodology. Previous studies have been limited by the resolution of their data, the unattainability of multiple, simultaneous measurements of environmental parameters and small sample sizes (especially for endothermic species). Our study overcame some of these limitations using cutting-edge technology that provides speed estimates of high precision and accuracy, and so provides the most representative speed information for this group of animals. Further refinements could come from directly measuring core body temperatures of each animal rather than estimating it from the environment or other studies (as we did). Technological developments are starting to facilitate such future work.

Our findings for the thermal niche expansion hypothesis contrast with those of numerous previous studies (Carey *et al.*, 1971, Carey and Lawson, 1973, Block, 1991, Block *et al.*, 1993, Dickson and Graham, 2004, Watanabe *et al.*, 2015). This may be because ours is the first to compare the thermal experience of a large number of species from both regional endotherms and ectotherms, at the individual level. Species-level thermal tolerance is influenced by factors such as abundance, migration and seasonality, and may obscure the temperature experience of individuals, with the individual-level being that at which niche expansion ought to provide benefit. Our finding that endothermy does not enhance thermal or vertical niches of individuals has broad implications, particularly in terms of climate change. It has previously been suggested that regionally endothermic fishes may be better able to deal with changing ambient temperatures by stabilising their tissue temperatures (Carey and Teal, 1969, Neill *et al.*, 1976, Stevens and Neill, 1978, Weng and Block, 2004), a situation which would be expected under current climate change scenarios, such as global ocean warming. Taken in conjunction with the assumption of thermal niche expansion, regionally endothermic fishes are often assumed to be less susceptible to the global and

local scale impacts of ocean warming (Block, 1991), due to their ability to escape thermal stress by expanding or shifting their distributions. That may be the case, but our results indicate that endothermy does not facilitate occupation of broader temperature or depth ranges, so the future climate resilience of such fishes may be overstated. Marine spatial planning and protection and re-introduction strategies, for conservation purposes, are largely informed by species distribution models (SDM's). SDM's are constructed from past and present distribution data of species, and then used to make spatially explicit predictions of environmental suitability for species and potential redistribution of the species (Jarvie and Svenning, 2018). This makes SDM's extremely useful tools in predicting species range shifts under climate change scenarios. While current SDM's for regionally endothermic fish species are based on current distribution data, the predictions they make for potential redistribution, under climate changes scenarios, may be susceptible to overestimation due to the long held assumption (Watanabe *et al.*, 2015, Dickson *et al.*, 2000, Weng *et al.*, 2005, Block, 1991, Block *et al.*, 1993) that regionally endothermic fishes can expand their thermal and vertical (Madigan *et al.*, 2015) niche and therefore exploit a wider spatial niche.

In conclusion, our quantitative and comparative analyses indicate that the significance of endothermy lies in the competitive advantages it confers to swimming performance rather than facilitating occupation of broader thermal niches. Moreover, our results suggest that the magnitude of the difference in swimming speed between ectotherms and regional endotherms is not as large as estimated previously. Rather than facilitating broader thermal niches, our data imply that convergent evolution of regional endothermy is more likely linked to advantages in ecological interactions, such as predator-prey interactions. Taken in conjunction with the fact that regional endothermy has evolved independently in lineages of fishes which are largely high-level predatory species, we consider the likely advantage of endothermy lies in the competitive advantage it confers to predation.

3. Chapter 3 Energetic costs increase with faster heating in an aquatic ectotherm.

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Author contribution: LH and NP conceived the ideas and designed methodology; LH collected the data; LH, AJ & NP analysed the data; LH led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Status: This manuscript is accepted with Conservation Physiology.

3.1. Abstract

The thermal sensitivity of metabolism is widely studied due to its perceived importance for organismal fitness and resilience to future climate change. Almost all such studies estimate metabolism at a variety of constant temperatures, with very little work exploring how metabolism varies during temperature change. However, temperature in nature is rarely static, so our existing understanding from experiments may not reflect how temperature influences metabolism in natural systems. Using closed chamber respirometry we estimated the aerobic metabolic rate of an aquatic ectotherm, the Atlantic ditch shrimp *Palaemonetes varians*, under varying thermal conditions. We continuously measured oxygen consumption of shrimp during heating, cooling, and constant temperatures, starting trials at a range of acclimation temperatures and exposing shrimp to a variety of rates of temperature change. In a broad sense, cumulative oxygen consumption estimated from static temperature exposures corresponded to estimates derived from ramping experiments. However, further analyses showed that oxygen consumption increases for both faster heating and faster cooling, with rapid heating driving higher metabolic rates than if shrimp were warmed slowly. These results suggest a systematic influence of heating rate on the thermal sensitivity of metabolism. With influential concepts such as the metabolic theory of ecology founded in data from constant temperature experiments, our results encourage further exploration of how variable temperature impacts organism energetics, and to test the generality of our findings across species. This is especially important given climate forecasts of heat waves that are characterised by both increased temperatures and faster rates of change.

3.2. Introduction

A broad body of research exists examining the thermal sensitivity of metabolism and the importance of this relationship reaches into many branches of biology and ecology (Brown *et al.*,

2004). This relationship is particularly paramount for ectotherms as temperature directly affects many facets of their physiology such as metabolism, and performance, as their body temperatures reflect their environments (Angilletta, 2009). This is ever more important given that 99% of species on Earth are ectothermic (Ohlberger, 2013) and that climate change is increasingly altering global temperatures and patterns (Kefford *et al.*, 2022).

An extensive suite of studies have explored the thermal sensitivity of metabolism and revealed many persistent patterns and trends. Firstly, when modelling the increase in metabolic rate with increasing temperature seen in ectotherms, biologists and ecologists widely used an Arrhenius function (Gillooly *et al.*, 2001, Robinson *et al.*, 1983), an application promoted by Brown *et al.* (2004) in the metabolic theory of ecology (MTE). However, although this could be used to construct the thermal performance curve (Huey and Stevenson, 1979) for many biological rates, it began to receive criticism for its inability to fully account for the varying thermal sensitivity of metabolic rate and several other models have been proposed to describe this relationship (Arroyo *et al.*, 2022, DeLong *et al.*, 2017, Padfield *et al.*, 2021). A key component of focus in these models is the activation energy (E_a). Dell *et al.* (2011) showed overwhelming evidence that the mean activation energy for metabolic reactions is 0.65 eV, a value which holds true for the thermal responses of many biological traits. An E_a value of ≈ 0.65 eV corresponds to a Q_{10} value in the range of 2 - 3 (Dell *et al.*, 2011), indicating a doubling or tripling in metabolic rate with every 10°C change in temperature. This understanding of the thermal sensitivity of metabolic rate is widely used to model and predict high level processes such as predicting ecosystem level responses (Dillon *et al.*, 2010, Rubalcaba *et al.*, 2020), understanding species climate resilience (Vajedsamiei *et al.*, 2021) and predicting population growth under a changing climate (DeLong *et al.*, 2018, Stearns, 1992).

Although the thermal sensitivity of metabolism has been widely studied, research has primarily focused on static temperature experiences (i.e., estimating metabolic rate at a range of constant temperatures). However, temperature in nature rarely remains static and so examining metabolic responses under static thermal conditions may not be an accurate reflection of what is occurring in nature. Therefore, we need to better understand how the thermal sensitivity of metabolism varies when temperature is undergoing change. Understanding this is essential to informing predictive models of ectotherm responses to climate change induced temperature change (Dillon *et al.*, 2010).

Some previous studies have investigated the effect of dynamic and stable temperature regimes on metabolism of ectotherms (Lake *et al.*, 2013, Vasseur *et al.*, 2014, Williams *et al.*, 2012, Zhang *et al.*, 2015, Latournerié *et al.*, 2011, García-Guerrero *et al.*, 2011, Guzzo *et al.*, 2019, Killen *et al.*, 2017, Semsar-kazerouni and Verberk, 2018, Via, 1985). However, the dynamic temperature scenarios used typically involve stepwise temperature changes (i.e., as opposed to continuous rate

of increase or decrease) or oscillating temperature regimes (i.e., multiple increases and decreases in temperature over a period of time). The average metabolic rate of the entire exposure period is then estimated and directly compared to a stable temperature regime. This approach makes it difficult to understand the direct influence of heating or cooling rate on the thermal sensitivity of metabolism. To the best of our knowledge, there exists only one study which measured metabolic rate continually under continuous temperature change (Lake *et al.*, 2013), which found mixed results. There could be several reasons to expect rates of temperature change to influence the thermal sensitivity of metabolism, which have been raised previously. For example, (i) cost of acclimation may differ with rate of temperature change (Rohr *et al.*, 2018). Faster rates of change may incur additional energetic costs for ectotherms, as they are forced to acclimate to a new temperature environment over a shorter period of time; (ii) the balance between supply and demand of resources may be altered as animals operating at higher temperatures, with higher metabolic rates, demand more resources, but also have a greater capacity to supply resources (Gillooly *et al.*, 2006); and (iii) overall metabolic cost may be impacted by rate of temperature change, specifically increasing metabolic cost with slower rates of temperature change, everything else being equal (Rezende *et al.*, 2011).

In this study, we examined whether the rate of temperature change affects the thermal sensitivity of aerobic metabolism. We do this by conducting closed chamber respirometry on an aquatic ectotherm, the Atlantic ditch shrimp *Palaemonetes varians*, to estimate oxygen consumption under varying thermal conditions. Closed chamber respirometry (which measures gas exchange between an animal and its environment) is widely recognised as a valid proxy for measuring aerobic metabolic rate of aquatic ectotherms (Nelson, 2016, Killen *et al.*, 2017), as the rate of oxygen uptake from the environment is expected to relate stoichiometrically to ATP production rate via mitochondrial oxidative phosphorylation (Nelson, 2016, Killen *et al.*, 2021, Clarke and Fraser, 2004). Previous respirometry experiments on shrimps demonstrated that oxygen consumption generally increases with an increase in temperature; *Litopenaeus stylirostris* (Spanopoulos-Hernández *et al.*, 2005) and *Penaeus chinensis* (Chen and Nan, 1993). Furthermore, *P. varians* has been used in temperature studies in the past (Oliphant *et al.*, 2011, New *et al.*, 2014, Ravaux *et al.*, 2012, Cottin *et al.*, 2010, Nielsen and Hagerman, 1998, Palma *et al.*, 2009) making it a suitable study species.

3.3. Materials & Methods

Closed chamber respirometry was used to estimate the aerobic metabolic rate of *P. varians* by recording the rate of decline in dissolved oxygen (DO) concentration (mg l^{-1}) over time, under varying thermal conditions. Measurements were taken individually on 161 shrimp with 38 experiencing stable temperature, 67 experiencing heating and 56 experiencing cooling.

Palaemonetes varians (Leach, 1814) is a shallow water shrimp native to Western Europe (Ravaux *et al.*, 2012). *P. varians* is known to inhabit areas where the environmental temperature can seasonally fluctuate from 0°C – 33°C (Lofts, 1956, Jefferies, 1964, Healy, 1997, Oliphant *et al.*, 2011). They are known to typically inhabit brackish waters but have been found in very low salinities, including freshwater (Hagerman and Uglow, 1984). These shrimps are often used for fishing bait or as live feed for aquarium fish (Palma *et al.*, 2008a, Palma *et al.*, 2009, Palma *et al.*, 2008b). This species was chosen as it has previously served as a model species for temperature studies (Ravaux *et al.*, 2012), due to their adaptation strategies to temperature (Cottin *et al.*, 2010) and their capacity to tolerate periods of severe hypoxia (Hagerman and Uglow, 1984), tolerating low oxygen tensions before entering anaerobic respiration (Nielsen and Hagerman, 1998, Peruzza *et al.*, 2018).

3.3.1. Data collection

3.3.1.1. Acclimation phase

Animals for this experiment were sourced from a specialist aquarium stockist. They were transported in transparent, plastic bags filled with brackish water at approx. 18°C, with transport from source location to laboratory taking approx. 6 days. Upon delivery to the laboratory, animals were removed from the bags and placed in 5 large buckets. Prior to experimental treatments, animals were acclimated stepwise to the five desired acclimation temperatures (10°C, 12°C, 15°C, 18°C, 21°C) during a 24 hour period, using temperature-controlled buckets with a photoperiod of 12 h:12 h light:dark. Shrimp were not fed during this period. Shrimp were then transferred to their corresponding acclimation tanks and fed. The laboratory set up consisted of 5 aerated tanks (37 x 23.5 x 26 cm) filled with unfiltered, treated tap water (~0.5‰), in a room kept with a 12:12 light:dark phase. Tank water was treated with 'Organic Aqua Start Up' water treatment and water quality was maintained with weekly 'Organic Aqua Fish Care'. Temperature in the tanks was maintained at stable temperatures, controlled by programmable units (Inkbird ITC-310T-B; constant desired temperature \pm 1.0°C) and shrimp were kept at these stable acclimation temperatures for 2 – 30 days before experiments commenced. A minimum acclimation phase duration of 2 days was chosen in accordance with previous studies of a similar nature on similar (or the same) species (González-Ortegón *et al.*, 2013, Miller *et al.*, 2002, Berglund and Bengtsson, 1981, Nielsen and Hagerman, 1998). The shrimp were provided with flake fish food approximately every second day. Prior to respirometry, shrimp were fasted for a minimum of 12 hours (average fasting time for stable trials was 26 ± 11 hours and for heating/cooling trials was 23 ± 12 hours).

3.3.1.2. *Temperature trials*

For the stable measurements, DO concentration was recorded for 1 – 2 hours at 5 stable treatments corresponding to the acclimation treatments (i.e., 10°C, 12°C, 15°C, 18°C, 21°C). For the dynamic temperature treatments, DO concentration was measured under four thermal regimes: (i) heating from 15°C to 21°C, and (ii) 10°C to 21°C, and then cooling from (iii) 15°C to 10°C, and (iv) 21°C to 10°C, with starting and ending temperatures corresponding to acclimation temperatures. These regimes were repeated at four ramping rates (λ : 0.0083 °C min⁻¹, 0.0167 °C min⁻¹, 0.0833 °C min⁻¹, and 0.1667 °C min⁻¹) where temperature was increased or decreased continuously. Individual shrimps were removed from the acclimation tanks and placed in 200ml plastic chambers, filled with water taken from the acclimation tanks. The chambers were then partially submerged in temperature-controlled water baths. The temperature of the water baths was controlled by a programmable unit (Inkbird ITC-310T-B; desired temperature \pm 0.5°C). Shrimp were allowed to settle in the chambers for 1 - 2 hours before commencing measurements, to allow them to recover from handling during transfer. Once settled, a lid was placed on the chamber, a dissolved oxygen probe (Go Direct® Optical Dissolved Oxygen Probe) was inserted through an opening in the top of the lid and the chamber was hermetically sealed. Probes were 100% calibrated before the beginning of each experimental phase following the manufacturer calibration procedure. Probes began recording as soon as the chamber was sealed, measuring DO concentration (mg l⁻¹), DO saturation (%), and temperature (°C) continuously. Sampling frequency of the probe was varied between temperature treatments due to probe memory limitations; when conducting experiments at λ = 0.0083, 0.0167, 0.0833, and 0.1667 °C min⁻¹, probes recorded at a frequency of 0.2, 0.5, 1, and 1 sample min⁻¹ respectively. All experiments were conducted during the photophase, on shrimp that had not been fed for 12 or more hours (for more details on acclimation & feeding times see Supp. Info. **Table B.2**). Individual shrimps were measured alongside 'control' chambers (chambers containing tank water but no shrimp), in order to record bacterial respiration and later correct the DO concentration data. Chambers were visually shielded from external disturbance during respirometry by the high, opaque walls on the water baths. Following data collection shrimp were euthanised by submersion in 90% ethanol, blotted dry and weighed (recording wet weight \pm 0.001g). Chambers were cleaned with 90% ethanol between all experiments to reduce bacterial growth within.

Animal ethics approval for all works was sought from and approved by Trinity College Dublin School of Natural Sciences (SNS) Research Ethics Committee (project number "2021-06 (revised)").

3.3.2. Data analyses

Several animals were removed from the analysis phase due to varying reasons; (i) 105T1021R5 was removed as it was found to have lost the ability to right itself at the end of the experiment, (ii) 28T2110R1 & 13T1021R0.5 died during the experiment, (iii) 37T2110R0.5 & 38T2110R0.5 had too short of a fasting period (5.5 hours), (iv) 122T1521R1 timer was set incorrectly. This resulted in a total of 117 ramping treatments and 38 stable treatments for use in the data analysis phase.

All animals were recorded concurrently with control “blank” chambers, containing water from the same source but no shrimp, in order to remove the effect of background (bacterial) respiration. A linear regression was fitted to the DO concentration of each blank chamber. The DO concentration for each animal was then corrected by subtracting the negative slope of the blank chamber from the slope of the DO concentration raw data (DO_{animal}), such that

$$DO_{\text{corrected}} = DO_{\text{animal}} - (-\text{slope}_{\text{background respiration}})$$

As this study used closed chamber respirometry, over periods of up to several hours, the potential occurrence of hypoxic conditions within the chamber required consideration. González-Ortegón *et al.* (2013) defined hypoxia for *P. varians* (and 5 other shrimp species) to be $DO \leq 3 \text{ mg O}_2 \text{ l}^{-1}$ and Berglund and Bengtsson (1981) noted hypoxia occurring $\leq 3 \text{ mg O}_2 \text{ l}^{-1}$ for *Palaemon adspersus*, a close relative of *P. varians* (Hagerman and Uglow, 1984). Therefore, a hypoxia threshold of $3 \text{ mg O}_2 \text{ l}^{-1}$ was used for this experiment. When this threshold was reached in a chamber, the experiment was ended; this occurred in 8 trials (49T1521R0.5, 50T1521R0.5, 52T1521R1, 54T1521R1, 62T1021R0.5, 74T2110R0.5, 78T2110R1, 97T1021R0.5).

