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Life in the slow lane: Estimating the metabolic rate and trophic impact of the Greenland shark (Somniosus microcephalus)

By

Eric Ste-Marie

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Life in the slow lane: Estimating the metabolic rate and trophic impact of the Greenland shark (Somniosus microcephalus)

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December 9th, 2020

DECLARATION OF CO-AUTHORSHIP / PREVIOUS PUBLICATION

I. Co-Authorship

I hereby declare that this thesis incorporates material that is result of joint research, as follows: All chapters of the author's thesis were written under supervision of Dr. Nigel Hussey. Both the general introduction and discussion were authored by E. Ste-Marie with editorial guidance by N.E. Hussey. The first data chapter was co-authored by E. Ste-Marie, Y.Y. Watanabe, J.M. Semmens, M. Marcoux, and N.E. Hussey. The text for all sections of this manuscript (Abstract, Introduction, Results, Discussion, Methods and Supplementary information) were written by E. Ste-Marie with co-authors contributing to the study design, interpretation of results, and to the editing of written text prior to submission and during the peer review process. The unpublished manuscript presented in the second data chapter was primarily written by E. Ste-Marie and revised by N.E. Hussey. Y.Y. Watanabe provided guidance and support with the data analysis for this chapter. Additionally, E. Ste-Marie, Y.Y. Watanabe, M. Marcoux, and N.E. Hussey all took part in the data collection process for both data chapters included in this thesis.

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II. Previous Publication

This thesis includes [*1*] original papers that have been previously published/submitted for publication in peer reviewed journals, as follows:

Thesis Chapter	Publication title/full citation	Publication status*
Chapter [2]	Ste-Marie E, Watanabe YY, Semmens JM, Marcoux M, Hussey NE. 2020. A first look at the metabolic rate of Greenland sharks (Somniosus microcephalus) in the Canadian Arctic. Sci Rep. 10(1):19297. doi:10.1038/s41598-020-76371-0.	*Published*

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ABSTRACT

Metabolic rate is intricately linked to the ecology of organisms and can provide a framework to study the behaviour, life history, population dynamics, and trophic impact of a species. Acquiring measures of metabolic rate, however, has proven difficult for large water-breathing animals such as sharks, greatly limiting our understanding of the energetic lives of these highly threatened and ecologically important fish. The following thesis presents the first estimates of metabolic rate for one severly understudied and near-threatened species, the long-lived Greenland shark (*Somniosus microcephalus*). Resting and active routine metabolic rates were estimated through field respirometry conducted on four relatively large-bodied individuals (33-126 kg), including the largest individual shark studied via respirometry. Despite recording very low whole-animal resting metabolic rates, estimates were well explained by derived interspecies allometric and temperature scaling relationships. Combining these results with data acquired from biologger deployments on free-roaming sharks allowed for the estimation of field metabolic rates for individuals inhabiting the Eastern Canadian Arctic. The estimated low energy needs of Greenland sharks in the wild translated to equally low estimates of prey consumpion rate at the individual level. However, when assessed at the scale of localized populations in two coastal fjord ecosystems and across all of Baffin Bay, prey consumption by Greenland sharks is assumed to play a key role in the top-down regulation of Arctic marine food webs, though important data deficiencies must be addressed before final conclusions can be drawn.

DEDICATION

I dedicate this thesis to my parents (both grand- and regular) for their never-ending support and for helping me develop a passion for science and a love of the ocean from a young age.

Je vous aime tous.

ACKNOWLEDGEMENTS

All scientific research requires extensive support and collaboration. While I am the primary author of this thesis, I received help from countless colleagues, faculty members, friends, family, therapists and swimming pool salespeople. Without their collective support, I would not have completed any of the research described in this thesis. In the remainder of this section, I will list the main people and organizations to whom I am endlessly thankful for.

First and foremost, I thank Dr. Nigel Hussey for recognizing my potential and for giving me the opportunity to conduct an insane set of experiments on one of the most unique species on the planet. Through his mentorship I developed a plethora of new skills and even managed to publish one of my thesis chapters before defending. Additionally, I would like to thank my co-authors Yuuki, Jayson and Marianne for their help planning, executing and publishing my first data chapter. I extend special thanks to Yuuki for hosting me at the Japanese polar institute (NIPR) in Tokyo in 2019, where he taught me the analysis techniques needed to analyze the biologged acceleration data for my second data chapter. I am also grateful for the guidance and encouragement provided by my two committee members Dr. Christina Semeniuk and Dr. Oliver Love.

A huge thank you to my amazing lab mates whose support ranged from discussing and workshopping ideas in the office to providing emotional support and friendship outside of the office (as well as rides to and from the airport). You have become some of my closest friends and I hope we will remain as such regardless of where we end up in the future. To Steph – our heroic lab manager –

thanks for all your help organising the field work component of this thesis, including making sure that I arrived in the North on time each year with all my equipment in hand. Although technically not an official Hussey Lab member, thank you to Nancy the graduate secretary for her help with scholarship applications and making sure I never forgot to submit any essential paperwork.

I would like to thank the peoples and HTOs of Mittimatalik (Pond Inlet) and Kanngiqtugaapik (Clyde River) for their continued support and contributions to this research. I also thank the many people who provided logistical support in the field, the crew of the MV Kiviuq II and partners at the EAT research camp in Tremblay Sound. Special thanks to Golder Associates for transporting our large respirometry setup to Tremblay Sound in 2018 and to Robert Hodgson for the organization of EAT. Funding for this thesis came from the Department of Fisheries and Oceans Canada, the Government of Nunavut, the Nunavut Fisheries Association, CanNor, the Molson Foundation, the Natural Sciences and Engineering Research Council of Canada, Mitacs, and the Garfield Weston Foundation. Additional funding was provided by the Japan Society for the Promotion of Science and the Arctic Challenge for Sustainability (ArCS) project.

Finally, thank you to my family (Marc, Jackie, Brianna, Alexandra and Josette), my partner Alexander, my best friends (Michelle, Kelsey and Mirella) and my grandmother Madelaine, whom I lost to COVID-19 while finishing this thesis. I love you all.

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CHAPTER 1

General Introduction

The primary purpose of this thesis is to demystify the ecological role of Greenland sharks (*Somniosus microcephalus*) in the Arctic through novel insight into their energetics and behaviour. The following chapter will serve as a general introduction and provide background information on the major topics of metabolism and ecology discussed in detail in the subsequent data chapters. Specifically, this section will introduce metabolism generally, how it can be applied to ecological studies, and why it is important that we do so in sharks – including the particularly elusive Greenland shark.

1.1 Metabolism

Metabolism is the driving force of life. It fuels the persistence of organisms by supplying the energy they require to maintain homeostasis, reproduce, grow and engage with their surroundings (Metcalfe and Norin 2019). In other words, life could not exist without all the chemical reactions involved in metabolism. The study of metabolic processes is a cornerstone of biology and is essential to developing a thorough understanding of the many patterns observed in nature. Metabolism is closely linked to ecology and consequently provides a basic framework on which we can build hypotheses concerning the behaviour, life history and trophic role of organisms living in a particular ecosystem (Brown et al. 2004). Studying the speed at which metabolism occurs in an organism, or its metabolic rate, is often an effective way to approach ecological questions, as this rate has been shown to correlate with many different physiological and environmental variables (Brown et al. 2004). Furthermore, metabolic rate can ultimately be used to predict if and how organisms are able to cope with changes in the conditions they experience, including most notably, those resulting from anthropogenic climate change (Dillon et al. 2010; Metcalfe and Norin 2019).