3.3.2.1. Modelling

Average metabolic rate (MO_2) was estimated for each animal held at one of the five stable temperature treatments. MO_2 was estimated following the methods of Svendsen *et al.* (2016), by fitting a linear model to all individual DO concentration data, extracting the slope (m) of this line and then correcting for ‘effective volume’ (volume of the chamber – volume of the animal). To avoid difficulties in measuring the volume of the animal, it is common practice to instead subtract the mass of the animal (in kg) from the volume of the chamber (in litres) (Svendsen *et al.*, 2016), as shrimp were assumed to be neutrally buoyant in water so densities are assumed equivalent and equal to 1. Metabolic estimates were also mass controlled and allometrically scaled (coefficient = 0.8; Christensen *et al.* (2020)):

$$MO_2 = (V_{\text{eff}}) \left(\frac{1}{\text{mass}^{0.8}} \right) (m)$$

where MO_2 is the metabolic rate in $\text{mg O}_2 \text{ min}^{-1} \text{ kg}^{-1}$, V_{eff} is the 'effective volume', mass is in kg, and m is the slope of the line of DO concentration vs time. These MO_2 values were then plotted against average temperature and a thermal performance curve (TPC) fitted using the 'rTPC' R package (Padfield and O'Sullivan, 2021). Several models were chosen for fitting based on their ecological applicability to data of this kind and the AICc score (used for small sample size, $n = 37$) calculated (Supp. Info. **Table B.1**) and used for model selection, based on the lowest AICc score. The "Rezende" model (Rezende and Bozinovic, 2019) gave the lowest AICc score and so was chosen for use. Total performance pf is calculated using the full model:

$$pf = \begin{cases} \left(Ce^{\frac{T \ln Q_{10}}{10}} \right) & \text{if } T < T_{th} \\ \left(Ce^{\frac{T \ln Q_{10}}{10}} \right) \times (1 - d(T - T_{th})^2) & \text{if } T > T_{th} \end{cases}$$

where Q_{10} defines the fold change in performance as a result of increasing the temperature by 10°C , d is a constant controlling the rate of decay from threshold temperature T_{th} upwards and Ce is the rate of dissolved oxygen decline in this scenario.

This TPC curve was used to predict the total oxygen consumption (mg O_2) for animals which experienced heating or cooling with bounds set as the starting (T_1) and ending temperatures (T_2) for each individual:

$$\int_{T_2}^{T_1} pf = \begin{cases} \left(Ce^{\frac{T \ln Q_{10}}{10}} \right) & \text{if } T < T_{th} \\ \left(Ce^{\frac{T \ln Q_{10}}{10}} \right) \times (1 - d(T - T_{th})^2) & \text{if } T > T_{th} \end{cases}$$

The relationship between predicted and observed total O_2 consumption was investigated to see if the stable temperature trials could be used to predict how much oxygen animals would consume in comparable thermal ranges but under differing rates and directions of temperature change. To do this the area under the curve was calculated by numerical integration using the 'integrate' function in R (Piessens *et al.*, 2011), with upper and lower limits set to the start and end temperature of each individual ramping trial. This integral was then converted to total predicted oxygen consumption (mg) by incorporating duration of the trial and mass of the organism using the following equation:

$$\text{Total predicted } O_2 \text{ consumption} = \frac{\text{integral}}{\lambda} (\text{mass}^{0.8})$$

where λ is the rate of temperature change and mass in kg. These predicted values were then plotted against the recorded (or observed) total oxygen consumption. Observed total oxygen consumption was calculated, using the recorded DO concentration data, by subtracting the average of the last 5 DO concentration values from the average of the first 5 DO concentration values and dividing by

the effective volume. These data were log transformed (to overcome the effect of larger O₂ measurements being prone to wider uncertainties) and plotted against each other.

In order to further investigate any potential effect of direction of temperature change the residuals of the previous plot were calculated (i.e., log of observed O₂ consumption minus log of predicted O₂ consumption) and the relationship between these residuals and λ was investigated. A breakpoint regression was fit, using Bayesian inference, using the 'JAGS' R package (Plummer *et al.*, 2022).

3.4. Results

In total 155 datasets were analysed: 64 heating trials, 53 cooling trials and 38 stable trials, with shrimp wet weight ranging 0.048 – 0.295 g (Supp. Info. **Table B.2**). We found that the relationship between metabolic rate (MO₂) and average temperature was best described by a thermal performance curve (**Figure 3.1**), specifically that modelled by Rezende and Bozinovic (2019) as it gave the lowest AICc score of 76.83 compared with the second lowest Pavar model AIC 77.295 (Supp. Info. **Table B.1**). This Rezende model yielded estimates of 3.03, 0.26, 17.93, and 0.05 for q_{10} , C_e , T_{th} , and d respectively.

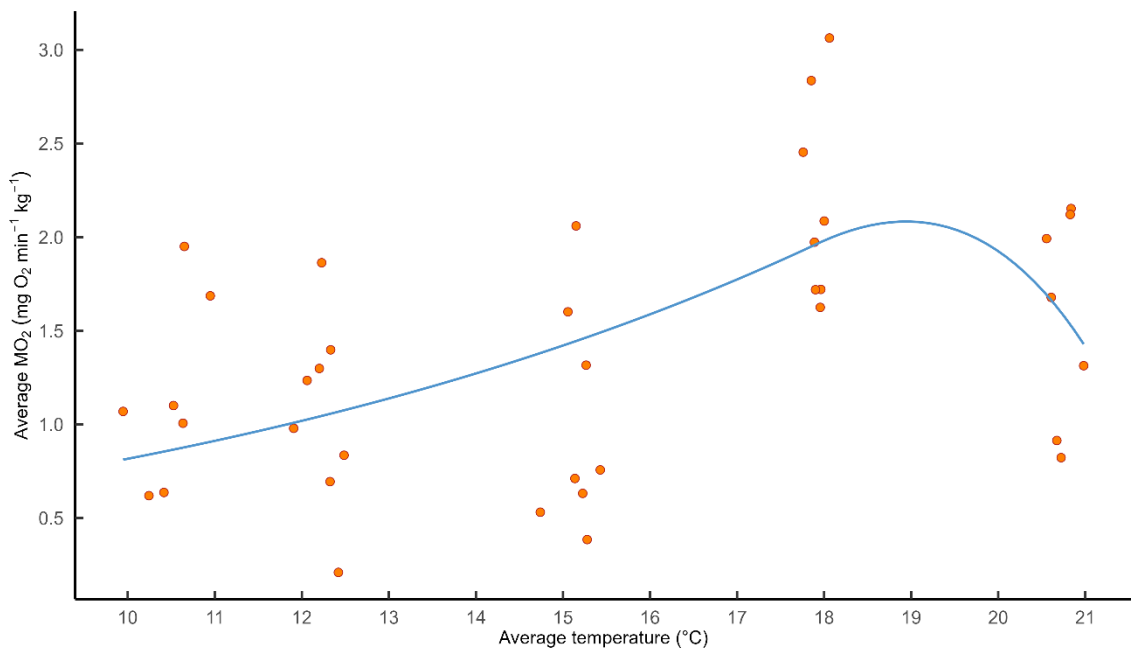


Figure 3.1: Average MO₂ (mg O₂ min⁻¹ kg⁻¹), for the duration of the trial, against average temperature (°C) for all stable temperature individuals, with thermal performance curve fitted, following the method of Rezende and Bozinovic (2019).

By integrating under this curve, total predicted oxygen consumption (mg O₂) was calculated for each individual which underwent heating or cooling (**Figure 3.2**). Three individuals (82T2110R10, 84T2110R10, 36T2110R10) were excluded from this analysis as they showed near zero O₂

consumption (-0.005, -0.02, -0.008 mg respectively), likely due to the fast cooling rate ($\lambda = 0.16 \text{ }^\circ\text{C min}^{-1}$) and short duration of exposure (approx. 60 mins).

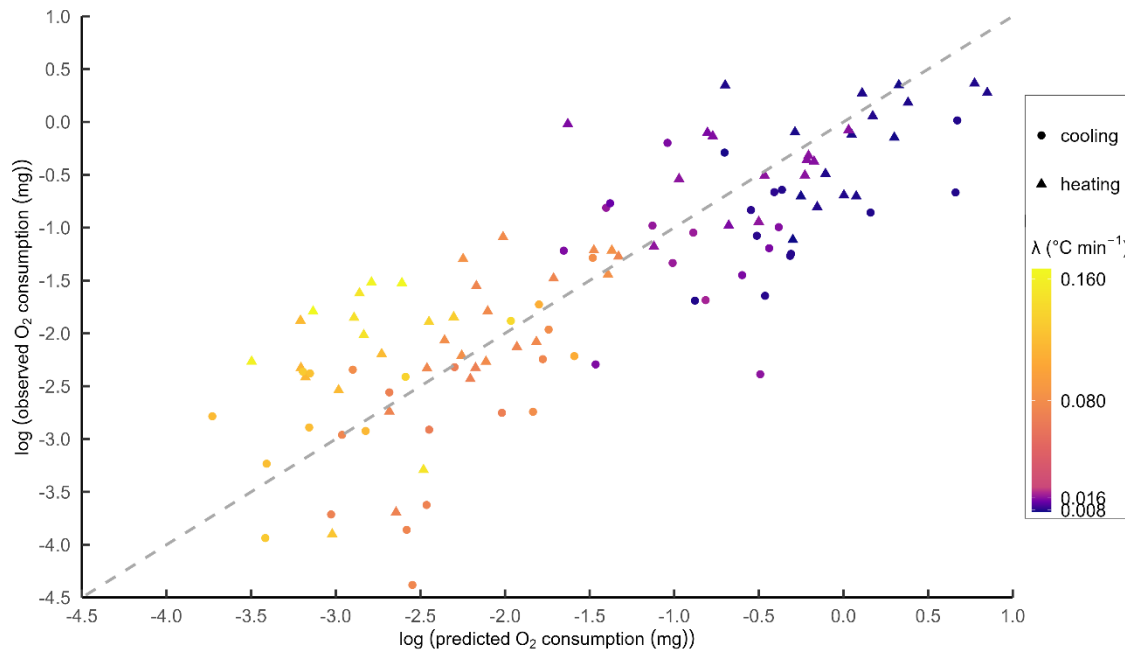


Figure 3.2: Log observed vs predicted O_2 consumption (mg) for each ramping individual, with points coloured by rate of temperature change ($\lambda \text{ }^\circ\text{C min}^{-1}$) and symbols indicating if the temperature was heating (triangle) or cooling (circle). The 1:1 (grey dashed) line indicates where we would expect the points to lie along if the stable treatments perfectly predicted the ramping trial O_2 consumption.

We see that generally the points are clustering along the 1:1 line (**Figure 3.2** grey dashed line), indicating that the stable temperature trials predict total oxygen consumption for the dynamic temperature trials. However, any potential effect of direction of temperature change is unclear. Therefore, the residuals of this were calculated (log of observed O_2 consumption minus log of predicted O_2 consumption) and the relationship between the residuals and λ investigated (**Figure 3.3**). The breakpoint regression was fit with one breakpoint forced through $\lambda = 0$ as all points greater than 0 related to heating trails and all points less than 0 related to cooling trails.

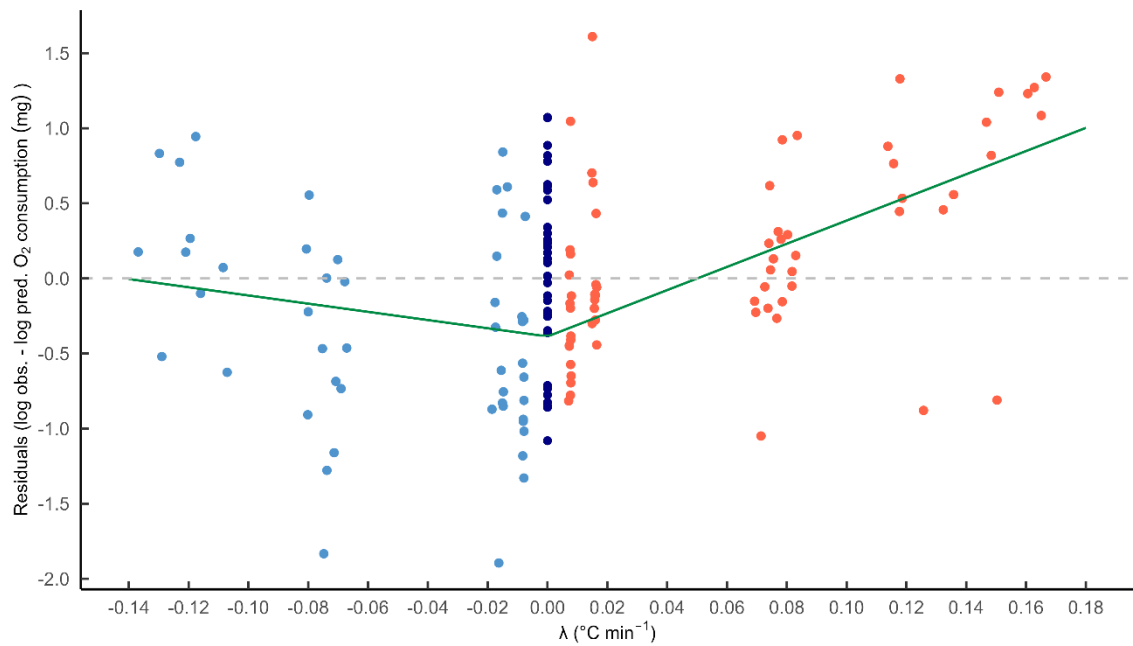


Figure 3.3: Residuals (i.e., log of observed O₂ consumption minus log of predicted O₂ consumption) against rate of temperature change (λ °C min⁻¹). Breakpoint regression line fitted (green line). Red points indicate heating trials and blue points indicate cooling trials. The residuals of the stable trials were calculated and overlaid (navy points). A 1:1 identity line is included (grey dashed line).

Figure 3.3 reveals that faster rates of heating and cooling tend to increase total oxygen consumption. However, there appears a weaker influence of rate of cooling than rate of warming on total oxygen consumption: the slope of the heating data and cooling data are significantly greater than zero ($\text{slope}_{\text{heating}} = 7.71$, $P(\text{slope} > 0) = 1.00$ for heating, and $\text{slope}_{\text{cooling}} = -2.73$, $P(\text{slope} < 0) = 0.96$ for cooling data) with cooling rate having a weaker influence on total oxygen consumption than heating rate.

Furthermore, as temperature increases more rapidly there is an increasing rate of oxygen consumption (as the regression line crosses the grey dashed line, with a continual positive slope). Additionally, animals consumed less oxygen when experiencing slow rates of temperature change, than when they were experiencing no change in temperature (evident in the heating and cooling datapoints, from $\lambda = -0.02 - 0.02$). By examining this relationship, between the residuals and λ , it is evident that at slower rates the stable temperature trials will tend to underestimate oxygen consumption of the dynamic temperature trials, and at faster rates the predictions will be overestimated.

3.5. Discussion

We show that the rate of temperature change has a systematic effect on the oxygen consumption of ectotherms. Perhaps most compellingly, we find that as temperature increases more rapidly, the rate of oxygen consumption increases and that the rate of cooling had less of an influence on the rate of oxygen consumption than the rate of warming. We also see that at slower

rates of temperature change the animals consumed less oxygen than when they were experiencing no change in temperature (i.e., stable temperature). These findings are somewhat surprising as previous literature indicates that dynamic or variable temperature environments are more energetically costly to ectotherms than stable environments (Morón Lugo *et al.*, 2020, Williams *et al.*, 2012), following Jensen's inequality (Ruel and Ayres, 1999) and that metabolic costs increase with decreasing heating rate, likely due to extended exposure duration (Rezende *et al.*, 2011, Chown *et al.*, 2009). However, these differing findings, may be related to Q_{10} values. Chown *et al.* (2009) assume a constant Q_{10} value throughout the temperature change, but "*a thermodynamically correct expression for Q_{10} shows it is a function of and changes with temperature*" (Rezende *et al.*, 2011, Gillooly *et al.*, 2001).

So why might we be seeing these higher metabolic costs at faster rates of temperature change? Previous studies have shown that accumulated metabolic costs of individuals under different ramping regimes are not equal and animals undergoing slower rates of temperature change may be undergoing acclimation, due to the associated longer exposure durations (Rezende *et al.*, 2011). Acclimation capacity may be allowing the animals to cope with the increased temperature (Vasseur *et al.*, 2014, Rohr *et al.*, 2018) and to down-regulate the increase in metabolism. Furthermore, the longer experiments (i.e., those with the slowest rates of temperature change) may be providing enough time for hardening to occur, a form of phenotypic plasticity (Hoffmann *et al.*, 2003) that protects cells from subsequent injury (Overgaard *et al.*, 2006). Another potential explanation could be that there may be a mismatch between metabolic supply and demand as the temperature increases and the rate of temperature change increases. This could result in "*internal entropy, stress and damage*", resulting in negative implications for performance over time (Vajedsamiei *et al.*, 2021, Pörtner, 2012, Ritchie, 2018).