Since the field's inception, those studying metabolic ecology have focused much of their attention on the predictable ways in which metabolic rate scales with mass and temperature. In 1932, Kleiber first proposed that metabolic rate scaled with mass to the 3/4 power across species. Since then, countless studies have provided support for and against this exponent; many showing that the allometry of metabolism depends on everything from the lifestyles of species to their habitat and phylogeny (Killen et al. 2010). Similar scaling relationships have also been described for the effect of body temperature on metabolic rate (Gillooly et al. 2001). In this case, metabolic rate tends to increase with increasing temperature. This effect is primarily explained by basic chemical kinetics (Gillooly et al. 2001), which define the rate of chemical reactions (r) in part as a function of temperature (T) according to the Boltzmann factor:

$$r \propto e^{-E_a/kT}$$

where (k) is a constant and (E_a) represents the activation energy of a given reaction. Since metabolism is the sum of reactions occurring in an organism, its rate should increase with a rise in body temperature (Brown et al. 2004). Most studies, however, approximate temperature's effect on metabolism using Q_{10} values which describe the factor by which metabolic rate changes over a ten degree centigrade range (Gillooly et al. 2001).

Unlike the effect of varying body temperature on an organism's metabolism, changes in environmental temperature do not have ubiquitous effects on metabolic rate. Metabolic processes occur internally and so animals that thermoregulate physiologically (i.e. endotherms) are not affected by changes in ambient temperature in the same ways as animals whose body temperatures vary according to their surroundings (i.e. ectotherms) (Peck 2002; Angilletta et al. 2010). In ectotherms, variable ambient temperatures can lead to large changes in body temperature, ultimately leading to highly variable metabolic rates (Sinclair et al. 2013).

Though undeniably important, mass and temperature are not the only factors responsible for determining the metabolic rate of an animal. In fact, life costs are determined by the amalgamation of many physiological, behavioural and environmental factors (Lear et al. 2017; Metcalfe and Norin 2019). Activity, for example, is a particularly important contributor to an animal's energetic costs in the wild. In general, metabolism scales positively with increases in activity, since movement results from muscle contractions which are themselves fueled by metabolic energy (Wilson et al. 2006). However, the extent to which behaviour affects metabolism differs based on factors such as the biomechanical efficiency of the behaviour, the physiology of the animal, and its phylogeny (Gleiss et al. 2011; Cooke et al. 2016; Auer et al. 2017). Quantifying the energetic costs of ecologically relevant behaviours is therefore essential to understanding the energetics of wild animals beyond the confines of the laboratory.

1.2 Shark Energetics

Sharks often play important roles in global marine ecosystems (Heithaus et al. 2010), yet relatively little is known regarding their energetics due to the inherent logistical and biological challenges associated with measuring metabolic rate in these typically large species (Sims 2000; Carlson et al. 2004; Lawson et al. 2019). As a result of this, evaluating the predatory impact of most sharks on their ecosystems has mostly been possible indirectly, through comparisons between healthy systems and those where sharks have been significantly depleted or extirpated (Stevens 2000), or qualitatively through assumptions based on trophic position (Hussey et al. 2015). Alternatively, developing an understanding of the energetic demands of sharks allows one to quantitatively estimate their impact on ecosystems (Semmens et al. 2013; Barnett et al. 2017). Metabolic rate defines their energetic requirements, which can then be transformed into prey consumption rates using information on the composition, caloric value and proportion of prey types in their diet (Semmens et al. 2013). Scaled to population, consumption rate can be used to estimate the overall trophic impact of a population inhabiting a specific ecosystem (Barnett et al. 2017).

Measuring the decline of oxygen resulting from respiration in a closed system (or respirometry) is widely accepted as the gold standard for estimating metabolic rate in fish, but can be challenging when dealing with large animals that are highly active in captivity (e.g. sharks; Carlson et al. 2004; Svendsen et al. 2016). Also challenging, is the requirement to build a respirometer capable of housing large fish and the associated high financial costs of doing so. To bypass these issues, some have identified methodological approaches that can estimate metabolism without the need for respirometry. For example, Sims and colleagues were able to estimate the metabolic rate of basking sharks using the prey density at which they cease foraging (Sims 2000). However, the use of such a method is restricted to filter feeders that forage optimally and is therefore not applicable for the majority of shark species. Furthermore, other common methods for estimating metabolic rate, such as the doubly labeled water method, are not effective on sharks (Green 2011; Treberg et al. 2016). On the other hand, methods such as electromyography and accelerometry, which have been used to effectively estimate the field metabolic rate (FMR) of some shark species (Scalloped hammerhead (*Sphyrna lewini)*, Lowe 2002; Lemon sharks (*Negaprion brevirostris*), Bouyoucos et al. 2018), still require calibration via respirometry trials (Cooke et al. 2016).

As previously discussed, the allometric and temperature based scaling of metabolic rate can provide insight into the ecology of wildlife, but defining such relationships requires data from a wide range of body sizes and experimental temperatures. For sharks, these relationships have been primarily derived from respirometry studies involving small individuals (~0.5-10kg) and warm temperatures (>10°C; See Table 7.1 in Carlson et al. 2004). In fact, there are only a few recent cases in which larger sharks have been studied in a respirometer and even those studies used individuals that weighed less than 50kg (Ezcurra et al. 2012; Payne et al. 2015). For example, Ezcurra et al. (2012) measured the oxygen consumption of one of the largest shark species, the white shark (*Carcharodon carcharias*); however, this was performed using young-of-year individuals weighing a fraction of what an average adult would weigh (22.6-36.2kg vs ~500-1000kg; Ezcurra et al. 2012). There is a clear gap in our understanding of shark metabolic rates and, as such, our knowledge on the topic is skewed towards small or young, tropical and temperate species. Therefore, obtaining metabolic rate estimates for large sharks living in cold environments is needed to improve our understanding of shark metabolism while strengthening the predictive power of metabolic scaling relationships across all shark species.

1.3 Greenland Sharks

Larger than all other polar fishes and inhabiting the often near-freezing waters of the Arctic, the Greenland shark (*Somniosus microcephalus*) is a unique species whose metabolism has yet to be studied in the lab or in the field (MacNeil et al. 2012; Edwards et al. 2019). Despite their slow recorded swim speeds, these sharks feed on a wide variety of prey, including marine mammals, fish and cephalopods. The extent to which Greenland sharks hunt versus scavenge is unknown, though anecdotal accounts and qualitative observations support the use of both foraging strategies (MacNeil et al. 2012; Nielsen et al. 2014). Overall, very little is currently known about the distribution, behaviour and ecology of this near-threatened species (IUCN 2020). Similarly, only local abundance estimates have been derived for Greenland sharks in certain parts of the Arctic, leaving their population status across most of their geographic range unknown (Devine et al. 2018). These slow swimming sharks are also slow to age, having an estimated lifespan of several centuries and a predicted size at maturity of 2.84 m for males and 4.19 m for females (Nielsen et al. 2020). Slow metabolic rates are frequently observed in species with slow life histories; and a causal link between these traits has even been demonstrated experimentally in some fishes (Auer et al. 2018). Given this, their size, and the temperatures they experience in the wild, Greenland sharks are predicted to have very low metabolic rates (Augustine et al. 2017; Shadwick et al. 2018).

1.4 Study System

The fieldwork component of this thesis took place in Scott Inlet (71°03'N 71°21'W) and Tremblay Sound (72°18'N 81°09'W), Nunavut, both located on the North-East coast of Baffin Island in the Eastern Canadian Arctic (Figure 1.1). These inlets are important fishing grounds for local communities and represent important summering habitats for narwhals (Heide-Jørgensen et al. 2002; Marcoux et al. 2017). Both locations are a part of the larger Baffin Bay area, where commercial fisheries for Greenland halibut (*Reinhardtius hippoglossoides*) and Northern prawn (*Pandalus borealis*) operate. Greenland shark bycatch is high in the commercial offshore Greenland halibut fishery (61 and 27 tons in sub division 0A in 2009 and 2010 respectively; DFO 2013) and could have a significant impact on shark populations, especially considering the increase in fishing effort over the last two decades (Figure 1.2; DFO 2013). However, the extent to which this may be affecting shark populations is not yet known because of the lack of comprehensive population data (Devine et al. 2018) and post release survival/mortality estimates following capture and release from commercial fishing gear. Even so, with an age at sexual maturity upwards of 1.5 centuries, as well as an 8-18 year predicted gestation period (Nielsen et al. 2016; Augustine et al. 2017), it is unlikely that Greenland shark populations are able to sustain much, if any, increased mortality resulting from bycatch. The importance of the Baffin Bay area to both Inuit and commercial fishers emphasizes the need for an improved understanding of the underlying ecology of the system, including the role of its largest ectothermic predator the Greenland shark.