To the best of our knowledge, there exists only one study which measures metabolic rate continually under continuous temperature change; Lake *et al.* (2013) carried out closed chamber respirometry on insects experiencing dynamic temperature change. Our study was conducted in a similar manner to that of Lake *et al.* (2013), who found that although estimates of thermal sensitivity of metabolism did not differ significantly between dynamic and stable treatments, absolute estimates of metabolic rate were higher under dynamic thermal conditions than stable, specifically they found that estimated oxygen consumption during cooling at a rate of $0.1^{\circ}\text{C min}^{-1}$ is significantly higher than stable temperature treatments. This finding however only occurred in the group of animals that had undergone repeated respirometry and did not occur in animals that were only tested once (as is the case with our study). This discrepancy led them to suggest that rate and direction of temperature changes effect on metabolic rate is an aspect that needs to be considered when extrapolating from laboratory studies to the field. At least in a broad sense, our findings

concur with those of Lake *et al.* (2013) and confirm that rate of temperature change does have an effect on metabolic rate.

A major consideration we acknowledge is the potential for a lag between the water temperature and the body temperature of the animals, and so to counteract this we intentionally selected a small-bodied aquatic animal (with body wet weight ranging 0.048 – 0.295 g), therefore increasing the potential for a large heat transfer coefficient and reducing the lag between body and water temperature. Notwithstanding this, should there have been a small lag present during our experiment, this would only increase the effect we show as it would mean that the higher metabolic rates are occurring at even slower rates of heating and cooling, as the body would heat and cool slower than the water, thereby increasing the slope of the heating and cooling relationships seen in **Figure 3.3**, meaning that the effect of λ is even more significant.

If the dependence of metabolism on heating rate that we document proves to be a general phenomenon seen across species, this would have implications for how we predict ectotherm responses to climate change. The magnitude, duration, and frequency of extreme thermal events (i.e., heat waves) is predicted to increase (Coumou and Rahmstorf, 2012, Kefford *et al.*, 2022) and ectotherms are likely more vulnerable to changing temperatures as their body temperature follows that of their environment (Åsheim *et al.*, 2020, Angilletta, 2009). With heatwaves increasing in frequency and intensity (Minuti *et al.*, 2021, Perkins *et al.*, 2012) our findings indicate that perhaps heat waves with faster rates of heating may be more costly to the animals than slower heat waves, even if they ultimately reach the same maximum temperature. This study is an important step in providing data on ectotherms capacity to adapt to change, through experimental manipulations, and feeding this into mechanistic models for predicting ectotherm responses to climate change.

To summarise, we show evidence that faster temperature changes are more energetically costly for ectotherms and rapid cooling is less costly than rapid heating. Along with another study (Lake *et al.*, 2013) that showed metabolic rate to vary with rates of temperature change, our results suggest a systematic influence of temperature change on energetics and encourage future work to determine the generality of this finding across species.

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4. Chapter 4 Capture heats up sharks

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Author contribution: L.H. and N.P. conceived the ideas and designed methodology; L.H., A.G., J.B., H.R.D., B.S., L.Harman, D.E., and N.P. collected the data; L.H., A.J. and N.P. designed the analysis and L.H. analysed the data; L.H. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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4.1. Abstract

Catch-and-release fishing is an important component of ecotourism industries and scientific research worldwide, but its total impact on animal physiology, health and survival is understudied for many species of fishes, particularly sharks. We combined biologging and blood biochemistry to explore how this fisheries interaction influenced the physiology of two widely distributed, highly migratory shark species: the blue shark (*Prionace glauca*), and the tiger shark (*Galeocerdo cuvier*). Nineteen sharks were caught by drum line or rod-and-reel angling; subcutaneous body temperature measurements were taken immediately upon capture, with 6 individuals also providing subsequent subcutaneous body temperature measurements via biologging as they swam freely for several hours post-release. We found that short-term capture caused shark body temperature to increase significantly and rapidly, with increases of 0.6 – 2.7°C for blue sharks (mean $1.2 \pm 0.6^\circ\text{C}$) and 0.5 – 0.9°C for tiger sharks (mean $0.7 \pm 0.2^\circ\text{C}$), and with capture-induced heating rates of blue sharks averaging $0.3^\circ\text{C min}^{-1}$ but as high as $0.8^\circ\text{C min}^{-1}$. Blue shark body temperature was even higher deeper into the white muscle. These heating rates were 3 - 8 times faster than maximum rates encountered by our biologging sharks swimming through thermally stratified waters, and faster than most acute heating experiments conducted with ectotherms in laboratory experiments. Biologging data showed that body temperatures underwent gradual decline after release, returning to match water temperatures approximately 10 – 40 mins post-release. Blood biochemistry showed variable lactate/glucose levels following capture; however, these concentrations were not correlated with the magnitude of body temperature increase, nor with body size or hooking time. These perturbations of the natural state could have immediate and longer-term effects on the welfare and ecology of sharks caught in catch-and-release fisheries and we encourage further study of the broader implications of this reported phenomenon.

4.2. Introduction

Catch-and-release fishing is a popular practice in recreational fisheries (Brownscombe *et al.*, 2017, Danylchuk *et al.*, 2014, Cooke and Schramm, 2007), and is often used in scientific research (Wosnick *et al.*, 2018), in particular tagging studies (Harding *et al.*, 2021, Royer *et al.*, 2020, Watanabe *et al.*, 2015). Catch-and-release can also occur on commercial fishing vessels where it has been estimated that approx. 9.1 million tonnes of non-target fish per year globally are caught and released in commercial fisheries (Sepulveda *et al.*, 2019, Gilman *et al.*, 2020). Numerous studies have investigated the physiological and ecological impacts of catch-and-release fishing on teleosts and elasmobranchs (Gale *et al.*, 2013, Mohan *et al.*, 2020, Sepulveda *et al.*, 2019, Gallagher *et al.*, 2019, Jerome *et al.*, 2017, Schlenker *et al.*, 2016, Gallagher *et al.*, 2014, Cooke *et al.*, 2013, Cooke and Schramm, 2007). Catch-and-release fishing is considered a multi-stressor interaction for individuals (Gale *et al.*, 2013), with the negative impacts broadly categorised as lethal or sub-lethal, with potential sub-lethal impacts including altered blood chemistry (Dapp *et al.*, 2016, Gallagher *et al.*, 2014), behavioural impairments (Raoult *et al.*, 2019), reduced growth and reproductive rates, and increased disease vulnerability (Gale *et al.*, 2013). Fish can experience oxygen deprivation (Schwieterman *et al.*, 2021), handling-related injuries (Cooke *et al.*, 2013, French *et al.*, 2015), and heat stress (Wosnick *et al.*, 2019, Wosnick *et al.*, 2018).

Many studies investigating the impacts of catch-and-release fishing have highlighted the potential importance of temperature in these interactions (Gale *et al.*, 2013, Schwieterman *et al.*, 2021, Bouyoucos *et al.*, 2018, Meka and McCormick, 2005, Schlenker *et al.*, 2016), whereby water temperature (T_a) can have a significant effect on post-release survival and a variety of sublethal impacts (Gale *et al.*, 2013). Furthermore, body temperature (T_b) is considered an important parameter when assessing an individual's response to stress, their metabolic rate, and their energy budgets, all of which may be affected by catch-and-release interactions. However, few studies have measured fish body temperatures during catch-and-release. Measurements of muscle temperature are especially rare, and while two recent studies have inferred surface temperature of sharks' post-capture using thermal imaging of shark skin (Wosnick *et al.*, 2018, Wosnick *et al.*, 2019), reflectance issues and effects of varying sun and water exposure likely complicate estimates of true operative body temperatures. Sharks are relatively large-bodied fishes with low heat-transfer coefficients (Nakamura *et al.*, 2020) so capture-induced heating could be a particularly relevant issue for them.

When hooked, sharks often exhibit intensive swimming acceleration (Gallagher *et al.*, 2017), and periods of exhaustive exercise (i.e., anaerobic exercise) (Schwieterman *et al.*, 2021), as they attempt to escape. Capture-related exercise and the resulting physiological stress can elevate the metabolic rate (Mohan *et al.*, 2020, Kieffer, 2000) resulting in, among other things, the generation of heat. Furthermore, fish are known to dissipate heat across the gill surface during

respiration (Stevens, 2011, Stevens and Fry, 1974, Nakamura *et al.*, 2020) and so during the period of fighting on the hook, these animals may be unable to swim freely which could provide a mechanism for reduction in heat loss. This excess heat may manifest as an elevation of body temperature in these animals and thus, this study aims to investigate this relationship and determine the extent to which sharks heat up when captured.

In addition to altered thermal dynamics, hooked fish may undergo altered blood biochemistry as a result of the event (Gallagher *et al.*, 2014, Dapp *et al.*, 2016, Schwieterman *et al.*, 2021, Mohan *et al.*, 2020). Capture can often result in hyperkalemia, metabolic and respiratory acidosis (Schwieterman *et al.*, 2021), and declines in blood oxygen concentration, as a result of the often exhaustive exercise and apneic asphyxia associated with capture (Schwieterman *et al.*, 2021). Lactate and glucose are two metabolites widely examined in studies investigating stress in sharks (Gallagher *et al.*, 2017, Gallagher *et al.*, 2014, Mandelman and Skomal, 2008, Hoffmayer and Parsons, 2001, Cliff and Thurman, 1984). Lactate is a metabolite that is produced anaerobically in the white muscle during exhaustive exercise (Moyes *et al.*, 2006). Glucose is measured as a proxy for the glucocorticoid hormone stress response whereby hepatic glycogen is converted to glucose during gluconeogenesis and released to fuel muscle tissues (Prohaska *et al.*, 2021, Hoffmayer and Parsons, 2001). Body temperature, and lactate and glucose are both key elements of metabolic processes. Therefore, by combining our investigations into the body temperature measurements with the blood biochemistry data we can explore how the two might be related during catch-and-release events.

4.3. Materials & Methods

4.3.1. Data collection

To properly evaluate body temperature dynamics in captured marine predatory fishes we incorporated all phases of the capture and release interaction, from moment of hooking to several hours post-release.

4.3.1.1. Biologging

We used biologging technology to collect fine-scale, physiological measurements from individuals free-swimming in the wild. Fishing was conducted across three locations: the Bahamas in May 2019, Cape Cod, U.S.A. in September 2019 and Co. Cork, Ireland in July - October 2021. We captured tiger sharks by drum lines and blue sharks by rod-and-reel angling. Tiger sharks were secured alongside the boat (remaining submerged during the procedure) and blue sharks were brought on deck with a deck hose placed in the mouth to constantly irrigate the gills with water taken from the ocean surface. Biologging packages were fitted to the first dorsal fin of four tiger

sharks (*Galeocerdo cuvier*), and two blue sharks (*Prionace glauca*) (**Table C.1**), which were then immediately released. A plastic cable was passed through two 1 cm incisions made in the dorsal fin, which was connected to a dissolvable time-release mechanism which secured the package to the fin. Biologging packages included a mixture of loggers such as accelerometers (recording tri-axial acceleration at 25Hz and depth at 1Hz; Techno-Smart AGM-1; 67 mm x 42 mm x 19 mm), animal-borne digital cameras (recording at 30 fps; Little Leonardo DVL400M065; 61 mm x 21 mm x 15 mm; 29 g in air; 4 x red LED lights), and temperature loggers (recording ambient and body temperature at 1Hz; Lotek LAT 1810; 11 x 38 mm, 7.6 g in air, & Wildlife Computers Mk9; 72 x 17 x 17mm, 34 g in air). Body temperature was measured via a sensor stalk inserted 4 – 8 cm into the dorsal musculature of the shark, adjacent to the dorsal fin. To enable retrieval tag packages also included a VHF transmitter (Advanced Telemetry Systems, MM100), and satellite position only tag (Wildlife Computers Model 258; ARGOS enabled). Once the time-release mechanism dissolved, the package detached from the fish and floated to the surface, as they were constructed of a positively buoyant material (Diab Syntactic © non-compressible foam). Packages were then located using the ARGOS system and a VHF receiver and retrieved from the ocean surface by boat. A total of 4 tiger sharks (ranging 155.7 – 206 kg body mass) and 2 blue sharks (ranging 25.4 – 30.7 kg body mass) were tagged.

4.3.1.2. *Additional body temperature measurements of blue sharks*

In addition to the biologging work, we collected body temperature measurements from 13 additional blue sharks, from the moment they were landed on deck, until the moment before release (**Table C.1**). Temperature probes were fitted to the sharks using the same method as the biologging. The temperature probe was left in place while a work-up was completed on the shark (e.g., recording biometrics, collecting blood samples, etc). Once the work-up was completed, the temperature probe was removed from the muscle and the shark released. Water temperature was recorded by subsequently placing the temperature logger in the surface water for approx. 2 mins. Additionally, secondary body temperature measurements were taken from 4 of these 12 sharks (i.e., BS32 – BS35) to generate a thermal profile of the shark's musculature. To do this, the temperature probe was inserted at a depth of 2 cm into the dorsomusculature, approx. 20 cm more anterior and closer to the gills than the first probe, left for 1 – 2 mins, pushed a further 2 cm into the dorsomusculature (to measure body temperature at 4 cm depth) and left for the remaining period of time that the shark was held on deck. The probe was then removed from the shark prior to release.

4.3.1.3. *Caudal peduncle blood sampling*

For 14 blue sharks, two blood samples were collected from the caudal peduncle using an 18-gauge needle: one immediately upon capture and one the moment before release (approximately

10 mins later), corresponding with the timing of insertion and removal of the temperature stalk. The time of collection was recorded, and the samples processed for lactate and glucose immediately after collection on deck, using a HaB direct Lactate Pro™ 2 lactate meter (HaB Direct, 2021) and Accu-Chek Performa blood glucose meter (Accu-Chek, 2021) respectively. A number of lactate/glucose readings could not be recorded due to logistical constraints and/or user error.

4.3.1.4. Ethics

All works carried out in Ireland were conducted under The Health Products Regulatory Authority (HPRA) Project Authorisation (AE19136/P127). All works carried out outside of Ireland were conducted under local licensing, obtained by Beneath the Waves.

4.3.2. Data analyses

Data handling and statistical analyses were carried out in R Version 4.0.3 (R Core Team, 2020), and IGOR Pro 8 (WaveMetrics, 2020) with Ethographer package (Sakamoto *et al.*, 2009). Time-series analyses were conducted on all biologging data with a focus on the body temperature, water temperature and depth data. A 500-point moving average smoother was applied to the temperature and depth data when plotting the time series (**Figure 4.4**).

Upon capture – meaning the moment individuals were landed on deck or secured alongside the boat – the metric ‘ ΔT ’ was calculated as the difference between body temperature T_b and water temperature T_a . The total ‘hooking time’ for each blue shark was calculated (i.e., the time from when the shark was hooked, to when it was brought on deck). Hooking time could not be calculated for the tiger sharks as they were caught using drum lines. Body mass was estimated for each individual using the length-weight relationship $W = aL^b$ where W is weight/body mass (kg), L is fork length (cm), and a & b are published, species-specific coefficients with $a = 3.184 \times 10^{-6}$ & $b = 3.1313$ for blue sharks and $a = 2.528 \times 10^{-6}$ & $b = 3.2603$ for tiger sharks (Kohler *et al.*, 1996).

Multiple gaussian generalised linear models were conducted to investigate potential relationships between ΔT and hooking time, body mass, lactate concentration, and glucose concentration (**Table C.2**). Initial and subsequent lactate and glucose concentrations were compared to investigate potential lags in stress biomarker elevations following capture.

4.4. Results

A total of 19 sharks were caught: 4 tiger sharks and 15 blue sharks. Biologging data were collected from 6 of these individuals (4 tiger sharks and 2 blue sharks), and blood samples were taken from 14 blue sharks and no tiger sharks (**Table C.1**). Subsequently, one individual (tiger shark, T2) was excluded from all analyses as it was found to exhibit faulty biologging data.

At the moment of capture, all sharks across both species exhibited elevated T_b relative to T_a (**Figure 4.1 A & B**), with elevations ranging from 0.6 – 2.7°C for blue sharks (mean \pm SD = 1.2 \pm 0.6°C) and 0.5 – 0.9°C for tiger sharks (mean \pm SD = 0.7 \pm 0.2°C) (**Table C.1**).

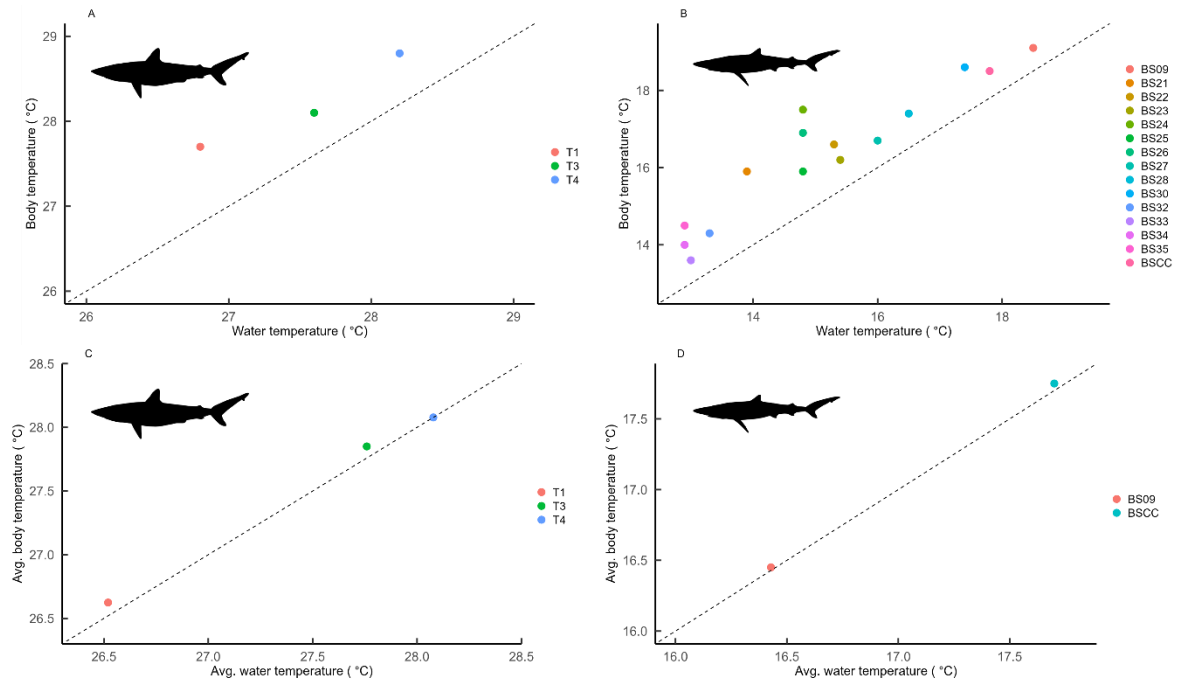


Figure 4.1: Body temperature elevation of tiger sharks and blue sharks recorded immediately upon capture (panels A & B), and average elevation of body temperature, during a 30-minute period under natural conditions several hours after release (panels C & D). Dashed black lines indicate a 1:1 identity line. [Blue shark image created by Ignacio Contreras and reproduced under the Creative Commons Attribution 3.0 Unported license: <https://creativecommons.org/licenses/by/3.0/legalcode>].

This elevation in temperature occurred over short periods of time (i.e., hooking time) which ranged from 1.4 – 13 mins for blue sharks ($n = 15$), indicating that warming occurred at an estimated rate of 0.1 – 0.8 $^{\circ}\text{C min}^{-1}$ (mean \pm SD = 0.3 \pm 0.23 $^{\circ}\text{C min}^{-1}$). These warming rates were unusually high when compared with the post-release data taken from biologged blue sharks BS09 & BS35 (**Figure 4.2**). Free-swimming blue sharks rarely exhibited heating rates greater than 0.1 $^{\circ}\text{C min}^{-1}$ (**Figure 4.2**).

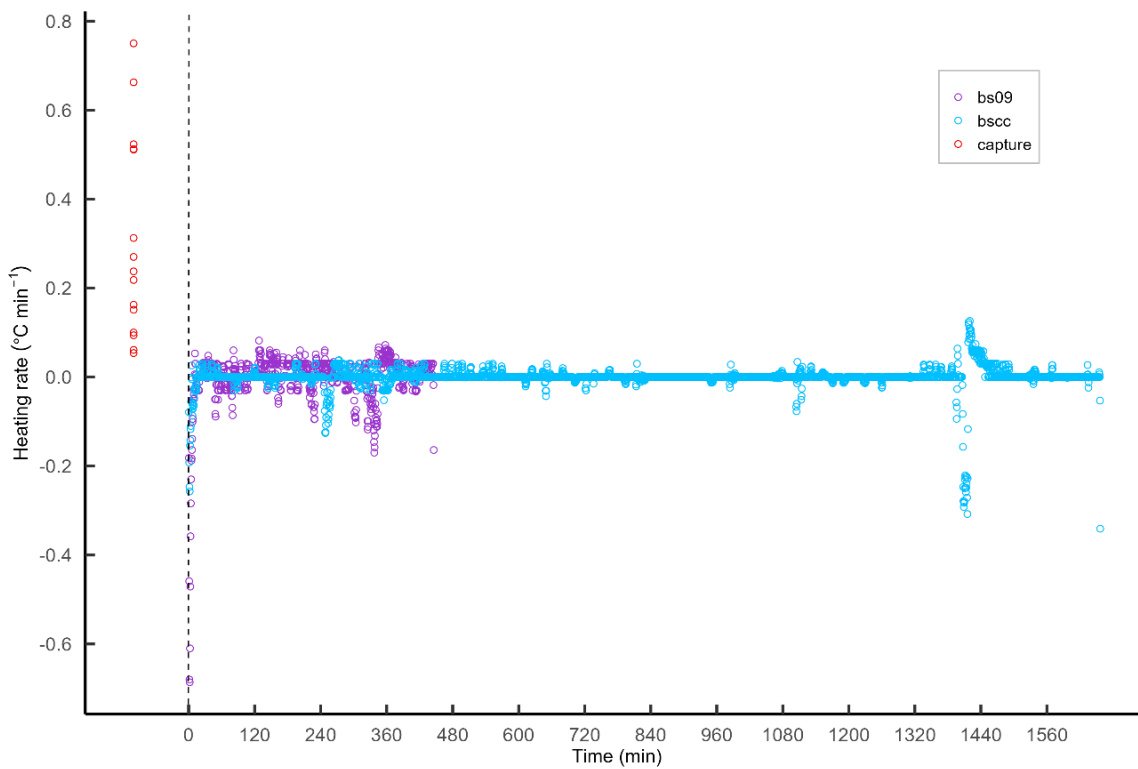


Figure 4.2: Average heating rate ($^{\circ}\text{C min}^{-1}$) for each blue shark during capture period (red circles; $n = 15$) and average heating rate every 30 sec for two biologged blue sharks (BSCC & BS09) during post-release phase ($n=4205$). Capture datapoints (red circles) are placed arbitrarily to left of x-axis to illustrate their collection before the beginning of the time series post-release.

The additional body temperature measurements taken from individuals BS32 – BS35 revealed a further increase in body temperature, the deeper the temperature probe was inserted, with the difference between readings at 2 cm penetration and 4 cm penetration ranging from $0.20 - 0.45^{\circ}\text{C}$ (Figure 4.3).

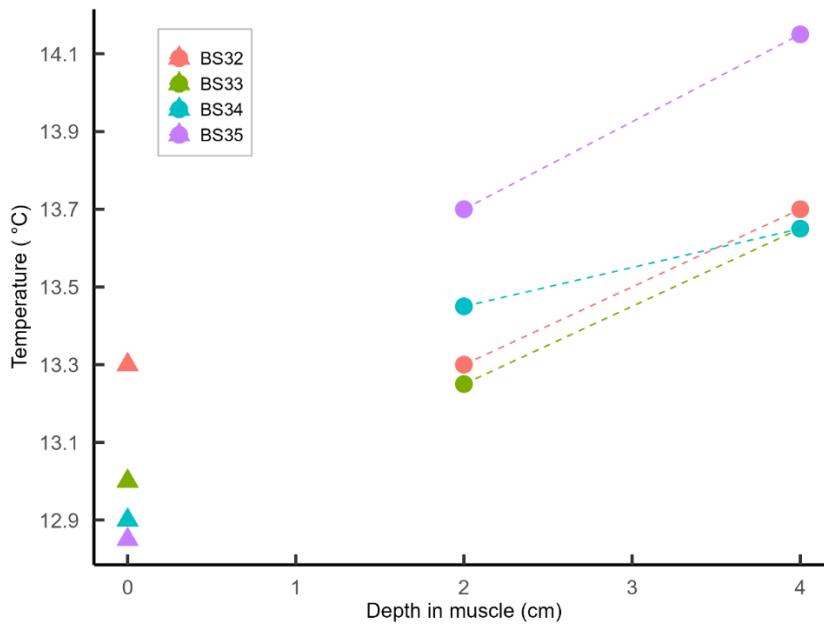


Figure 4.3: Water temperature measurements (triangles) and body temperature measurements (circles) taken at 2cm and 4cm penetration into the dorsal musculature of 4 blue sharks.

The relationship between water temperature and muscle temperature at 4cm depth was approximately linear despite a somewhat variable relationship between water temperature and shallow muscle temperature (**Figure 4.3**), perhaps representing an uncertainty as to what depth and therefore temperature these sharks were initially hooked at. For all sharks equipped with biologging packages and subsequently released, following the initial elevation of T_b upon capture, T_b underwent a gradual decline, over the first 30 mins for tiger sharks and 15 mins for blue sharks, before returning to match water temperature. During this period of body temperature decline, there was no corresponding decline in water temperature or depth (**Figure 4.4**). Several hours after release, T_b essentially matched T_a during extended periods (**Figure 4.1 C & D**).

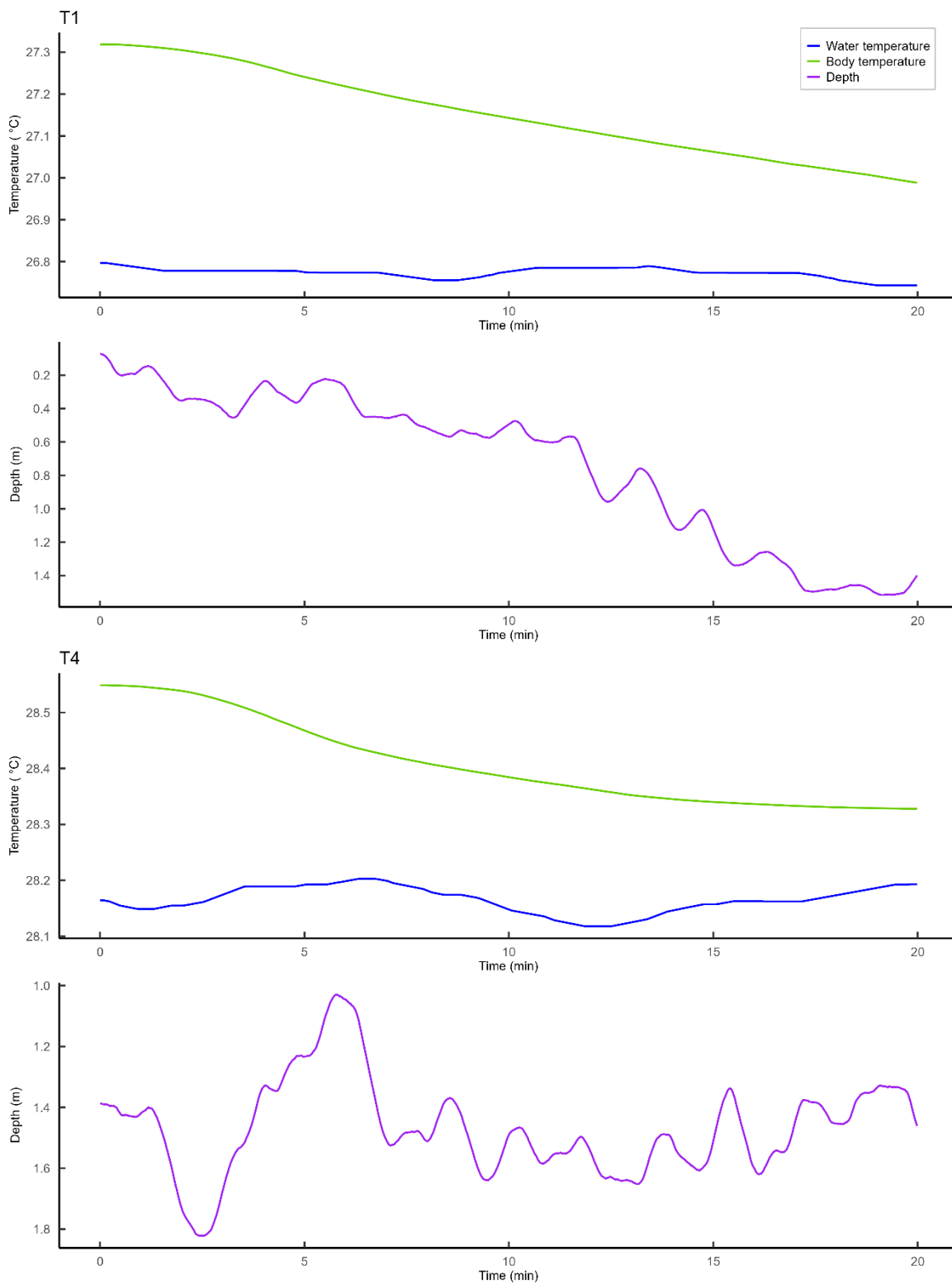


Figure 4.4: Body temperature, water temperature and depth data for tiger sharks T1 (top panel) and T4 (bottom panel) from moment of release. A 500-point moving average smoother was applied to all data.

Regression analyses showed hooking time had no significant influence on ΔT (**Figure 4.5 A**; $p = 0.44$); log transformed body mass had no significant influence on ΔT (**Figure 4.5 B**; $p = 0.12$); lactate concentration had no significant influence on ΔT (**Figure 4.5 C**; $p = 0.45$); and glucose concentration had no significant influence on ΔT ($p = 0.34$).

Multiple linear regressions with ΔT as the response variable and hooking time, body mass, lactate concentration, and glucose concentration as predictor variables showed no significant relationships (**Table C.2** for more detail).

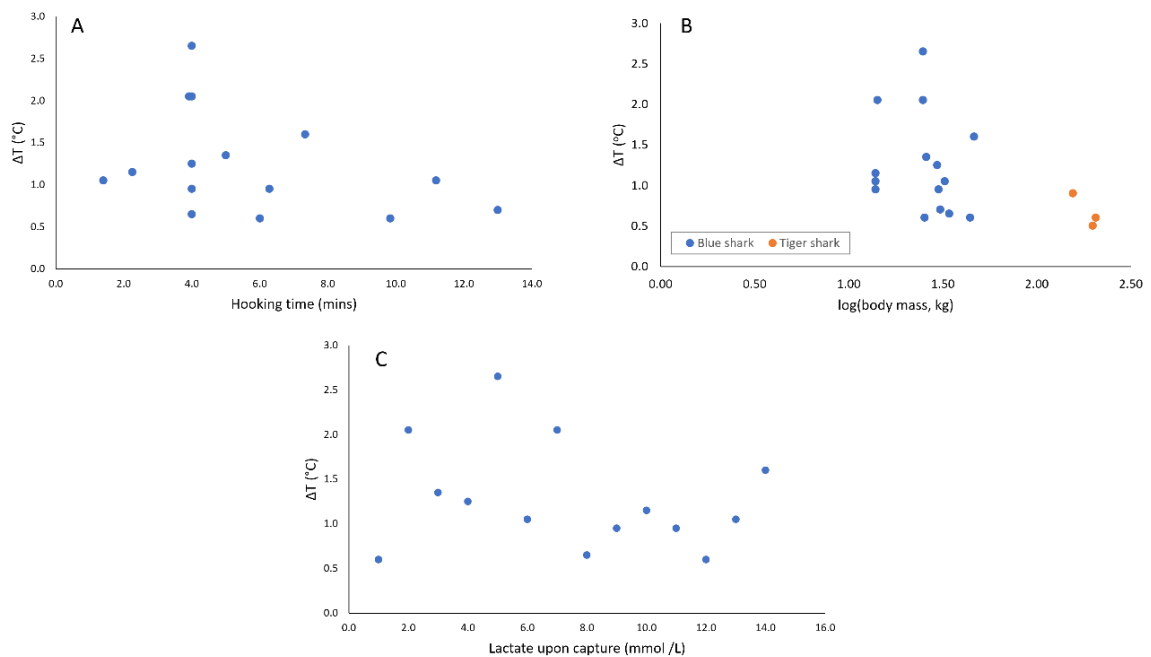


Figure 4.5 (A - C): (A) Temperature differential (ΔT) against hooking time for blue sharks with no significant relationship; (B) temperature differential (ΔT) against log (body mass) with no significant relationship; (C) temperature differential (ΔT) against lactate upon capture for blue sharks with no significant relationship.

Blue shark blood analysis showed lactate levels upon capture ranged from 1.2 – 9.0 mmol l^{-1} (mean = 3.1 mmol l^{-1} , $n = 13$). Following time on deck lactate levels ranged from 2.9 – 9.0 mmol l^{-1} (mean = 5.4 mmol l^{-1} , $n = 11$). Furthermore, nine out of eleven blue sharks tested twice showed increased lactate levels following time on deck (mean increase \pm SD = 2.5 \pm 1.2 mmol l^{-1}), one showed no change and one showed a decline (**Table C.1**). Glucose levels upon capture ranged from 3.1 – 19.7 mmol l^{-1} (mean = 8.6 mmol l^{-1} , $n = 9$). Following time on deck glucose levels ranged from 2.9 – 22.7 mmol l^{-1} (mean = 6.9 mmol l^{-1} , $n = 11$). Of the seven sharks tested twice, only two showed increased glucose levels following time on deck and five showed a decline (mean decrease \pm SD = 3.3 \pm 6.9 mmol l^{-1}) (**Table C.1**).