1.5 Objectives

Considering the threats facing Greenland sharks and their potential importance with regards to top down regulation of Arctic marine food webs, there is a clear need for research on the ecology of this species. Since metabolism and ecology are intricately linked, an understanding of the energy requirements of these sharks would provide a solid foundation for future studies on Greenland shark ecology and would allow quantification of their impact as consumers in a rapidly changing ecosystem. Nevertheless, there are currently no metabolic rate estimates in the literature for this species. Chapter 2 will focus on bridging this knowledge gap through the estimation of resting and active metabolic rates in this species using custom-built field respirometers. These estimates will then be added to those for all previously studied ectothermic species of shark and used to derive interspecific allometric and temperature scaling relationships for this threatened group of fish. Building on these results, Chapter 3 will focus on modeling the field metabolic rate (FMR) and prey consumption rates of Greenland sharks using biologged activity and temperature data.

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TABLES AND FIGURES

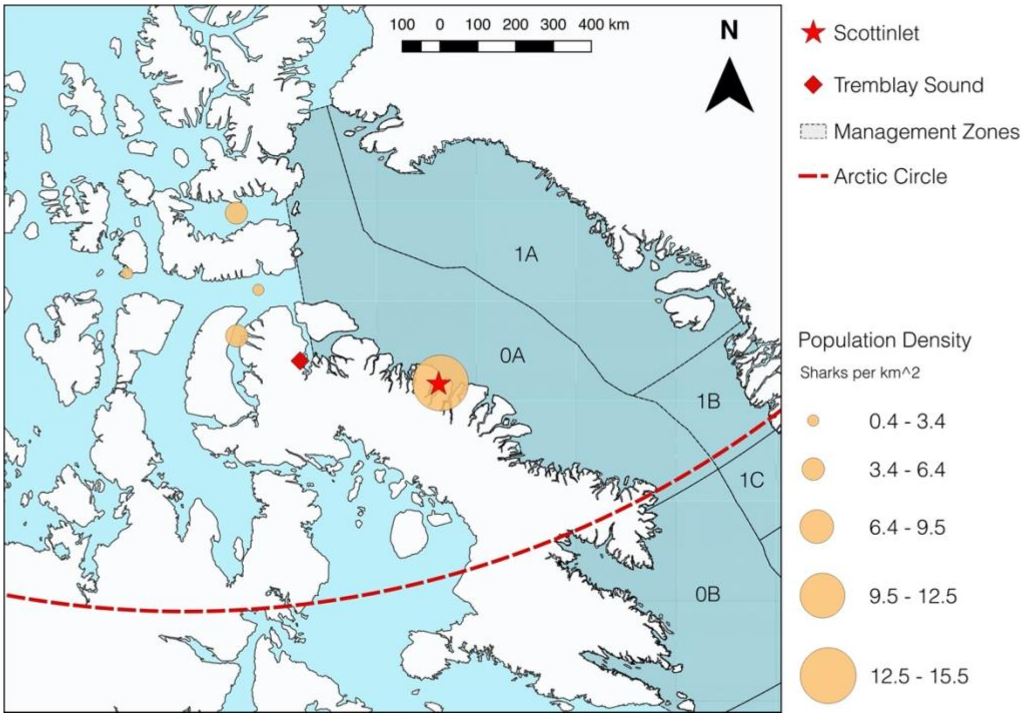

Figure 1.1: Map of the greater Baffin Bay area. Red icons designate the two field locations (i.e. Scott Inlet [star] and Tremblay Sound [diamond]) where sharks underwent respirometry trials or were equipped with biologger packages between 2015 and 2019. Shaded regions represent NAFO fisheries management divisions for Baffin Bay. Orange circles represent local population density estimates of Greenland sharks in the Eastern Canadian Arctic (data from Devine et al. 2018).

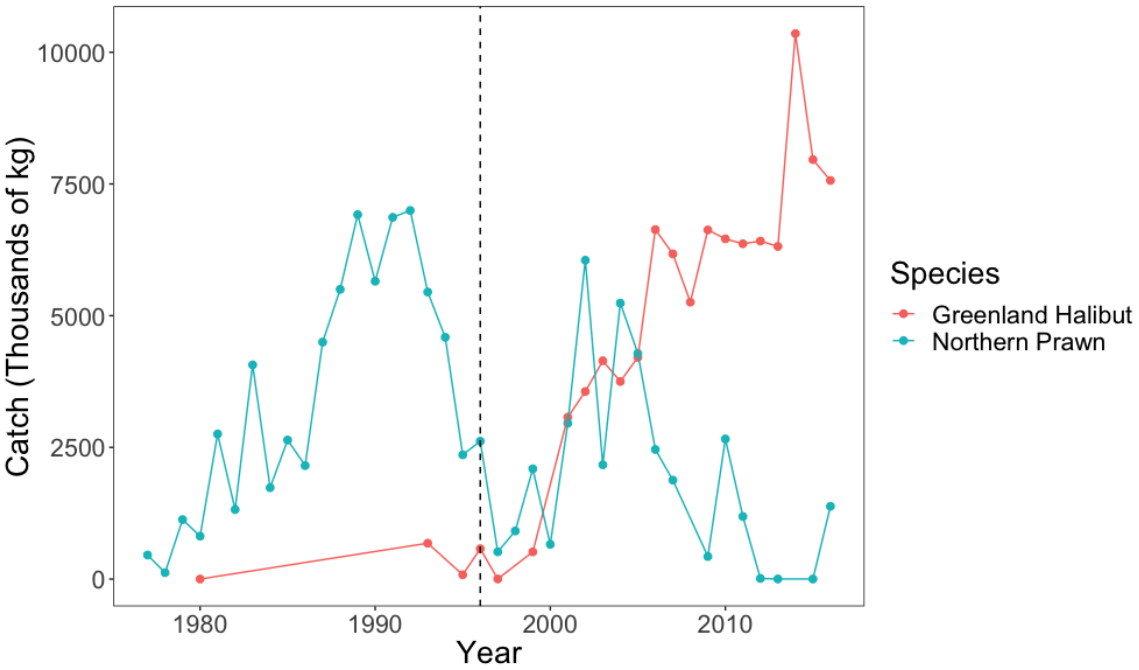

Figure 1.2: Total catch is plotted over time for the two commercial fisheries operating in our study region (management zone 0A). The dashed vertical line represents the start of the Greenland halibut commercial fishery in 1996. Data was acquired from NAFO's 21A database.