4.5. Discussion

By combining biologging, temperature measurements immediately after capture, and blood biochemistry, we show that capture significantly and rapidly (up to $0.8^\circ\text{C min}^{-1}$) elevates the body temperature of sharks. Subcutaneous muscle temperature was elevated by as much as 2.7°C immediately after capture, and temperature increased deeper into the white muscle, but the magnitude of the temperature elevation above ambient was unrelated to shark size, capture duration, and blood lactate or glucose levels. Following release, T_b rapidly declined toward T_a during

the first 30 mins for tiger sharks and 15 mins for blue sharks, and generally approximated T_a within one hour after release. These results provide new insight into the stress physiology of capture in sharks and highlight the significant influence the fishing process has on shark body temperatures.

Although body temperature elevation has been acknowledged to be of importance when assessing the negative physiological impacts of catch-and-release fishing in the past, it has not been directly recorded under these conditions before. Only through these direct, fine-scale measurements were we able to show definitively that catch-and-release events caused an elevation of the body temperature of sharks. Acute body temperature elevations have been known to cause a number of physiological, ecological and behavioural consequences; in terms of physiology, rapid elevations of body temperature can speed up digestion rates (Carey *et al.*, 1984), increase the expression of heat shock proteins (Renshaw *et al.*, 2012) and affect biological rates, such as metabolism (Morley *et al.*, 2019), potentially contributing to a deficit in the sharks' daily energy budget, as has been shown before (Bouyoucos *et al.*, 2018, Bouyoucos *et al.*, 2017). Regarding behavioural changes, elevations of body temperature can result in distributional changes as sharks are known to adjust their position in the water column as a means to behaviourally thermoregulate (Watanabe *et al.*, 2021, Nakamura *et al.*, 2020, Sims *et al.*, 2006), or may expand their horizontal range if topographically limited (e.g. the tiger sharks in the Bahamas are depth limited and therefore may travel further offshore to seek out colder, deep waters) (Gallagher *et al.*, 2021). While the magnitude of the measured temperature increase deeper into the muscle (0.7 – 1.2°C on average) may not seem dramatic, muscles deeper into the body were higher than subcutaneous tissues for blue sharks, and the subcutaneous temperatures likely underestimate the true temperature elevation of those tissues. This is because we could not measure T_b of sharks prior to capture, so calculated our estimates of T_b elevation based on sea surface temperatures at the point of capture, and our biologging data which showed shark T_b matches water temperature following sufficient equilibration time after release. Accordingly, our estimates of capture-induced heating of subcutaneous tissues are likely conservative because shark T_b may have been lower than surface temperatures if they had been inhabiting cooler (deeper) waters immediately prior to taking the hook, i.e., the true magnitude of heating could be higher than what we report. We do however acknowledge the limited sample size in our study; further collection of measurements of this kind from additional species and individuals could investigate any potential interindividual or interspecies variation. Future work could build on ours and other studies (Wosnick *et al.*, 2019, Wosnick *et al.*, 2018) that explore how heat is distributed throughout the body of sharks and the associated physiological implications. It is also noteworthy that we report T_b to match T_a for these animals after they have recovered from capture (**Figure 4.1 C & D**), because few studies have equivocally shown this to be the case for large ectotherms that have significant thermal inertia (low temperature rate constants; (Nakamura *et al.*, 2020)).

The simultaneous elevation of body temperature and lactate concentration are undoubtedly due to higher metabolic rates during capture, which is partially through anaerobic pathways. Nevertheless, temperature elevation was not correlated with lactate concentration, and neither were correlated with hooking duration (if anything, all these relationships were slightly negative; **Figure 4.5**). These results were somewhat unexpected, notwithstanding the known lag issues associated with using blood lactate as a direct proxy of the extent of cumulative anaerobic metabolism (blood lactate is chiefly a measure of anaerobic metabolism as it shifts from the white muscle to the blood when an animal switches from aerobic to anaerobic respiration during periods of increased energetic demands (Prohaska *et al.*, 2021)), and that other studies have also shown hooking duration as a poor proxy of blood lactate levels (Shea *et al.*, 2022). Further studies with increased sample sizes would be beneficial to investigating this relationship further. Notwithstanding this, our data show that shark body temperature rapidly responds to capture but is not a proxy of blood lactate concentrations over the same time scales. Body temperature should therefore be treated as a new physiological proxy of exhaustion in captured sharks that reflects increased aerobic exercise as well as the mismatch between heat generated in the skeletal muscles and lost at the gills.

Capture-induced heating rates were far more rapid than what our biologged sharks exhibited naturally; some blue sharks heating almost 8 times faster than did wild sharks swimming throughout thermally stratified waters. An important next step would be to determine the physiological implications of heating at these rates and magnitudes. There exists a rich literature on physiological responses to acute heating in the laboratory, which provides useful context. For example, Morley *et al.* (2019) compiled data on studies testing the upper temperature limits of marine, freshwater and terrestrial ectotherms under varying rates of warming. The maximum heating rates used in most experimental studies were approx. $1^{\circ}\text{C min}^{-1}$, with most commonly used rates being much lower. These higher rates are often considered to be so fast as to be not ecologically meaningful (Payne *et al.*, 2021, Payne *et al.*, 2016b) whereas our sharks heated close to those maximum heating rates manipulated in the lab ($0.8^{\circ}\text{C min}^{-1}$). Heating rate has a well-recognised impact on an ectotherm's thermal limit (Peck *et al.*, 2009, Kingsolver and Umbanhowar, 2018), so it could be instructive to determine physiological implications of this fast heating over the magnitude of temperature increases we documented. This could take the form of laboratory-based studies on physiological indicators of stress in sharks which are undergoing thermal ramping, such as blood biochemistry, behavioural changes, and response to stimuli. Observations from these controlled environments may aid our understanding of how this rapid heating is occurring and affecting the animals physiologically. Another avenue of research could be to explore behaviour post-release through biologging and investigate any relationship with ΔT . Increasing the number of

individuals and species, of varying lifestyles (e.g., sedentary, active predators) tagged with biologgers would greatly aid these studies.

Future research of this kind, and our own study, have numerous physiological and fisheries-based implications. Firstly, the findings of this study could be incorporated into future ecological models aimed at predicting mortality following catch-and-release angling, perhaps by incorporating a thermal threshold value. Moyes *et al.* (2006) constructed a model to predict the long-term survival of fish released following capture based on several blood markers (including lactate). This study noted that the inclusion of water temperature could have improved their model, with lower water temperatures likely resulting in reduced mortality post-release. We posit that this model could be further improved by the inclusion of body temperature in conjunction with water temperature, as we have shown that body temperature does not directly mimic water temperature in these ectothermic sharks for the first hour(s) after release. We are not aware of any other published studies that documented capture-induced changes in body temperature in large fishes, aside from a report on bluefin tuna captured in nets which reported a $\sim 2^{\circ}\text{C}$ increase in body temperature (Addis *et al.*, 2009). Tunas, along with some other species such as lamnid sharks, have specialised physiology which allows them to retain metabolically derived heat through vascular countercurrent heat exchangers, so could be expected to exhibit even greater temperature elevation during capture than ectothermic species. Many of those species are also of conservation concern, so it could be instructive to explore how catch-and-release fishing might impact welfare of these animals via T_b elevations.

In summary, we show that catch-and-release angling causes a measurable and rapid increase in the body temperature of sharks. With fast temperature elevations of up to 2.7°C , and possibly greater, it might be important for future research to explore any physiological impacts that this heating might cause, to better manage catch-and-release programs. Welfare outcomes of different handling protocols have been examined in other species (Raoult *et al.*, 2019, Brownscombe *et al.*, 2017, Danylchuk *et al.*, 2007) and exploring implications of factors such as removing sharks from the water (versus leaving them submerged) or catching them near the upper limit of their thermal niche could be helpful for this group of animals.

5. Discussion

Understanding the role of temperature in shaping animal's physiology, behaviour and interactions with nature is key to making predictions of how they will respond to change in their environment in the future. Throughout the course of this thesis, I have addressed fundamental, unanswered questions in the field of aquatic thermal ecology and provided novel insights into the pathways by which temperature influences several key physiological parameters at an individual level.

5.1. The role of endothermy in fishes

By comparing the encountered temperature ranges of ectothermic and regionally endothermic fishes (**Chapter 2**), I was able to provide the first evidence in contradiction of the thermal niche expansion hypothesis. Moreover, by directly recording the cruising speed of several ectothermic and regionally endothermic fish species I showed that regional endotherms swim faster than their ectothermic counterparts. These findings support my hypothesis that the significance of endothermy lies in the competitive advantages it confers to swimming performance rather than facilitating occupation of broader thermal niches. My findings contradict that of previous studies of endothermy's role in thermal niche expansion (Weng *et al.*, 2005, Block *et al.*, 2001, Dickson and Graham, 2004, Carey and Lawson, 1973), challenging long-held assumptions that are central to many other studies in the field of thermal ecology, for example the latitudinal diversity gradient (Stevens, 1989). My findings in relation to swim speed however, remain in support of the findings of Watanabe *et al.* (2015). Nonetheless, I found a smaller difference when comparing swim speed of ectotherms and regional endotherms, with regional endotherms swimming 1.6 times faster than ectotherms, compared to 2.7 times faster found by Watanabe *et al.* (2015).

These data provide new evidence for the role of endothermy and call into question our understanding of this specialised physiologies role in the thermal niches of fishes. It casts doubt on the assumption that regionally endothermic fishes are less susceptible to the negative impacts of global warming and compel us to re-examine how we forecast these species responses to global warming. When it came to testing the hypothesis that regional endothermy facilitates faster swimming speeds, I identified one drawback of my approach; I was unable to directly measure core body temperatures of each animal, of which I had recorded swim speed, and so instead had to estimate it from the environment (for the ectotherms) or from other studies (for the regional endotherms). However, technological developments are starting to facilitate such future work, such as internal temperature loggers, seen used in **Chapter 4** of this thesis.

5.2. Rate of temperature needs to be accounted for

Studies investigating the thermal sensitivity of metabolism abound, driven by its importance in many fields of biology and ecology (Brown *et al.*, 2004). However, the potential importance of rate of temperature change receives very little attention. **Chapter 3** of this thesis aimed to address this gap and provided evidence that the rate of temperature change has a systematic effect on the oxygen consumption of ectotherms, a proxy of aerobic metabolic rate, and as temperature increases more rapidly, the rate of oxygen consumption increases. Furthermore, the rate of cooling had less of an influence on the rate of oxygen consumption than the rate of warming. This response necessitates further investigation and consideration as global ocean temperatures continue to increase, and marine heat wave events increase in magnitude and rate of change.

A key finding of **Chapter 3**, that at slower rates of temperature change the animals consumed less oxygen than when they were experiencing no change in temperature (i.e., stable temperature), contradicts that of previous dynamic temperature studies which found that variable temperature environments are more energetically costly to ectotherms than stable environments (Morón Lugo *et al.*, 2020, Williams *et al.*, 2012). Furthermore, my finding that rapid heating was driving higher metabolic rates contradicts Rezende *et al.* (2011) and Chown *et al.* (2009) who found metabolic costs increase with decreasing heating rate, postulated to be due to extended exposure duration. My findings however, broadly concur with those of Lake *et al.* (2013) and confirm the rate of temperature change does have an effect on metabolic rate. Given our experiment was conducted in the same manner as Lake *et al.* (2013), this highlights the importance of experimental design and identifies a factor not previously considered in this field.

These data provide new evidence that rate of temperature change plays a role in the thermal sensitivity of aquatic ectotherms, a relationship previously unknown. This study was however limited to one species, with small body size. Future studies could extend this investigation to larger-bodied species and endothermic species to explore potential effects of body size and/or thermoregulatory strategy (and its associated specialised physiology) on this relationship.

5.3. Capture heats up sharks

Catch-and-release fishing remains a widespread practice both in the commercial and recreational fishing industries (Brownscombe *et al.*, 2017, Danylchuk *et al.*, 2014, Cooke and Schramm, 2007, Gilman *et al.*, 2020, Sepulveda *et al.*, 2019) and the numerous physiological and ecological impacts it has on teleosts and elasmobranchs have been widely documented (Gale *et al.*, 2013, Mohan *et al.*, 2020, Sepulveda *et al.*, 2019, Gallagher *et al.*, 2019, Jerome *et al.*, 2017, Schlenker *et al.*, 2016, Gallagher *et al.*, 2014, Cooke *et al.*, 2013, Cooke and Schramm, 2007).

However, until now, one major physiological impact on elasmobranchs remained undocumented. Through the use of biologging technology, I show that capture significantly and rapidly elevates the body temperature of ectothermic sharks, elevating the subcutaneous temperature by as much as 2.7°C.

It is known that sharks exhibit intensive swimming acceleration (Gallagher *et al.*, 2017) and periods of exhaustive exercise (i.e., anaerobic exercise) (Schwieterman *et al.*, 2021) when attempting to free themselves from fishing hooks. We also know stress and exercise can elevate metabolic rate (Kieffer, 2000, Mohan *et al.*, 2020) and that heat loss across the gills is likely impeded during capture, and so it is logical that capture elevates the body temperature. The potential for body temperature elevation has been acknowledged in the past but had not been directly recorded until now and my data confirm this phenomenon. Acute elevations of body temperature can result in a variety of physiological and behavioural impacts for the animal and given that sharks are relatively large-bodied fishes with low heat-transfer coefficients (Nakamura *et al.*, 2020) this capture-induced heating could be a particularly relevant issue for them. One potential behavioural response that is of importance is resultant changes in the shark's distribution. Sharks may alter their vertical or horizontal range (if topographically limited) in the water column as a means of behaviourally thermoregulating (Nakamura *et al.*, 2020, Sims *et al.*, 2006, Watanabe *et al.*, 2021). One key limitation I identified in this study relates to my approach to recording the differential between body temperature and water temperature; as I was unable to directly measure core body temperatures of each animal at the moment of hooking, the body temperature recorded at the moment of capture was used instead.

5.4. Practical applications of this work

This body of research not only contributes to advancing scholarly understanding but also has a range of practical applications, especially for those seeking to spatially manage natural resources. Given this new evidence that regionally endothermic fishes do not have broader thermal niches than their ectothermic counterparts, it throws into question their resilience to climate change, as they had previously been assumed to be less susceptible than ectotherms. If global ocean temperatures continue to rise, their thermal niche may contract in a similar manner as for ectotherms, perhaps putting them at similar risk of loss of habitat (both vertical and horizontal), loss of foraging grounds, and increased risk of fisheries interactions. Understanding this response will allow us to better inform spatial management planning for these threatened species, as most regionally endothermic fish are large, predatory species which are in global decline. Therefore, by exploring fundamental questions (as I have done in **Chapter 2**) we can help build a mechanistic understanding into how temperature regulates the distribution of fishes.

Without research into the thermal ecology of ectothermic fishes, and advances in technology, we might still be unaware of the elevation of body temperature of sharks during capture. But, by documenting this (**Chapter 4**), I hope to improve catch-and-release practices, aiming to reduce mortality outcomes of this widespread fisheries activity. Actions could include (i) reducing the occurrence of removal of sharks from the water, opting instead to keep the shark submerged or partially submerged in the surface water during unhooking, measuring, etc.; (ii) where it is deemed necessary to remove the animal from the water and bring it onboard, sharks should have a hose placed in the mouth flushing the gills with (colder than air) water; and (iii) restricting catch-and-release fishing in locations and/or seasons when the animals will be inhabiting waters which are near the warm range edge for their species, aiming to reduce the risk of pushing the animals outside their maximum critical temperature. The findings of **Chapter 4** of this thesis will hopefully encourage further lines of investigation, perhaps investigating potential physiological impacts caused by this acute elevation in body temperature. Taking this finding into account and given what I learned about how acute temperature increases influence aerobic metabolism (**Chapter 3**), I believe these physiological understandings will be of interest to ecosystem modellers, who seek realistic parametrisation of how temperature influences metabolism and its impacts on individual and population growth.

The many findings of this thesis could imply a need to incorporate organismal thermal responses in predictions of species responses to global warming. Incorporation of ecophysiological patterns could be a powerful tool in predicting species range shifts under climate change scenarios and could aid marine spatial planning and protection and inform re-introduction strategies for conservation purposes. Predictions could be strengthened by information at an individual level, such as how increasing rates of temperature change will elevate metabolic cost, and at a population level, such as how regional endothermy does not facilitate thermal niche expansion for fishes. By synthesising this empirical data, we can further strengthen predictions by development of indicators for predicting future shifts in abundance. This will hopefully improve conservation efforts and bolster policy makers to improve protection of the oceans against global warming, a key mission if we are to maintain food security for coastal communities under future climate shifts.