CHAPTER 2

A First look at the metabolic rate of Greenland sharks (Somniosus microcephalus) in the Canadian Arctic

2.1 Introduction

Organisms inhabiting extreme environments have long been of special interest to ecologists, physiologists and evolutionary biologists alike (Cavicchioli et al. 2011; Riesch et al. 2015), particularly as these environments, including the poles, deserts and the deep sea are not rare, but in fact cover vast expanses of the planet (Wharton 2007). To assess the mechanisms facilitating life in extreme environments, the study of metabolic rate is regarded as a powerful tool given it combines insight into both the physiology and ecology of an organism (Elliott et al. 2013; Lear et al. 2020). This is based on the premise that the rates at which lifeforms acquire and expend energy are intricately linked to the abiotic and biotic conditions that constrain individual life on a daily basis (Brown et al. 2004). In ectotherms, body mass (biotic) and environmental temperature (abiotic) are amongst the most studied variables known to influence metabolic rate (Clarke and Johnston 1999; Brown et al. 2004; Schulte 2015). Since Kleiber first published his seminal work linking body mass to metabolic rate (Kleiber 1932), much research has focused on defining this relationship within and across taxonomic boundaries (Clarke and Johnston 1999; Glazier 2010; Jerde et al. 2019). Although the exact extent to which metabolic rate changes with the mass of organisms can vary (van der Meer 2006), the general pattern that mass-adjusted metabolic rate decreases with increasing body mass is widely observed and accepted as a fundamental biological concept (Brown et al. 2004).

Temperature’s effect on metabolic rate, similar to that of mass, can be assessed across species (i.e. interspecific; Clarke and Johnston 1999), as well as within species (i.e. intraspecific; Luongo and Lowe 2018). While intraspecific scaling relationships can be useful when modeling the energetic needs of a specific animal under natural conditions (Lear et al. 2020), interspecific relationships are useful as a reference point for the comparison of species (White et al. 2011). Understanding these patterns is important since changes in energetic demand have been shown to systematically impact behaviour, life history (e.g. longevity, age at maturity, reproductive periodicity), and feeding requirements of individuals, which in turn affect population dynamics and ecosystem function (Brown et al. 2004). Furthermore, unique data for extreme-temperature adapted species can broaden the scope and confidence of interspecific metabolic scaling relationships that aid in the development of ecologically relevant bioenergetic and evolutionary hypotheses (Glazier 2010). For example, it has long been argued that species adapted to polar environments maintain relatively elevated metabolic rates to enable physiological processes that would otherwise be hindered by the extreme cold temperatures they inhabit (Krogh 1914). In other words, a polar species is expected to have a metabolic rate that is higher than that predicted by the interspecies scaling relationship for a given temperature (Messamah et al. 2017). While data from more recent studies contradict this theory, demonstrating that polar species are not metabolically cold adapted (Holeton 1974; Clarke and Johnston 1999; Steffensen 2002; Peck 2016), a few studies also provide support for the theory (White et al. 2011), indicating further investigation is needed across a wider phylogenetic range.

In fish, standard metabolic rate (SMR) is a fundamental measure of metabolism. It describes the basic energetic maintenance costs of an unfed individual at rest. For many species, SMR cannot be feasibly estimated under laboratory or field conditions, so resting routine metabolic rate (rRMR) is often used as a proxy (Chabot et al. 2016). This metric generally describes the same conditions as SMR, but is used when the latter's strict assumptions cannot be met (e.g. if the fish exhibits minor postural fin movements during respirometry trials). Measuring SMR (or rRMR) poses additional challenges when studying sharks, as respirometry trials are expensive and logistically difficult to perform on large bodied individuals (Lawson et al. 2019). As such, SMR estimates for sharks are relatively rare and often skewed towards small species and juveniles (Lowe 2001; Luongo and Lowe 2018). In addition, active metabolic rates are often used to extrapolate SMR in obligate ram-ventilating species (Lear et al. 2020), which can lead to variable estimates depending on the methodology used and the range of swim speeds covered (Chabot et al. 2016). Recent studies have found creative ways to curtail some of these challenges (Payne et al. 2015; Byrnes et al. 2020), but overall, the metabolic rates of sharks remain relatively understudied.

The Greenland shark (*Somniosus microcephalus*) is one of the largest carnivorous fish species that is widely distributed across the North Atlantic and Arctic oceans, yet many aspects of its physiology and ecology remain a mystery including its metabolic rate (MacNeil et al. 2012; Edwards et al. 2019). While previous work has used dynamic energy budget (DEB) models to estimate certain life history characteristics in this species (e.g. gestation period), these have yet to be validated experimentally (Augustine et al. 2017). Greenland sharks occur at higher latitudes than all known species of shark and, as such, experience some of the coldest water temperatures on the planet (as low as -1.8 °C; MacNeil et al. 2012). At adult lengths reaching greater than 5 metres and with an estimated lifespan of 392 ± 120 years, they are the largest fish inhabiting the Arctic and the oldest known vertebrate species on the planet (MacNeil et al. 2012; Nielsen et al. 2016). Paradoxically, they are also among the slowest fish in the ocean when accounting for body size, with a maximum recorded swim speed of only 0.74 $m \cdot s^{-1}$ (Watanabe et al. 2012). Despite the obvious uniqueness of Greenland sharks, their size and tendency to inhabit deep and remote areas of the ocean has made studying them expensive and logistically difficult (Edwards et al. 2019). Even so, their relatively high trophic position (4.2-7.7; Hussey et al. 2014) and abundance (up to 15.5 individuals per km^2; Devine et al. 2018) imply that they are important top-down regulators in Arctic food webs. In addition, through the scavenging of large carcasses (e.g. whale falls), Greenland sharks contribute to nutrient cycling which could aid in stabilizing food webs (Wilson and Wolkovich 2011).

Drawing from a novel dataset comprised of oxygen consumption rates measured through field respirometry trials, we provide the first estimates of resting and active routine metabolic rate (rRMR and aRMR) for the Greenland shark. Representing an extreme in terms of both body size and experimental temperature, we integrate our estimates with those of all sharks studied to date to derive a shark-specific interspecies metabolic scaling relationship for mass and temperature. We then compare our metabolic rate estimates for Greenland sharks with the values predicted by this derived equation in order to test for metabolic cold adaptation in this species. As a large and slow-moving species inhabiting extreme low temperatures, and given that most recent work has found little evidence supporting metabolic cold adaptation in polar species (Peck 2016), we hypothesized that Greenland sharks have predictably low metabolic rates when compared to all other sharks studied to date (Clarke and Johnston 1999; Lear et al. 2017; Luongo and Lowe 2018).

2.2 Results

2.2.1 Respirometry

Using two large custom-built field respirometers, we measured the metabolic oxygen consumption rates of four Greenland sharks with individuals reaching body masses exceeding those used in previous studies on other fish (33-126 kg; Table 2.1). The largest of these individuals, held in a 16,570 L swimming pool in the high Arctic (Tremblay Sound, Nunavut), had an estimated mass that was more than double that of the largest shark previously studied in a respirometer (Previous record = 47.7 kg; Payne et al. 2015). Both resting and active routine metabolic rate (rRMR and aRMR) were estimated for this individual at an experimental temperature of 3.8 °C. Average mass-adjusted rRMR across measurement intervals for this shark was 23.07 ± 4.62 (SD) $mgO_2h^{-1}kg^{-0.84}$, while aRMR during an approximate twenty-minute period when the shark swam volitionally with a constant tailbeat frequency (TBF) of 0.18 Hz was 30.96 $mgO_2h^{-1}kg^{-0.84}$. Of the three individuals studied using a smaller rectangular respirometer aboard the MV Kiviuq II the following year (Scott Inlet, Nunavut), two were inactive for extended periods providing estimates of rRMR of 22.29 ± 2.90 and 17.23 ± 0.90 (SD) $mgO_2h^{-1}kg^{-0.84}$, at 4.9-5.1 °C. The third individual remained active throughout the trial yielding an aRMR estimate of 40.46 ± 2.17 (SD) $mgO_2h^{-1}kg^{-0.84}$, at 4.9 °C; however, this individual's movement was inhibited by the holding tank, so we excluded it from further analysis.