5.5. Future research

Given my finding that rate of temperature change has effects on the thermal sensitivity of aerobic metabolism, we must consider the implications this has going forward as it brings into question the universality of the MTE and Q_{10} effect. Future studies would benefit from the inclusion of rate of temperature change in their estimations of metabolism, and for that matter all biological rate responses to thermal change. Furthermore, a retrospective review of studies investigating the thermal sensitivity of metabolism under dynamic conditions could be conducted to possibly identify

any previously unidentified physiological responses. Expansion of studies exploring the effect of rate of temperature change on biological rates could contribute to this knowledge gap. Moreover, it is advised that any future experiments which utilise thermal ramping to establish physiological or behavioural responses or limits must take this effect into consideration. As this finding may have implications for animal growth, energy budgets and distribution, it also warrants further exploration in the field, with the goal of linking mechanistic insights with physiological responses. Investigating the influence of rate of temperature change on endothermic and regionally endothermic species could provide a more holistic understanding of the physiological mechanisms at play and strengthen our predictions of how global warming will impact energy budgets of aquatic organisms.

Given this new understanding of how rapid increases in temperature elevate the aerobic metabolism of ectotherms (**Chapter 3**), what could this imply for my captured sharks (**Chapter 4**)? Sharks captured during this study heated at rates as fast as $0.8^{\circ}\text{C min}^{-1}$, significantly faster than any of the rates tested in **Chapter 3**, implying an even greater magnitude of metabolic increase should this relationship extend to ectothermic sharks. Future research could investigate whether this relationship occurs in ectothermic sharks under similar conditions, i.e., using intermittent-flow respirometry. By better understanding this relationship, better predictions could be made as to the impact of temperature change on shark energy budgets, distributions (perhaps as they seek out additional foraging grounds to counteract elevated energy demands) and population growth.

As I found that regional endothermy does not facilitate thermal niche expansion for fishes, this brings into question their susceptibility to climate change. I encourage future research into how regionally endothermic fishes will be affected by ocean warming and to examine whether they will be pushed beyond their thermal tolerance breadth and/or change their distributions (both vertical and horizontal). Should it be found that by climate change induced reduction of suitable habitats, fishes are shifting their distributions, consideration should be given to the knock-on impacts this could have, such as increased risk of fisheries interactions, or increased encounters with bathers (if the animals move inshore) driving increased implementation of bather control measures, risking entanglement and mortality. Understanding this is of great importance if we are to better protect these largely high-level predatory species, many of whom are already threatened by extinction globally.

5.6. Conclusions

Temperature lies centrally at the junctions between physiology and behaviour, which in turn shape a species ecology. Organisms experience temperature differently and through exploring these differences we can better predict how they will respond to changing thermal environments.

Through investigating the drivers of endothermy in fishes, documenting the influence of the rate of temperature change on aerobic metabolism and discovering a thermal, stress response in captured ectothermic sharks, I have answered long held questions within thermal ecology, and contributed novel findings to an ever-expanding field.

6. Bibliography

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Appendix A Supplementary information for Chapter 2: Endothermy makes fishes faster but does not expand their thermal niche

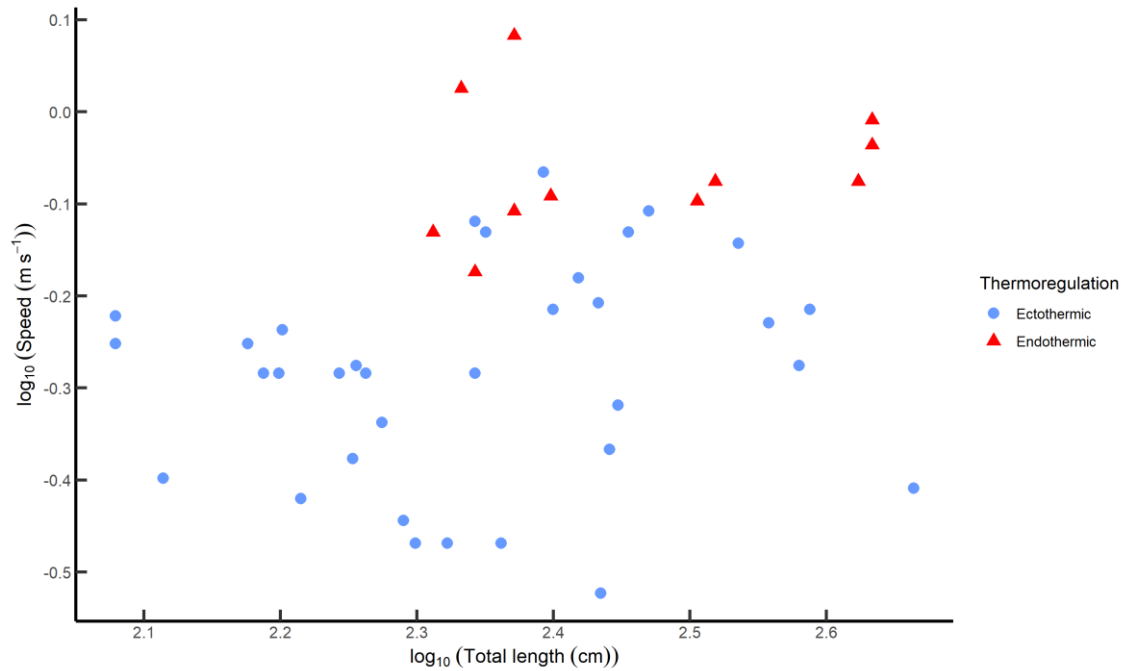


Figure A.1: Cruising speed (\log_{10} transformed; m s^{-1}) as a function of total length (\log_{10} transformed; cm): cruising speed of fishes with regional endothermy (red triangles) and fishes without it (light blue circles) recorded in the wild.

Table A.1: Length and weight conversion equations used during both studies. Length-weight relationships represented by $W = aL^b$ where W is weight/body mass (kg), a & b are species specific coefficients and L is a measure of length: TL is total length (cm), PCL is precaudal length (cm) and FL is fork length (cm).

Species	a	b	Length measure	Source
<i>Thunnus thynnus</i>	0.00000002	2.96	TL	(Sinovčić <i>et al.</i> , 2004)
<i>Carcharhinus melanopterus</i>	0.00001242	2.85	TL	(Motta <i>et al.</i> , 2014)
<i>Prionace glauca</i>	0.0000031841	3.1313	FL	(Kohler <i>et al.</i> , 1996)
<i>Carcharhinus leucas</i>	0.0000001	2.406	TL	(Shiple, 2005)
<i>Carcharhinus galapagensis</i>	0.0000136	3	TL	(Curran and Bigelow, 2016)
<i>Sphyrna mokarran</i>	0.00000123	3.24	TL	(Stevens and Lyle, 1989)
<i>Carcharhinus amblyrhynchos</i>	0.00000878	3.050	TL	(Letourneur <i>et al.</i> , 1998)
<i>Carcharhinus longimanus</i>	0.0000254	2.691	TL	(Lessa <i>et al.</i> , 2004)
<i>Lamna ditropis</i>	0.000044	2.875	PCL	(Goldman and Musick, 2006)
<i>Carcharhinus plumbeus</i>	0.000010885	3.0124	FL	(Kohler <i>et al.</i> , 1996)
<i>Sphyrna lewini</i>	0.00255	3.130	TL	(Motta <i>et al.</i> , 2014)
<i>Hexanchus griseus</i>	0.0000002	3.6060	TL	(İşmen <i>et al.</i> , 2009)
<i>Galeocerdo cuvier</i>	0.0000025281	3.2603	FL	(Kohler <i>et al.</i> , 1996)
<i>Carcharodon carcharias</i>	0.0000075763	3.0848	FL	(Kohler <i>et al.</i> , 1996)

Table A.2: Length and weight conversion equations used during both studies, where WT is weight/body mass (kg), and TL is total length (cm).

Species	Equation	Length measure	Source
<i>Notorynchus cepedianus</i>	Females: $WT = 0.003TL^2 - 0.42TL + 19.501$ Males: $WT = 0.002TL^2 - 0.22TL + 8.803$	TL	(Barnett <i>et al.</i> , 2017, Blower <i>et al.</i> , 2012)

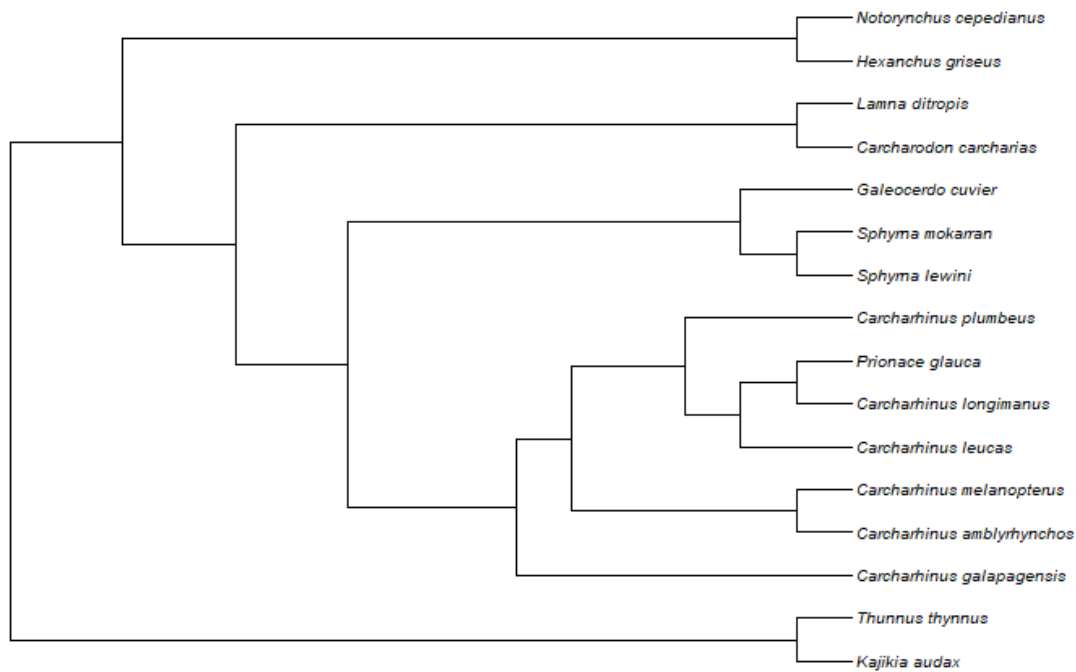


Figure A.2: Phylogenetic tree of species contained in elevated cruising speeds study dataset.

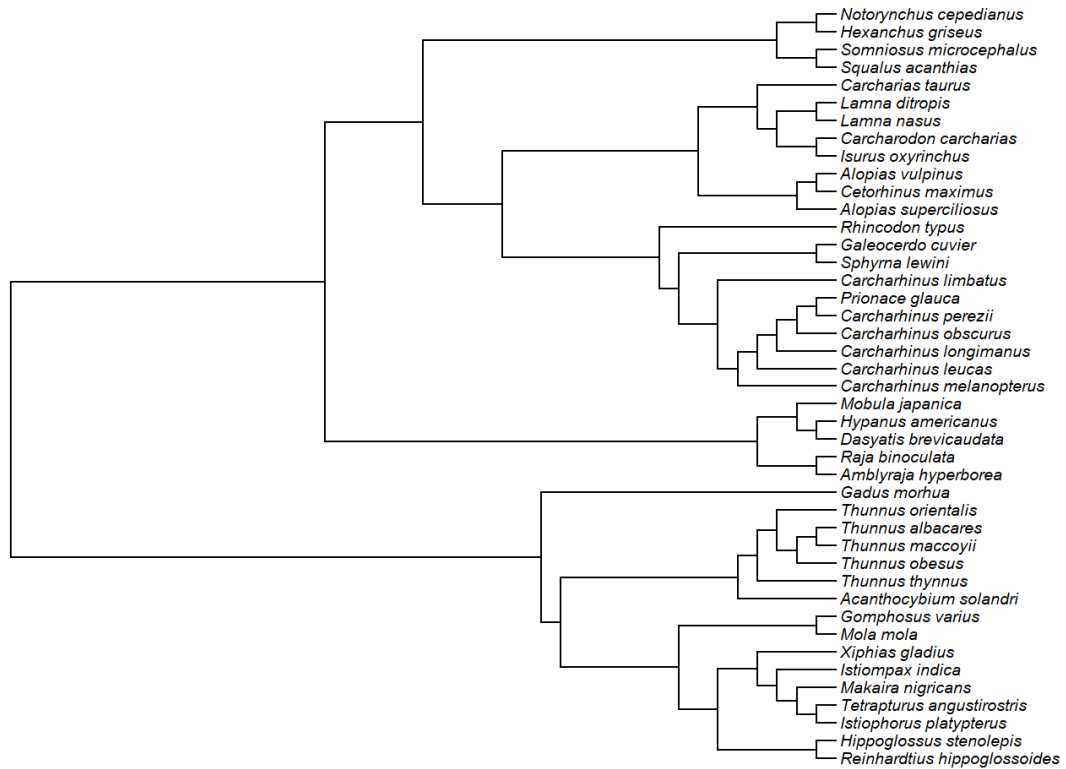


Figure A.3: Phylogenetic tree of species contained in thermal niche expansion dataset.

Table A.3: Fitting of nonphylogenetic regression models for thermal niche expansion hypothesis, where 'XT' is absolute thermal range, 'XT₈₀' is 80th percentile thermal range, N is number of individuals, 'XD₈₀' is 80th percentile depth range, and 'DAL' is days at liberty. Final models used in phylogenetic informed regression models (MCMCglmm) shown in bold.

Model	R ²	AIC
XT ~ log₁₀DAL + N + log₁₀BodyMass + Thermoregulation	0.2433	577.4679
XT ~ log ₁₀ DAL	0.09506	587.2058
XT ~ log ₁₀ DAL + N	0.09974	588.7493
XT ~ log ₁₀ DAL + N + log ₁₀ BodyMass	0.2159	578.5965
XT ~ log ₁₀ DAL + N + Thermoregulation	0.12	588.7485
XT₈₀ ~ log₁₀DAL + N + log₁₀BodyMass + Thermoregulation	0.2362	185.3211
XT ₈₀ ~ log ₁₀ DAL + N + log ₁₀ BodyMass	0.2046	184.6200
XT ₈₀ ~ log ₁₀ DAL + N + Thermoregulation	0.21	184.4006
XD₈₀ ~ log₁₀DAL + N + log₁₀BodyMass + Thermoregulation	0.4925	434.5407

Table A.4: Fitting of nonphylogenetic regression models for elevated cruising speeds hypothesis. Final models used in phylogenetic informed regression models (MCMCglmm) shown in bold.

Model	R ²	AIC
log₁₀Speed ~ log₁₀BodyMass + log₁₀Bodytemp + Thermoregulation	0.6095	-79.42704
log ₁₀ Speed ~ log ₁₀ BodyMass + log ₁₀ AmbTemp	0.2098	-49.71088
log ₁₀ Speed ~ log ₁₀ BodyMass + log ₁₀ Bodytemp	0.4301	-64.42017
log ₁₀ Speed ~ log ₁₀ BodyMass + log ₁₀ AmbTemp + Thermoregulation	0.5803	-76.18531
log ₁₀ Speed ~ log ₁₀ BodyMass + log ₁₀ AmbTemp + Thermoregulation + log ₁₀ AmbTemp*Thermoregulation	0.6097	-77.44784
log ₁₀ Speed ~ log ₁₀ BodyMass + log ₁₀ Bodytemp + Thermoregulation + log ₁₀ AmbTemp*Thermoregulation	0.6104	-75.53347

Table A.5: Elevated cruising speeds dataset; Biologging summary data for individuals caught and tagged for elevated cruising speeds study.