2.2.2 Metabolic Scaling in Sharks

From previous experimental studies, we extracted rRMR and SMR estimates for eighteen shark species spanning nine families (SI Table 2.1). These experimental studies were conducted on animals ranging in size from <0.5 to 12.4 kg and in experimental temperatures from 6.5 to 32.5 °C. Combining estimates with our rRMR results for Greenland sharks, we derived interspecific mass and temperature scaling coefficients for whole-animal metabolic rate via multiple regression analysis with each species weighted evenly (adjusted $R^2 = 0.761$, $n = 34$, $p < 0.0001$; Figure 2.1). The resulting mass coefficient translates to an allometric scaling exponent of 0.84, whose 95% confidence intervals (0.67-1.01) include the range of values published for global teleost fish (0.70-0.89; Clarke and Johnston 1999; Killen et al. 2010; Jerde et al. 2019). The coefficient describing the effect of temperature on $\log_{10}$ metabolic rate (0.035) can be approximated by an overall interspecific Q_{10} of 2.23 across a ~29 °C temperature range (3.8-32.5 °C). This interspecific Q_{10} is within the wide range of intraspecific values derived for individual shark species (1.34-2.99; full Q_{10} list provided in SI Table 2.2), and its 95% confidence intervals include both the overall interspecific Q_{10} and median intraspecific Q_{10} values derived for teleost fish (1.83 and 2.40; Clarke and Johnston 1999). Additionally, we found that the rRMR estimates for the Greenland sharks studied here were all within the confidence intervals predicted by our overall interspecies metabolic scaling model.

2.3 Discussion

Our whole-animal rRMR results for Greenland sharks indicate that these fish have very low energetic needs. However, the rRMR of examined Greenland sharks is well within the 95% confidence intervals predicted by our interspecific metabolic scaling relationship for mass and temperature across sharks. As such, our findings suggest that Greenland sharks are not metabolically cold adapted. While these results present a preliminary look at the metabolic ecology of this species, further investigation into the effect of mass and temperature on metabolic rate across individual Greenland sharks is required to accurately predict the dynamics of metabolic rate for this species in the wild.

The analysis of resting metabolic rate across shark species provided an allometric scaling exponent that was comparable to those derived for teleost species (0.70-0.89; Clarke and Johnston 1999; Killen et al. 2010; Jerde et al. 2019). Due to the limited number of studies reporting respirometer derived SMR or rRMR estimates for sharks, and variability in the methods used to acquire these estimates (Lear et al. 2018), we could not be as stringent with our study selection criteria as those used in previous analyses of teleosts. Nevertheless, our results identify that allometric scaling of metabolic rate in sharks across a large mass spectrum falls within the range of values for teleost fish examined at a global scale. However, scaling exponents for individual shark species, similar to teleost fish, will likely differ from the interspecific value according to lifestyle (e.g. pelagic vs. benthic), metabolic level, and swimming style of the species in question (Killen et al. 2010). These factors vary immensely across shark species and can likely explain some of the variation observed around our interspecies scaling relationship. For example, the nurse shark (*Ginglymostoma cirratum*) has the lowest mass and temperature adjusted SMR among studied shark species because it is adapted to a relatively inactive lifestyle (Whitney et al. 2016). So far, only two studies have assessed intraspecific metabolic allometry in sharks, both of which yielded similar scaling exponents to our overall interspecific value of 0.84 (0.86 for lesser spotted dogfish [*Scyliorhinus canicula*], Sims 1996; 0.80 for zebra sharks [*Stegostoma fasciatum*], Payne et al. 2015).

Allometric scaling of metabolic rate is often used to estimate the energy requirements of large sharks (e.g. white shark [*Carcharodon carcharis*]; Semmens et al. 2013), yet most respirometry is conducted on small species (Giacomin et al. 2017), or juveniles of large species which could have metabolic rates that differ from their adult counterparts (Lowe 2002; Ezcurra et al. 2012). When extrapolating the metabolic rates of large individuals using estimates derived for individuals that are order(s) of magnitude smaller, minor differences among commonly used scaling exponents can lead to large discrepancies in estimated results (Payne et al. 2015; Lawson et al. 2019). For example, extrapolated metabolic rates for whale sharks weighing 5000 kg varied by a factor of 6.5 depending on the scaling exponent used (Payne et al. 2015). This example, albeit extreme, emphasizes the need for metabolic rate data for large-bodied sharks, thus reducing the need for extrapolation. In the absence of such information, studies attempting to model the energetics of wild sharks typically rely on interspecific scaling equations or those borrowed from other species (Semmens et al. 2013; Barnett et al. 2017; Watanabe et al. 2019), which undoubtedly increases the uncertainty surrounding estimates.

As with mass, the effect of temperature on metabolic rate is known to vary across species (SI Table 2.2). Several studies have addressed temperature dependent intraspecific scaling of metabolic rate in sharks, with metabolic Q_{10} estimates ranging from 1.34 in scalloped hammerhead sharks (*Sphyrna lewini,* Lowe 2001) to 2.99 in nurse sharks (*Ginglymostoma cirratum,* Lear et al. 2017). Due to our limited sample size and narrow range of experimental temperatures across respirometry trials, we could not address intraspecific scaling in Greenland sharks. However, the addition of metabolic oxygen consumption data for this cold-living species to the pooled data for all studied sharks, allowed for the assessment of how metabolic rate scales with temperature interspecifically across this diverse group of cartilaginous fish. We report that the across-shark Q_{10} of 2.23 is slightly higher than that derived for teleost fish (Q_{10} = 1.83) across a similar range of temperatures (Clarke and Johnston 1999). This could mean that, overall, the metabolic rates of sharks are more sensitive to temperature than those across teleost fish; however, the broad confidence intervals surrounding our Q_{10} estimate (1.74-2.85) include the value published for teleost fish, suggesting this small difference may not represent a real evolutionary difference between both groups of fish.

Conducting field respirometry trials on Greenland sharks in remote regions of the Arctic presents many logistical and methodological challenges. While the results of the present study provide novel insight into the metabolism of a large Arctic shark, several caveats must be acknowledged. Notably, short acclimation periods (2.5 hours) prior to conducting respirometry trials could have led to inflated rRMR estimates arising from stress/recovery costs (Chabot et al. 2016). Additionally, we were unable to confirm if individuals were in a post-absorptive state, consequently specific dynamic action (SDA) could have increased the rate of oxygen uptake in our experimental animals if they were actively digesting a meal at the time of study (Secor 2009; Chabot et al. 2016). Though important to consider, fasting a large polar ectotherm such as the Greenland shark could take weeks and would not have been feasible under field conditions. Even if the rRMR estimates provided here represent an over-estimate of the true SMR of Greenland sharks, we found no indication that Greenland sharks are metabolically cold-adapted. Given the methodological caveats outlined above, their true SMR might actually be lower than expected for a species inhabiting the extreme cold waters of the Arctic. The latter point would seem feasible given their longevity and proclivity for deep-sea environments, both of which have been linked to reduced metabolic rates in other fish (Drazen and Seibel 2007; Auer et al. 2018).

Despite having a seemingly unremarkable mass and temperature adjusted metabolic rate in comparison to other sharks, it is important to consider the implications of the extremely low whole-animal metabolic rates measured here at ecologically relevant experimental temperatures, as it relates to the ecological role of Greenland sharks in the Arctic. With such low energetic needs, Greenland sharks may be capable of surviving extended periods of time without feeding following the consumption of energy rich prey (Edwards et al. 2019). For example, assuming an assimilation efficiency of 73% (Brett and Groves 1979), and that 1 mol O_2 is equal to 434 kJ (Widdows 1987), the aRMR of the 126 kg shark studied in the Tremblay Sound respirometer would translate to a daily caloric requirement of only 192 kcal. If we further assume Greenland sharks can store energy in their tissues or as undigested food in their gut (Armstrong and Schindler 2011), the consumption of a whole juvenile seal weighing 25 kg could theoretically allow the shark to survive >365 days without subsequent feeding events (caloric value of ringed seal taken from Stirling and McEwan 1975). This preliminary estimate accepts that aRMR measured at a specific activity level and temperature is not necessarily representative of the individual's field metabolic rate but serves to contextualize its low metabolic rate in ecological terms.

Furthermore, the consumption of large meals by Greenland sharks combined with their slow metabolism could facilitate life in resource scarce environments, such as the Arctic, and allow this species to maximize the use of seasonally abundant or migratory prey such as marine mammals. This is further supported by evidence that a fish's tendency to exhibit hyperphagia increases dramatically at cold temperatures (Furey et al. 2016). However, the mechanisms driving the feeding and digestive physiology of wild free roaming animals remain largely unknown and understudied, making it difficult for ecologists to explain or predict feeding behaviour in the wild. As such, energetic models for animals under natural conditions require significant assumptions (Armstrong and Schindler 2011). Further study of the digestive physiology and field metabolism of Greenland sharks is necessary to increase our understanding of hyperphagia and feeding frequency in this highly vulnerable species.

Among the world's largest fish and inhabiting some of the deepest and coldest waters on the planet, the long-lived Greenland shark provides a unique model to study animal physiology under extreme conditions. Despite this, our results suggest the Greenland shark's resting metabolic rate is unremarkable when the effects of temperature and mass are accounted for, but further investigation is needed to uncover how metabolic rate scales within the species. The logistics of measuring the metabolic rates of large sharks continues to prevent the widespread application of standardized respirometry practices commonly used to assess the metabolism of small fish. Despite this, we show that interspecific metabolic scaling with mass and temperature across sharks yields similar scaling coefficients as those derived for teleost fish, even with the inclusion of data for sharks at much larger body sizes than previously studied. As the use of metabolic data in ecological modeling grows in popularity, there is a pressing need to improve our understanding of the dynamics of metabolic rate within and across shark species.

2.4 Methods

2.4.1 Respirometry

To estimate the metabolic demands of Greenland sharks, respirometry trials were conducted on temporarily captive wild sharks (see SI appendix for details on all fishing and fieldwork protocols). We built two types of respirometer for this study (Figure 2.2). The first was a 16570 L circular static respirometer in Tremblay Sound that allowed the measurement of the routine oxygen consumption rate of a shark at rest and while swimming volitionally (i.e. rRMR and aRMR). The second was a smaller (600-910 L) rectangular tank in which we were able to measure the rRMR of sharks aboard a commercial fishing vessel (MV Kiviuq II) in Scott Inlet. Submersible pumps were used to homogenize dissolved oxygen levels in both respirometers during trials and plastic drop sheeting was used to seal the water surface area to prevent gas exchange with air. Due to the logistical challenges of conducting respirometry trials on large animals in the field and the assumed slow digestion rate of Greenland sharks at low temperatures, we could not starve individuals ahead of measuring their oxygen consumption rates. As such, we refer to our estimates as routine metabolic rate instead of true standard or active metabolic rate according to Chabot et al. (2016).

In both experimental setups, trials for each shark began after an acclimation period of 2.5 hours at the same water temperatures recorded during the trials themselves (i.e. 3.7-3.8 °C in Tremblay Sound and 4.9-5.1 °C in Scott Inlet). Three to five 60-minute trials were run intermittently for each shark in Scott Inlet (individual trial estimates available in SI Table 2.3), with twenty-minute intervals between each trial to replenish dissolved oxygen levels in the tank. Due to the large volume of the Tremblay Sound respirometer, dissolved oxygen levels remained high (>95% original concentration) so only one depletion was performed. Timed notes were taken to track behavioural changes of individuals (i.e. swimming, resting, rolling) throughout each trial in both setups, allowing the selection of periods of continuous rest to estimate rRMR and periods of sustained swimming to estimate active routine metabolic rate (i.e. aRMR). Background respiration rates were measured daily (immediately following shark trials) and subsequently used to correct the slopes observed during Greenland shark trials. Dissolved oxygen concentrations were measured every ten seconds using an HQ40d meter and two LDO101 probes (HACH).

All trials conducted in the Scott Inlet respirometer setup resulted in dissolved oxygen depletions with high R^2 values (> 0.95). The R^2 values for the individual studied in the Tremblay Sound respirometer were lower (0.67-0.93), despite depletions being linear (i.e. residuals were evenly scattered around fitted line). This was a result of the large volume of water in the respirometer, the very slow rate of oxygen uptake by the shark, and the level of sensitivity of the dissolved oxygen probe over short sampling intervals. Dissolved oxygen levels decreased at a rate that was too slow to be sensed every ten seconds by our probes, leading to greater spread in the raw data and the lower observed R^2 values over the short measurement periods when the shark maintained continuous resting or swimming behaviour (roughly 20-60 mins). While using a smaller respirometer would have improved the R^2 value, it would have also impeded the shark’s ability to swim, leading to inflated metabolic rate estimates.

2.4.2 Calculating Oxygen Consumption Rate

Raw oxygen depletion data was used to estimate mass adjusted metabolic oxygen consumption (MO_2) according to the following equation:

$$MO_2 = (V \times \Delta O_2) / (\Delta t \times m^{0.84})$$

where (V) is the volume of water in the respirometer (total volume – estimated volume of the shark; Svendsen et al. 2016), (m) is the body mass of the shark adjusted using the interspecies allometric scaling exponent derived here (0.84), and (ΔO_2) is the change in oxygen concentration over time (Δt)(Clark et al. 2013). Shark mass was either measured directly for smaller sharks (n = 2 individuals) or estimated using a published Fork length (FL)-Body mass relationship for larger individuals (n = 2; m = 1.109 × 10−6 × FL3.41990; Leclerc et al. 2012). The slope of each oxygen depletion trial was adjusted using the slope of a blank trial of equal duration (i.e. $\text{slope}_{[\text{with shark present}]} - \text{slope}_{[\text{with shark absent}]}$). In doing so, we accounted for any background respiration occurring in the unfiltered seawater used in the respirometers.

2.4.3 Interspecies Comparison of rRMR in Sharks and Relative to Global Teleosts

We conducted a literature search and compiled mean SMR and rRMR estimates for all shark species previously studied via respirometry, excluding data for endothermic species (SI Table 2.1). Due to the logistic challenges of measuring metabolic rate in large-bodied sharks, most of these experiments were conducted on juveniles. We estimated the relative contributions of $\log_{10}$-mass and temperature on the $\log_{10}$-metabolic rate (whole-animal estimates) of sharks using multiple regression analysis. To avoid statistical imbalances arising from some species being overrepresented in the data (i.e.

multiple studies on one species and/or multiple estimates derived at different temperatures or masses), data were weighted by species (weight = 1/number of points for a given species). Whereas previous meta-analyses on teleost fish have dealt with this issue by selecting a single representative study for each species in the regression (Clarke and Johnston 1999; Killen et al. 2010), we opted to use weighted points to avoid having to omit studies from the already limited number published for sharks (further details available in SI appendix). The model output provided coefficients “a” and “b” describing the contribution of $\log_{10}$-mass and temperature to $\log_{10}$ whole-animal SMR/rRMR such that:

$$\mathrm{Log}_{10}\ \mathrm{SMR} = b(\mathrm{Log}_{10}\ \mathrm{Mass}) + a(\mathrm{Temperature})$$

Where “b” represents the interspecies allometric scaling exponent for sharks (i.e. $\mathrm{SMR} \propto \mathrm{Mass}^{b}$) and where “a” can be used to derive an overall Q_{10} value by calculating metabolic rates (R_1 and R_2) at both temperature extremes in our data set (T_1 and T_2) using the equation above and holding mass constant, then subsequently plugging these values into the Q_{10} equation below:

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{10/(T_2-T_1)}$$

For visualization purposes, we plotted the effect of temperature and mass on metabolic rate separately (Figure 2.1). We also extracted high and low allometric scaling exponents from published meta-analyses on teleost fish, as well as intraspecific Q_{10} values for sharks, to use as reference points when assessing our interspecific values.