Animal ID	Scientific name	Common name	Total length (cm)	Body mass (kg)	Recording duration (h)	Mean ambient temperature (°C)	Mean body temperature (°C)	Cruising speed (m s ⁻¹): mode
1	<i>Thunnus thynnus</i>	Atlantic bluefin tuna	205	139.26	25.12	14	24.9	0.74
2	<i>Thunnus thynnus</i>	Atlantic bluefin tuna	220	171.63	15.70	12	23.9	0.67
3	<i>Thunnus thynnus</i>	Atlantic bluefin tuna	235	208.64	7.46	13	24.4	1.21
4	<i>Thunnus thynnus</i>	Atlantic bluefin tuna	235	208.64	8.01	13	24.4	0.78
5	<i>Carcharhinus melanopterus</i>	Blacktip shark	130	13.15	71.58	24	24	0.40
6	<i>Prionace glauca</i>	Blue shark	199	28.94	13.03	15.5	15.5	0.34
7	<i>Prionace glauca</i>	Blue shark	230	45.38	15.97	16	16	0.34
8	<i>Carcharhinus leucas</i>	Bull shark	150	17.21	13.96	28	28	0.56
9	<i>Carcharhinus leucas</i>	Bull shark	164	21.33	37.50	27	27	0.38
10	<i>Carcharhinus galapagensis</i>	Galapagos shark	280	298.55	132.76	25	25	0.48
11	<i>Sphyrna mokarran</i>	Great hammerhead shark	295	123.63	17.98	28	28	0.78
12	<i>Carcharhinus amblyrhynchos</i>	Grey reef shark	154	41.25	68.88	28.2	28.2	0.52
13	<i>Carcharhinus amblyrhynchos</i>	Grey reef shark	158	44.61	70.03	27	27	0.52
14	<i>Carcharhinus amblyrhynchos</i>	Grey reef shark	159	45.47	127.97	28.2	28.2	0.58
15	<i>Carcharhinus longimanus</i>	Oceanic whitetip shark	220	51.08	19.31	26	26	0.76
16	<i>Carcharhinus longimanus</i>	Oceanic whitetip shark	262	81.75	41.89	25	25	0.66
17	<i>Carcharhinus longimanus</i>	Oceanic whitetip shark	271	89.53	86.62	26	26	0.62
18	<i>Carcharhinus longimanus</i>	Oceanic whitetip shark	285	102.52	41.01	26	26	0.74
19	<i>Lamna ditropis</i>	Salmon shark	215	121.28	10.66	13.5	25.9	1.06
20	<i>Carcharhinus plumbeus</i>	Sandbar shark	175	35.76	121.34	24	24	0.52
21	<i>Carcharhinus plumbeus</i>	Sandbar shark	179	38.23	49.35	22.5	22.5	0.42
22	<i>Carcharhinus plumbeus</i>	Sandbar shark	180	38.87	113.06	23.6	23.6	0.53

Animal ID	Scientific name	Common name	Total length (cm)	Body mass (kg)	Recording duration (h)	Mean ambient temperature (°C)	Mean body temperature (°C)	Cruising speed (m s⁻¹): mode
23	<i>Carcharhinus plumbeus</i>	Sandbar shark	183	40.82	116.45	23.6	23.6	0.52
24	<i>Sphyrna lewini</i>	Scalloped hammerhead	120	8.21	36.89	23	23	0.56
25	<i>Sphyrna lewini</i>	Scalloped hammerhead	120	8.21	39.95	23	23	0.60
26	<i>Hexanchus griseus</i>	Sixgill shark	461	806.00	24.04	13	13	0.39
27	<i>Galeocerdo cuvier</i>	Tiger shark	220	56.34	85.35	25	25	0.52
28	<i>Galeocerdo cuvier</i>	Tiger shark	224	60.01	6.60	24	24	0.74
29	<i>Galeocerdo cuvier</i>	Tiger shark	247	84.38	29.37	25.5	25.5	0.86
30	<i>Galeocerdo cuvier</i>	Tiger shark	276	123.93	206.21	23.5	23.5	0.43
31	<i>Galeocerdo cuvier</i>	Tiger shark	343	261.19	11.62	25	25	0.72
32	<i>Galeocerdo cuvier</i>	Tiger shark	361	310.93	30.16	25.5	25.5	0.59
33	<i>Galeocerdo cuvier</i>	Tiger shark	380	370.17	177.14	26	26	0.53
34	<i>Galeocerdo cuvier</i>	Tiger shark	387	393.84	13.19	25	25	0.61
35	<i>Carcharodon carcharias</i>	White shark	320	319.67	22.16	15	26.4	0.80
36	<i>Carcharodon carcharias</i>	White shark	330	352.14	17.07	15	26.4	0.84
37	<i>Carcharodon carcharias</i>	White shark	420	750.22	19.98	15	26.4	0.84
38	<i>Carcharodon carcharias</i>	White shark	430	807.55	2.08	15	26.4	0.92
39	<i>Carcharodon carcharias</i>	White shark	430	807.55	39.67	15	26.4	0.98
40	<i>Kajikia audax</i>	Striped marlin	250	122.19	18.61	22	22.4	0.81
41	<i>Notorynchus cepedianus</i>	Broadnose sevengill shark	195	41.95	83.33	17	17	0.36
42	<i>Notorynchus cepedianus</i>	Broadnose sevengill shark	210	63.60	22.15	17.62	17.6	0.34
43	<i>Notorynchus cepedianus</i>	Broadnose sevengill shark	188	38.13	69.31	17.27	17.3	0.46
44	<i>Sphyrna mokarran</i>	Great hammerhead shark	251	73.26	20.42	24.2	24.2	0.61
45	<i>Sphyrna mokarran</i>	Great hammerhead shark	272	95.04	19.42	27.9	27.9	0.3

Table A.6: Data sources for thermal niche expansion dataset: Citation & additional individual information for all sources used in comparative analysis.

Study species	Thermoregulatory strategy	Mean body mass (kg)	Min. ambient temp. (°C)	Max. ambient temp. (°C)	10%ile ambient temp.	90%ile ambient temp.	Mean Days at Liberty (DAL)	Max depth (m)	Publication
Arctic skate	Ectothermic	3.02	1.2	2.9	NA	NA	40	1355	(Peklova et al., 2014)
Atlantic Bluefin tuna	Regionally endothermic	122.36	12	29.6	NA	NA	250	1000	(Block et al., 2001)
Atlantic Bluefin tuna	Regionally endothermic	160.60	3.4	28.7	7	23	115	672	(Wilson et al., 2005)
Atlantic Bluefin tuna	Regionally endothermic	171.23	14	26	14	24	167	800	(Stokesbury et al., 2004)
Atlantic Bluefin tuna	Regionally endothermic	152.53	5.8	24.7	12	19	196	958	(Stokesbury et al., 2007)
Atlantic cod	Ectothermic	7.34	-0.9	11.4	NA	NA	320	741	(Pálsson and Thorsteinsson, 2003)
Atlantic cod	Ectothermic	2.59	-1.54	19.45	NA	NA	251	851.6	(Righton et al., 2010)
Basking shark	Ectothermic	1702.36	5.8	21	12.5	15	70	320	(Skomal et al., 2004)
Basking shark	Ectothermic	1540.34	8	17	NA	NA	137	1000	(Sims et al., 2003)
Big eye thresher	Ectothermic	67.55	11.1	21.6	12.5	20	14	600	(Stevens et al., 2010)
Big eye thresher	Ectothermic	183.48	NA	NA	6	24	44	NA	(Weng and Block, 2004)
Big skate	Ectothermic	20.74	2	18	NA	NA	287	500	(Farrugia et al., 2016)
Bigeye tuna	Regionally endothermic	30.73	3	28.5	NA	NA	117	1500	(Schaefer and Fuller, 2002)
Bigeye tuna	Regionally endothermic	49.81	7	23	NA	NA	1	466.5	(Musyl et al., 2003)
Bigeye tuna	Regionally endothermic	12.10	9.6	26.5	NA	NA	371	1826	(Fuller et al., 2015)
Black marlin	Regionally endothermic	113.40	16	28	22.5	31.5	39	190	(Gunn et al., 2003)
Black marlin	Regionally endothermic	196.40	7.4	31.3	NA	NA	46	536	(Williams et al., 2017)
Blacktip reef shark	Ectothermic	12.44	27.4	31.4	NA	NA	4	14.5	(Papastamatiou et al., 2015)
Blue marlin	Regionally endothermic	90.65	5.4	30.6	NA	NA	107	712	(Carlisle et al., 2017)
Blue shark	Ectothermic	28.05	4	27	8	22	114	499	(Weng et al., 2005)

Study species	Thermoregulatory strategy	Mean body mass (kg)	Min. ambient temp. (°C)		Max. ambient temp. (°C)	10%ile ambient temp.	90%ile ambient temp.	Mean Days at Liberty (DAL)	Max depth (m)	Publication
Blue shark	Ectothermic	88.06	4.8	22.5	22.5	11.7	19.2	50	980	(Stevens <i>et al.</i> , 2010)
Blue shark	Ectothermic	20.32	10.6	24.6	24.6	NA	NA	28	696	(Queiroz <i>et al.</i> , 2010)
Bluntnose sixgill shark	Ectothermic	169.16	5.4	20.6	20.6	NA	NA	82	NA	(Comfort and Weng, 2015)
Broadnose sevengill shark	Ectothermic	53.52	8	18.2	18.2	NA	NA	82	360	(Stehfest <i>et al.</i> , 2014)
Bull shark	Ectothermic	26.68	20	29.5	29.5	24	28	18	205	(Brunnschweiler <i>et al.</i> , 2010)
Caribbean reef shark	Ectothermic	205.09	12.4	30.8	30.8	NA	NA	14	356	(Chapman <i>et al.</i> , 2007)
Common thresher shark	Regionally endothermic	4.33	9	21	21	11	19	150	192	(Cartamil <i>et al.</i> , 2016)
Common thresher shark	Regionally endothermic	14.89	9.1	21.3	21.3	10	20	491	320	(Cartamil <i>et al.</i> , 2011)
Dusky shark	Ectothermic	168.77	10.2	26.1	26.1	NA	NA	11	498	(Barnes <i>et al.</i> , 2016)
Greenland halibut	Ectothermic	1.76	-0.1	4.2	4.2	NA	NA	131	1000	(Boje <i>et al.</i> , 2014)
Greenland shark	Ectothermic	224.96	0	6	6	0.5	5.5	122	1562	(Campana <i>et al.</i> , 2015)
Greenland shark	Ectothermic	923.46	2.6	17.2	17.2	5.5	10	175	1816	(Campana <i>et al.</i> , 2015)
Greenland shark	Ectothermic	256.36	-1.5	7.4	7.4	-1	5	105	1560	(Fisk <i>et al.</i> , 2012)
Greenland shark	Ectothermic	130.94	-1.1	8.6	8.6	NA	NA	60	352	(Stokesbury <i>et al.</i> , 2005)
Greenland shark	Ectothermic	210.90	-1.2	3.4	3.4	NA	NA	1	273	(Watanabe <i>et al.</i> , 2012)
Ocean sunfish	Ectothermic	147.75	2.6	22	22	10	18	5	350	(Nakamura <i>et al.</i> , 2015)
Ocean sunfish	Ectothermic	91.08	6.6	24	24	8	18	186	556	(Thys <i>et al.</i> , 2015)

Study species	Thermoregulatory strategy	Mean body mass (kg)	Min. ambient temp. (°C)	Max. ambient temp. (°C)	10%ile ambient temp.	90%ile ambient temp.	Mean Days at Liberty (DAL)	Max depth (m)	Publication
Oceanic whitetip shark	Ectothermic	NA	6.79	29.52	15.73	22.2	185	1190.2	(Howey <i>et al.</i> , 2016)
Oceanic whitetip shark	Ectothermic	436.37	7.75	30.48	NA	NA	142	1082	(Howey-Jordan <i>et al.</i> , 2013)
Pacific bluefin tuna	Regionally endothermic	3.68	1.4	28.4	NA	NA	145	117	(Itoh <i>et al.</i> , 2003)
Pacific bluefin tuna	Regionally endothermic	43.00	5.7	25	NA	NA	99	382	(Domeier <i>et al.</i> , 2005)
Pacific bluefin tuna	Regionally endothermic	15.06	11.43	26.17	NA	NA	359	NA	(Boustany <i>et al.</i> , 2010)
Pacific halibut	Ectothermic	29.01	0.2	10	NA	NA	195	844	(Seitz <i>et al.</i> , 2011)
Pacific halibut	Ectothermic	26.45	3.2	9	NA	NA	204	748	(Seitz <i>et al.</i> , 2008)
Pacific sleeper shark	Ectothermic	84.69	4.4	11.8	NA	NA	214	724	(Hulbert <i>et al.</i> , 2006)
Porbeagle shark	Regionally endothermic	66.47	9.8	18.5	NA	NA	44	552	(Pade <i>et al.</i> , 2009)
Porbeagle shark	Regionally endothermic	26.58	9	17	NA	NA	122	700	(Saunders <i>et al.</i> , 2010)
Sailfish	Regionally endothermic	19.67	20	24.3	NA	NA	1	27.9	(Hoolihan, 2005)
Salmon shark	Regionally endothermic	281.58	2	24	4	18	163	499	(Weng <i>et al.</i> , 2005)
Sand tiger shark	Ectothermic	132.55	9.7	20.55	NA	NA	43	86	(Smale <i>et al.</i> , 2012)
Sand tiger shark	Ectothermic	71.13	13	26	NA	NA	122	188	(Teter <i>et al.</i> , 2015)
Sandbar shark	Ectothermic	56.41	14.1	25.9	NA	NA	12	302.5	(Barnes <i>et al.</i> , 2016)
Scalloped hammerhead shark	Ectothermic	80.22	4.8	27.8	NA	NA	74	980	(Jorgensen <i>et al.</i> , 2009)
Shortbill spearfish	Regionally endothermic	16.00	17.6	26.6	24	26	8	208	(Arostegui <i>et al.</i> , 2019)
Shortfin mako	Regionally endothermic	46.60	4.6	24.1	12	22	59	888	(Abascal <i>et al.</i> , 2011)
Shortfin mako	Regionally endothermic	88.40	10.4	28.6	NA	NA	60	556	(Loefer <i>et al.</i> , 2005)
Shortfin mako	Regionally endothermic	59.17	5.2	31.1	NA	NA	73	866	(Vaudo <i>et al.</i> , 2016)

Study species	Thermoregulatory strategy	Mean body mass (kg)	Min. ambient temp. (°C)	Max. ambient temp. (°C)	10%ile ambient temp.	90%ile ambient temp.	Mean Days at Liberty (DAL)	Max depth (m)	Publication
Southern stingray	Ectothermic	23.69	23.8	34.4	24	29	34	77.5	(Branco-Nunes et al., 2016)
Spine-tail devil ray	Ectothermic	98.14	NA	NA	15	27.5	83	3267	(Croll et al., 2012)
Spine-tail devil ray	Ectothermic	125.60	5	26	NA	NA	30	1112	(Francis and Jones, 2017)
Spiny dogfish	Ectothermic	2.71	5.2	14.9	NA	NA	127	559	(Sulikowski et al., 2010)
Spiny dogfish	Ectothermic	3.07	2.8	22.1	NA	NA	195	481.5	(Carlson et al., 2014)
Swordfish	Regionally endothermic	83.16	3.2	28.8	5	22	95	1227	(Abecassis et al., 2012)
Swordfish	Regionally endothermic	65.00	4	31	NA	NA	62	980	(Dewar et al., 2011)
Swordfish	Regionally endothermic	113.50	7.2	22.8	13.7	23.7	3	425	(Stoehr et al., 2018)
Tiger shark	Ectothermic	257.06	14.6	27.6	NA	NA	0	247	(Nakamura et al., 2011)
Tiger shark	Ectothermic	198.42	5.6	32.2	NA	NA	67	91	(Werry et al., 2014)
Tiger shark	Ectothermic	26.02	4	31.2	18	26	61	1112	(Afonso and Hazin, 2015)
Tiger shark	Ectothermic	121.38	6	33	NA	NA	137	400	(Ferreira et al., 2015)
Tiger shark	Ectothermic	14.76	13	29	NA	24	45	304	(Hazin et al., 2013)
Tiger shark	Ectothermic	85.17	5.9	29.5	20	26	20	920	(Holmes et al., 2014)
Wahoo	Ectothermic	12.55	11.1	27.9	NA	NA	22	253	(Sepulveda et al., 2011)
Whale shark	Ectothermic	909.68	4.4	30.8	NA	NA	101	980	(Graham et al., 2006)
Whale shark	Ectothermic	1396.16	2.2	28.7	NA	NA	151	980	(Wilson et al., 2006)
Whale shark	Ectothermic	1619.58	3.4	29.9	14	28	47	1286	(Brunnsweller et al., 2009)
Whale shark	Ectothermic	1336.34	17.6	35.4	NA	NA	111	344	(Robinson et al., 2017)
Whale shark	Ectothermic	1574.44	18	36	NA	NA	91	208	(Robinson et al., 2017)
Whale shark	Ectothermic	322.43	6.1	31.4	NA	NA	143	NA	(Hsu et al., 2007)

Study species	Thermoregulatory strategy	Mean body mass (kg)	Min. ambient temp. (°C)	Max. ambient temp. (°C)	10%ile ambient temp.	90%ile ambient temp.	Mean Days at Liberty (DAL)	Max depth (m)	Publication
Whale shark	Ectothermic	1690.86	4.2	33	18	27	83	1928	(Tyminski <i>et al.</i> , 2015)
Whale shark	Ectothermic	1156.42	18.5	29.7	NA	NA	26	NA	(Rohner <i>et al.</i> , 2018)
White shark	Regionally endothermic	876.55	4.8	26.2	NA	NA	109	692	(Boustany <i>et al.</i> , 2002)
White shark	Regionally endothermic	547.35	6.4	23.8	NA	NA	140	901	(Bonfil <i>et al.</i> , 2010)
White shark	Regionally endothermic	467.03	12.4	20.6	NA	NA	1	108.3	(Watanabe <i>et al.</i> , 2019b)
White shark	Regionally endothermic	31.56	9	22	NA	NA	28	240	(Dewar <i>et al.</i> , 2004)
White shark	Regionally endothermic	547.35	3.9	25.2	7.5	20	141	495	(Domeier and Nasby-Lucas, 2008)
White shark	Regionally endothermic	593.78	3.9	24.8	5	20	223	979.5	(Nasby-Lucas <i>et al.</i> , 2009)
White shark	Regionally endothermic	56.49	8.4	24	NA	NA	67	NA	(Weng <i>et al.</i> , 2007)
White shark	Regionally endothermic	461.98	5.4	24.2	NA	NA	305	644	(Weng <i>et al.</i> , 2007)
White shark	Regionally endothermic	658.02	1.6	30.4	11	23	316	1128	(Skomal <i>et al.</i> , 2017)
Yellowfin tuna	Regionally endothermic	60.68	18	26.3	21.1	26.3	39	260.4	(Brill <i>et al.</i> , 1999)
Yellowfin tuna	Regionally endothermic	10.14	4.5	28.5	NA	NA	172	1173	(Schaefer <i>et al.</i> , 2007)

Appendix B Supplementary information for Chapter 3: Energetic costs increase with faster heating in an aquatic ectotherm.