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TABLES AND FIGURES

Table 2.1: Summarized data for Greenland sharks (*Somniosus microcephalus*) that underwent respirometry trials in Tremblay Sound and Scott Inlet, Nunavut, Canada (n=4). Reported study temperatures represent the mean recorded temperature throughout the trials.

							Mean Mass-adjusted Metabolic Rate (mgO_2 h^{-1} $kg^{-.084}$)							
Shark ID	**Sex**	**FL (cm)**	**Mass (kg)**	**Date**	**Location**	**Study Temp (℃)**	**rRMR**	**±**	**SD**	**aRMR**	**±**	**SD**	**TBF (Hz)**	**Respirometer**
1	M	227	126[a]	2018-09-01	Tremblay Sound	3.8	23.07	±	4.62	30.96	±	NA	0.18	Circular
2	F	163	40.8[a]	2019-09-20	Scott Inlet	4.9	22.29	±	2.90	-	-	-	-	Rectangular
3	F	172	52.4	2019-09-21	Scott Inlet	4.9	-	-	-	40.46	±	2.17	0.23[b]	Rectangular
4	F	155	33.4	2019-09-21	Scott Inlet	5.1	17.23	±	0.90	-	-	-	-	Rectangular
mean	-		63.1	-	-	4.7	20.86	±	3.17	-		-	-	-

[a] Mass estimated from Leclerc's 2012 equation using fork-length (FL).

[b] Movement was restricted by wall of respirometer.

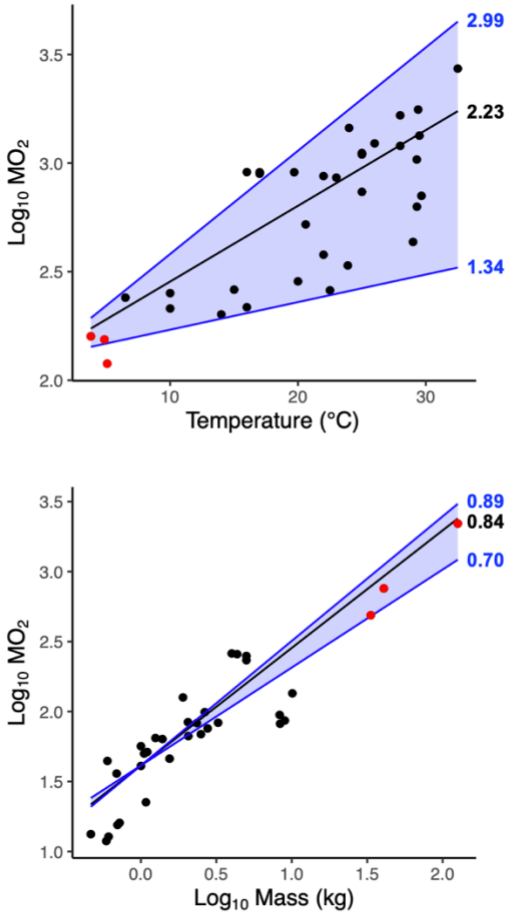

Figure 2.1: Comparison of literature derived whole-animal SMR and rRMR estimates for eighteen ectothermic shark species from nine families (MO_2 units = log10 [$mgO_2\ h^{-1}$]). Each black point represents the study-specific mean whole-animal MO_2 provided for a species at a specific experimental temperature and mass. Red points represent rRMR estimates for the Greenland shark (*Somniosus microcephalus*). Panel (A) depicts $\log_{10}$-transformed SMR and rRMR estimates (adjusted to a standard mass of 10 kg) against experimental temperature. The black line represents the SMR of a shark species predicted using the interspecies Q_{10} value derived from our multiple regression analysis, while the blue lines represent the maximum and minimum Q_{10} values observed for specific shark species (*Ginglymostoma cirratum* and *Sphyrna lewini* respectively). Panel (B) depicts $\log_{10}$-transformed SMR and rRMR estimates (adjusted to a standard temperature of 10 °C) against the $\log_{10}$-transformed mean mass of sharks used in each study. The black line represents the SMR of a shark species predicted using the interspecies allometric scaling exponent derived from our multiple regression analysis, while the blue lines encompass the range of predicted SMR values calculated with commonly used allometric scaling exponents derived for global teleost fish in previous meta-analyses (see Methods).

Figure 2.2: Photographs of the two respirometers used in this study. Panel A depicts the large "circular" type respirometer used in Tremblay Sound in 2018 (Photo by Eric Ste-Marie). Panel B depicts the smaller "rectangular" type respirometer used in Scott Inlet in 2019 (Photo of E. Ste-Marie taken by Jena Edwards and used with permission).

SUPPLEMENTARY INFORMATION

Fishing & Data collection

In Tremblay Sound in 2018-2019, Greenland sharks were captured using longlines composed of 6-10 hooks spaced ten metres apart baited with char, seal or narwhal donated by Inuit from subsistence fishing/hunting. Lines were set for 3-8 hours and subsequently pulled to the surface by hand. In Scott Inlet sharks were captured using longlines composed of 50 hooks set for 12 hours baited with squid. Lines were pulled using a motorized winch aboard the MV Kiviuq II. Sharks were not tagged, measured or sampled until after the trials took place to avoid unnecessary stress. Instead, individuals were immediately transferred into the respirometer following capture and allowed to acclimate to their surroundings. Only healthy sharks were used in respirometry trials (i.e. No visible injuries and responsive to a nose touch or tail pinch). In Tremblay Sound (2018), we fished for respirometry sharks nearshore to avoid having to tow animals more than two hundred metres to where our large circular field-respirometer was set up on the beach. Once at the beach, our team used an Extra-Large Shark Carrier (121 Animal Handling Products Ltd, Derbyshire, UK) to rapidly transfer the shark from the fjord to the respirometer (~30 seconds air exposure). A similar protocol was used to release the shark following experimentation. In Scott Inlet (2019), sharks were transferred directly from the longline to our rectangular respirometer aboard the MV Kiviuq II. Following experimentation, sharks were lowered back into the fjord using a makeshift sling.

Interspecies Metabolic Scaling Model

We conducted multiple regression analysis using the “lm” (linear model) function in R (version 3.5.2). Since neither mass nor temperature scales linearly with metabolic rate, metabolic rate and mass data were log transformed. Since some species of shark were represented by several data points (i.e. multiple studies per species or multiple estimates at different masses or temperatures), the regression analysis was balanced using the weights argument, with weights for each data point set to the inverse of the total number of data points for that species. Typical weighted regressions also incorporate the variance or standard deviation associated with data points in the model. These values, however, were not available for all species/experiments due to a lack of standardized reporting practices in respirometry studies on sharks. The variance or standard deviation for each study was therefore not included in the regression analysis. Furthermore, most studies only provided a mean mass-specific SMR estimate across individuals of varying mass, without providing the mean mass of individuals used in their study (SI Table 2.1). In such cases, we assumed that the mean mass of individuals was the midpoint between the max and min masses used in the study (a range of masses was always provided when the mean was not). Additionally, three studies provided mass-adjusted values instead of mass-specific estimates. In such cases, we converted the estimate into the mass-specific equivalent for an individual of average mass. Whole animal metabolic rates were then estimated by multiplying mass-specific metabolic rate by the average mass of an individual used in the study. This undoubtedly increased the error surrounding our model; however, most studies covered a relatively narrow range of masses (~2 kg range on average) which likely limited its overall influence on the output of our analysis covering a range of approximately 126 kg.

S.I. Table 2.1: Literature derived mass-specific SMR (or rRMR) estimates for sharks.