Table B.1: Thermal performance curve models fitted to stable temperature data using rTPC R package (Padfield and O'Sullivan, 2021) and associated AICc scores.

Thermal performance curve model	AICc score
Beta (Niehaus <i>et al.</i> , 2012)	81.664
Boatman (Boatman <i>et al.</i> , 2017)	81.999
DeLong enzyme-assisted Arrhenius (DeLong <i>et al.</i> , 2017)	84.642
Flinn (Flinn, 1991)	77.903
Gaussian (Lynch and Gabriel, 1987)	79.088
Pawar (Kontopoulos <i>et al.</i> , 2018)	77.295
Rezende (Rezende and Bozinovic, 2019)	76.838
Sharpe-Schoolfield model (high temperature inactivation only) (Schoolfield <i>et al.</i> , 1981)	77.296
Sharpe-Schoolfield model (low temperature inactivation only) (Schoolfield <i>et al.</i> , 1981)	82.060
Spain (Spain, 1982)	77.542

Table B.2: Experimental data for all temperature trials and individuals, where in Direction, H is heating, C is cooling, and S is stable.

ID	Wet weight (g)	Fasting period (hours)	Acclimation duration (days)	Thermal range (°C)	Direction	λ (°C/min)	Mean temperature (°C)
10T1521R10	0.071	24	23	6	H	0.1178	NA
110T1021R10	0.100	75	25	11	H	0.1628	NA
111T1510R1	0.224	21	26	5	C	-0.0176	NA
114T1510R5	0.178	28.5	26	5	C	-0.0714	NA
117T1521R0.5	0.152	15.5	27	6	H	0.0080	NA
118T1521R0.5	0.140	15.5	28	6	H	0.0079	NA
119T1510R0.5	0.214	15.5	28	5	C	-0.0083	NA
11T1521R10	0.138	24.5	9	6	H	0.1186	NA
121T1510R0.5	0.151	15.5	28	5	C	-0.0084	NA
12T1521R10	0.100	24.5	9	6	H	0.1177	NA
15T1021R0.5	0.076	15	4	11	H	0.0075	NA
18T1021R1	0.138	13	11	11	H	0.0160	NA
19T1021R5	0.235	18	21	11	H	0.0746	NA
1T1521R0.5	0.122	13	6	6	H	0.0078	NA
20T1021R5	0.092	18	21	11	H	0.0771	NA
24T1021R10	0.088	19	5	11	H	0.1484	NA
25T1510R0.5	0.176	15	6	5	C	-0.0079	NA
27T2110R0.5	0.170	26	7	11	C	-0.0079	NA
2T1521R0.5	0.133	13	6	6	H	0.0077	NA
30T2110R1	0.108	21	19	11	C	-0.0155	NA
32T2110R5	0.133	19	17	11	C	-0.0752	NA
34T2110R10	0.295	57	16	11	C	-0.1071	NA

ID	Wet weight (g)	Fasting period (hours)	Acclimation duration (days)	Thermal range (°C)	Direction	λ (°C/min)	Mean temperature (°C)
39T1510R0.5	0.195	15	6	5	C	-0.0081	NA
3T1521R0.5	0.075	22	4	6	H	0.0071	NA
41T1510R1	0.241	12	4	5	C	-0.0186	NA
42T1510R1	0.090	21	5	5	C	-0.0151	NA
43T1510R5	0.105	14.5	10	5	C	-0.0708	NA
46T1510R10	0.179	17	5	5	C	-0.1160	NA
47T1510R10	0.132	20.5	5	5	C	-0.1290	NA
48T1510R10	0.175	27	5	5	C	-0.1195	NA
49T1521R0.5	0.125	30	9	6	H	0.0075	NA
4T1521R1	0.167	20	7	6	H	0.0165	NA
50T1521R0.5	0.077	30	9	6	H	0.0077	NA
51T1521R0.5	0.088	24	10	6	H	0.0073	NA
52T1521R1	0.128	20	7	6	H	0.0148	NA
54T1521R1	0.071	15	12	6	H	0.0150	NA
55T1521R5	0.097	27	3	6	H	0.0755	NA
56T1521R5	0.126	27	3	6	H	0.0696	NA
57T1521R5	0.070	27	3	6	H	0.0727	NA
58T1521R10	0.077	24.5	9	6	H	0.1138	NA
59T1521R10	0.080	24.5	9	6	H	0.1157	NA
60T1521R10	0.070	16	12	6	H	0.1606	NA
61T1021R0.5	0.117	15	4	11	H	0.0077	NA
62T1021R0.5	0.115	27	5	11	H	0.0073	NA
63T1021R0.5	0.197	27	5	11	H	0.0078	NA
64T1021R1	0.141	13	11	11	H	0.0160	NA
65T1021R1	0.189	13.5	11	11	H	0.0158	NA
66T1021R1	0.138	13.5	11	11	H	0.0158	NA
67T1021R5	0.107	14.5	7	11	H	0.0785	NA
68T1021R5	0.095	14.5	7	11	H	0.0785	NA
69T1021R5	0.150	16	10	11	H	0.0740	NA
6T1521R1	0.077	20	7	6	H	0.0165	NA
71T1021R10	0.085	20	9	11	H	0.1509	NA
72T1021R10	0.136	20	9	11	H	0.1503	NA
73T2110R0.5	0.171	26	7	11	C	-0.0079	NA
74T2110R0.5	0.093	26	7	11	C	-0.0074	NA
75T2110R0.5	0.090	26	7	11	C	-0.0079	NA
80T2110R5	0.215	22	10	11	C	-0.0806	NA
81T2110R5	0.138	22	10	11	C	-0.0802	NA
82T2110R10	0.135	16	7	11	C	-0.1419	NA
83T2110R10	0.236	22.5	9	11	C	-0.1416	NA
84T2110R10	0.103	17.5	12	11	C	-0.1286	NA
85T1510R0.5	0.094	15	6	5	C	-0.0079	NA
88T1510R1	0.112	21	5	5	C	-0.0151	NA
91T1510R5	0.115	14.5	10	5	C	-0.0739	NA
92T1510R5	0.184	20	10	5	C	-0.0748	NA

ID	Wet weight (g)	Fasting period (hours)	Acclimation duration (days)	Thermal range (°C)	Direction	λ (°C/min)	Mean temperature (°C)
93T1510R5	0.150	20	10	5	C	-0.0701	NA
94T1510R10	0.117	15	12	5	C	-0.1210	NA
95T1510R10	0.077	15	12	5	C	-0.1176	NA
96T1510R10	0.151	19	12	5	C	-0.1298	NA
97T1021R0.5	0.104	25.5	9	11	H	0.0077	NA
98T1021R5	0.114	16	10	11	H	0.0737	NA
99T1521R0.5	0.175	24	10	6	H	0.0073	NA
108T1021R1	0.105	16	26	11	H	0.0162	NA
100T1521R10	0.118	16	12	6	H	0.1667	NA
103T1021R5	0.087	71	25	11	H	0.0835	NA
104T1021R5	0.257	71	25	11	H	0.0830	NA
112T1521R5	0.143	26.5	26	6	H	0.0818	NA
113T1521R5	0.122	26.5	26	6	H	0.0803	NA
116T1521R0.5	0.108	15.5	27	6	H	0.0078	NA
120T1521R5	0.231	23	27	6	H	0.0767	NA
123T1521R10	0.100	15	29	6	H	0.1257	NA
14T1021R0.5	0.219	27	22	11	H	0.0077	NA
16T1021R1	0.075	15.5	21	11	H	0.0149	NA
17T1021R1	0.145	15.5	21	11	H	0.0157	NA
21T1021R5	0.208	21	4	11	H	0.0781	NA
22T1021R10	0.156	42	20	11	H	0.1323	NA
23T1021R10	0.134	16	21	11	H	0.1358	NA
53T1521R1	0.129	20	7	6	H	0.0152	NA
5T1521R1	0.091	17.5	23	6	H	0.0162	NA
70T1021R10	0.082	14.5	7	11	H	0.1468	NA
7T1521R5	0.138	15.5	23	6	H	0.0743	NA
8T1521R5	0.133	15.5	23	6	H	0.0692	NA
9T1521R5	0.081	27	3	6	H	0.0714	NA
106T1021R5	0.248	73	25	11	H	0.0817	NA
107T1021R10	0.131	75	25	11	H	0.1651	NA
102T1510R10	0.160	19	12	5	C	-0.1230	NA
101T2110R10	0.106	17.5	12	11	C	-0.1368	NA
31T2110R5	0.091	16	17	11	C	-0.0690	NA
29T2110R1	0.104	17.5	18	11	C	-0.0163	NA
115T1510R5	0.124	28.5	26	5	C	-0.0797	NA
45T1510R5	0.234	15.5	23	5	C	-0.0678	NA
33T2110R5	0.048	21	19	11	C	-0.0738	NA
89T1510R1	0.178	15	9	5	C	-0.0169	NA
44T1510R5	0.192	15.5	23	5	C	-0.0671	NA
90T1510R1	0.125	15	9	5	C	-0.0169	NA
40T1510R1	0.125	17.5	23	5	C	-0.0134	NA
79T2110R5	0.153	17	7	11	C	-0.0800	NA
35T2110R10	0.232	57	16	11	C	-0.1084	NA

ID	Wet weight (g)	Fasting period (hours)	Acclimation duration (days)	Thermal range (°C)	Direction	λ (°C/min)	Mean temperature (°C)
86T1510R0.5	0.162	24	8	5	C	-0.0083	NA
87T1510R0.5	0.172	24	8	5	C	-0.0086	NA
26T1510R0.5	0.195	15	6	5	C	-0.0081	NA
36T2110R10	0.117	22.5	9	11	C	-0.1453	NA
77T2110R1	0.085	25	5	11	C	-0.0148	NA
76T2110R1	0.103	25	5	11	C	-0.0148	NA
78T2110R1	0.158	24	8	11	C	-0.0150	NA
109T1510R1	0.193	21	26	5	C	-0.0174	NA
s27_stable14_15	0.096	14	22	NA	S	NA	15.1
s28_stable14_15	0.190	14	22	NA	S	NA	14.7
s29_stable15_15	0.050	23.5	22	NA	S	NA	15.2
s30_stable15_15	0.199	23.5	22	NA	S	NA	15.1
s31_stable16_18	0.090	18	26	NA	S	NA	18.0
s32_stable17_18	0.154	20	26	NA	S	NA	18.0
s33_stable18_12	0.258	40	27	NA	S	NA	12.2
s34_stable19_12	0.163	42	27	NA	S	NA	12.2
s35_stable20_12	0.127	44	27	NA	S	NA	12.3
s36_stable21_12	0.086	14	28	NA	S	NA	11.9
s37_stable22_12	0.160	21	30	NA	S	NA	12.1
s38_stable23_12	0.119	25	2	NA	S	NA	12.5
s39_stable23_12	0.115	25	2	NA	S	NA	12.3
s40_stable24_12	0.100	25	2	NA	S	NA	12.4
s41_stable25_18	0.118	28	2	NA	S	NA	17.9
s42_stable25_18	0.110	28	2	NA	S	NA	17.8
s43_stable26_18	0.123	28	2	NA	S	NA	17.9
s44_stable26_18	0.139	28	2	NA	S	NA	18.1
s45_stable27_18	0.158	30	2	NA	S	NA	18.0
s46_stable27_18	0.117	30	2	NA	S	NA	17.9
s47_stable28_21	0.116	21	3	NA	S	NA	21.0
s48_stable28_21	0.229	21	3	NA	S	NA	20.8
s51_stable30_10	0.133	23	3	NA	S	NA	10.2
s52_stable30_10	0.113	23	3	NA	S	NA	10.7
s53_stable31_21	0.216	23	3	NA	S	NA	20.7
s54_stable31_21	0.125	23	3	NA	S	NA	20.6
s55_stable32_21	0.215	26	3	NA	S	NA	20.7
s56_stable32_21	0.143	26	3	NA	S	NA	20.6
s57_stable33_10	0.142	26.5	3	NA	S	NA	10.4
s59_stable34_10	0.115	29	3	NA	S	NA	10.6
s60_stable34_10	0.131	29	3	NA	S	NA	10.9
s61_stable35_10	0.129	29	3	NA	S	NA	9.9
s62_stable35_10	0.087	29	3	NA	S	NA	10.5
s63_stable36_15	0.165	13	3	NA	S	NA	15.2

ID	Wet weight (g)	Fasting period (hours)	Acclimation duration (days)	Thermal range (°C)	Direction	λ (°C/min)	Mean temperature (°C)
s64_stable36_15	0.163	13	3	NA	S	NA	15.3
s65_stable37_15	0.173	13	3	NA	S	NA	15.4
s66_stable37_15	0.138	13	3	NA	S	NA	15.3
s67_stable38_21	0.160	71	25	NA	S	NA	20.8

Appendix C Supplementary information for Chapter 4: Capture heats up sharks.

Table C.1: Biometrics and measurements taken of all animals included in this study; for restraint method, OD = on deck, & SB = secured alongside the boat; TL = total length (cm), FL = fork length (cm), BM = estimated body mass (kg), HT = hooking time (mins), T_b = body temperature upon capture (°C), T_a = water temperature upon capture (°C), Lac1 = lactate upon capture (mmol/L), Lac2 = lactate immediately prior to release (mmol/L), Gluc1 = glucose upon capture (mmol/L), Gluc2 = glucose immediately prior to release (mmol/L).

Date	Animal ID	Species	Sex	Fishing method	Restraint method	Biologging package	TL (cm)	FL (cm)	BM (kg)	HT (mins)	T _b (°C)	T _a (°C)	Lac1	Lac2	Gluc1	Gluc2
02.05.2019	T1	Tiger shark	Female	Drum line	SB	Yes	298	245	155.67	NA	27.7	26.8	NA	NA	NA	NA
04.05.2019	T2	Tiger shark	Female	Drum line	SB	Yes	311	266	203.5	NA	NA	NA	NA	NA	NA	NA
06.05.2019	T3	Tiger shark	Female	Drum line	SB	Yes	316	264	198.59	NA	28.1	27.6	NA	NA	NA	NA
07.05.2019	T4	Tiger shark	Female	Drum line	SB	Yes	323	267	206.04	NA	28.8	28.2	NA	NA	NA	NA
27.09.2019	BSCC	Blue shark	Male	Angling	OD	Yes	213	170	30.70	13	18.5	17.8	NA	NA	NA	NA
17.07.2021	BS09	Blue shark	Female	Angling	OD	Yes	195	160	25.39	6	19.1	18.5	NA	9.0	NA	22.7
18.08.2021	BS21	Blue shark	Female	Angling	OD	No	162	133	14.24	4	15.9	13.9	2.0	4.4	NA	NA
18.08.2021	BS22	Blue shark	Female	Angling	OD	No	196	161	25.90	5	16.6	15.3	1.9	3.4	4.4	4.1
18.08.2021	BS23	Blue shark	Female	Angling	OD	No	211	168	29.59	4	16.2	15.4	9.0	5.7	NA	2.9
18.08.2021	BS24	Blue shark	Female	Angling	OD	No	193	159	24.90	4	17.5	14.8	7.5	7.5	NA	3.6
18.08.2021	BS25	Blue shark	Female	Angling	OD	No	161	132	13.90	1.4	15.9	14.8	1.2	NA	18.9	NA
18.08.2021	BS26	Blue shark	Female	Angling	OD	No	193	159	24.90	3.9	16.9	14.8	1.5	3.0	19.7	4.1
19.08.2021	BS27	Blue shark	Female	Angling	OD	No	212	176	34.23	4	16.7	16.0	1.5	2.9	NA	4.1
19.08.2021	BS28	Blue shark	Male	Angling	OD	No	161	132	13.90	4	17.4	16.5	3.5	7.1	15.6	19.5
15.09.2021	BS30	Blue shark	Female	Angling	OD	No	159	132	13.90	2.25	18.6	17.4	3.3	4.4	4.5	4.3
05.11.21	BS32	Blue shark	Female	Angling	OD	No	204	169	30.14	6.3	14.3	13.3	1.4	5.7	3.1	3.4
05.11.21	BS33	Blue shark	Female	Angling	OD	No	232	191	44.22	9.8	13.6	13.0	1.8	5.8	3.6	3.4
05.11.21	BS34	Blue shark	Female	Angling	OD	No	191	173	32.43	11.2	14.0	12.9	2.1	NA	3.7	NA
05.11.21	BS35	Blue shark	Female	Angling	OD	No	237	194	46.43	7.3	14.5	12.9	3.1	5.6	3.7	3.4

Table C.2: Fitting of regression models where “deltaT” is $T_b - T_a$ (i.e. ΔT) upon capture; “Lact” is lactate concentration upon capture; “Gluc” is glucose concentration upon capture; “log_bm” is the log of body mass (kg); and “hooking_time” is duration of time from moment of hooking to moment of landing on deck (mins).

Model	R²	AIC
deltaT ~ Lact + Gluc + log_bm + hooking_time	0.4452	16.51698
deltaT ~ Lact + Gluc + log_bm*hooking_time + hooking_time	0.584	15.92566
deltaT ~ log_bm + hooking_time	0.07667	32.80171
deltaT ~ Lact + hooking_time	0.1852	28.98296