Ref	Species	Temp (C)	Mass avg. (kg)	Mass Range (kg)	N	MO_2 ($mgO_2kg^{-1}h^{-1}$)	SD	SE	Method[b]
Carlson et al. 1999	Carcharhinus acronotus	28	1	0.45-3.51	10	239.8			extrapolated
Lear et al. 2020	Carcharhinus leucas	19.7	5	3-7	9	101.4[c]			extrapolated
Lear et al. 2020	Carcharhinus leucas	32.5	5	3-7	9	304.1[c]			extrapolated
Lear et al. 2017	Carcharhinus limbatus	29.4	1.25[a]	1.03-1.47	7	246			extrapolated
Bouyoucos et al. 2018	Carcharhinus melanopterus	29.66	1.08		8	100.92	11.3		real
DiSanto & Bennett 2011	Chiloscyllium plagiosum	24	0.6		7	227.8[c]		14.8	real
Fournier 1996	Ginglymostoma cirratum	23	2.65[a]	1.3-4	5	106			real
Whitney et al. 2016	Ginglymostoma cirratum	22.5	8.37	5-12.4	5	26.7[c]	8		real
Lear et al. 2017	Ginglymostoma cirratum	23.9	8.31[a]	5.5-11.12	8	34.8	6		real
Lear et al. 2017	Ginglymostoma cirratum	29.3	10.1[a]	7.8-12.4	8	62.9	8		real
Whitney et al. 2016	Ginglymostoma cirratum	29	8.99	5.6-12.4	6	44.1[c]	17		real
Luongo and Lowe 2018	Heterodontus francisci	14	0.7225	0.44-0.94	4	30.6		3.4	real
Luongo and Lowe 2018	Heterodontus francisci	16	0.61	0.41-0.94	10	33.9		2.3	real
Luongo and Lowe 2018	Heterodontus francisci	20	0.59	0.41-0.94	9	44.9		2.4	real
Luongo and Lowe 2018	Heterodontus francisci	22	0.7	0.44-0.94	3	57.9		2.7	real
Molina et al. 2020	Heterodontus portusjacksoni	17	1.9	1-4.3	5	116.6[c]		20.4	real
Molina et al. 2020	Mustelus antarcticus	17	4.35	0.9-10.6	13	103.74[c]		61.9	real
Bouyoucos et al. 2018	Negaprion acutidens	29.29	1.55		3	139.95	12.07		real
Lear et al. 2017	Negaprion brevirostris	20.6	2.77[a]	2.07-3.46	20	64.1	16		real
Bushnell et al.	Negaprion	22	1.05[a]	0.8-1.3	13	125		5.68	real

1989	brevirostris								
Scharold and Gruber 1991	Negaprion brevirostris	25	1.39	1.11-1.61	7	152.6		7.3	extrapolated
Lear et al. 2017	Negaprion brevirostris	29.5	2.35[a]	1.74-2.95	16	168.5	23		real
Sims 1996	Scyliorhinus canicula	15	0.466[a]	0.0029-0.929	33	42.67			real
Piiper et al. 1977	Scyliorhinus stellaris	25	2.5[a]		12	92			real
Ste Marie et al (Present)	Somniosus microcephalus	4.86	40.77		1	12.3			real
Ste Marie et al (Present)	Somniosus microcephalus	5.08	33.4		1	9.83			real
Ste Marie et al (Present)	Somniosus microcephalus	3.8	126		1	10.63			real
Lowe 2001	Sphyrna lewini	26	0.69	0.506-0.927	17	189	15		extrapolated
Carlson 2000	Sphyrna tiburo	25	1.1[a]	0.8-1.4	12	156			extrapolated
Carlson and Parsons 2003	Sphyrna tiburo	28	1		8	173.4		11.3	paralyzed
Brett and Blackburn 1978	Squalus acanthias	10	2.06	1.87-2.4	18	32.4		2.6	real
Hanson and Johansen 1970	Squalus suckleyi	6.5	2.05[a]	1.6-2.5	9	30.95	8.37		real
Hanson and Johansen 1970	Squalus suckleyi	10	3.25[a]	2.16-4.3	9	25.62	3.3		real
Scharold et al. 1989	Triakis semifasciata	16	4[a]	2.2-5.8	5	105.3		35.6	extrapolated

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[a] Only a mass range was provided by the source, so this value represents the midpoint between the maximum and minimum mass instead of a true average.

[b] Method refers to whether the SMR value quoted in the original paper was a direct product of respirometry on a shark that was volitionally at rest (i.e. real), or if it was derived by extrapolating estimates measured while the shark was active to a swim speed of zero (i.e. extrapolated). One study conducted respirometry on chemically immobilized sharks (i.e. paralyzed)

[c] MO_2 estimate was presented in original paper as mass-adjusted value. The value presented here was converted into a mass-specific value using the same allometric scaling exponent used by the paper.

S.I. Table 2.2: Literature derived Q_{10} values for sharks. If multiple values were provided in the original study, only those calculated over an ecologically relevant temperature range are presented here.

Paper	Shark	Q_{10}	Temp range (°C)
Lear et al. 2020	Carcharhinus leucas	1.88	19.7-32.5
Lear et al. 2017	Carcharhinus limbatus	2.67	21.6-29.4
Dowd et al. 2006	Carcharhinus plumbeus	2.5	24-28
Tullis and Baillie 2005	Chiloscyllium plagiosum	2.7	15-30
Whitney et al. 2016	Ginglymostoma cirratum	2.42	23-30
Lear et al. 2017	Ginglymostoma cirratum	2.99	23.9-29.3
Luongo and Lowe. 2018	Heterodontus francisci	2.01	14-22
Lear et al. 2017	Negaprion brevirostrus	2.96	20.6-29.5
Butler and Taylor 1975	Scyliorhinus canicula	2.1	7-17
Lowe 2001	Sphyrna lewini	1.34	21-29
Carlson and Parsons 1999	Sphyrna tiburo	2.34	20-30
Giacomin et al. 2017	Squalus acanthias	2.59	7.5-12
Miklos et al. 2003	Triakis semifasciata	2.51	12-24

S.I. Table 2.3: Individual trial estimates (mass-adjusted) for the Greenland sharks studied via respirometry. rRMR estimates are presented in white and aRMR estimates are in blue. Red estimates are for trials where the shark exhibited sporadic movement throughout the trial making it impossible to estimate true rRMR or aRMR. Durations for each measurement interval are provided in minutes (min).

Trial Estimates ($mgO_2kg^{-1}h^{-0.84}$)

Shark ID	Respirometer	1			2			3			4			5		
		MO_2	min	R^2	MO_2	min	R^2	MO_2	min	R^2	MO_2	min	R^2	MO_2	min	R^2
1	Circular	26.01	30	0.790	30.96	20	0.757	16.26	40	0.673	25.89	60	0.935	24.10	33	0.760
2	Rectangular	24.97	29	0.994	19.22	30	0.955	33.27	60	0.997	31.29	60	0.999	22.67	15	0.975
3	Rectangular	38.32	60	0.994	42.66	60	0.999	40.38	60	0.999						
4	Rectangular	16.00	60	0.996	17.25	60	0.998	18.12	60	0.998	17.57	60	0.999			

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CHAPTER 3

Modeling the Field Metabolic Rate and Prey Consumption Rate of Greenland Sharks (Somniosus microcephalus) Using Archival Biologgers

3.1 Introduction

All lifeforms consume energy in one form or another, but the quantity required by each individual, population or species varies tremendously across the tree of life. Studies of metabolism have shown that the energy requirements of animals are influenced — often predictably — by their behaviour (e.g. variable activity costs in seabirds; Elliott et al. 2013), physiology (e.g. stress metabolism in fish; Nadler et al. 2016), and environment (e.g. thermoregulatory costs in mammals; Maloney et al. 1999). As such, a holistic estimate of the energy utilization of wildlife in the context of their ecosystem, referred to as field metabolic rate (FMR), can be very informative of their ecology and fitness (Treberg et al. 2016).

Several methodologies have been employed to estimate FMR in wildlife; however, no single technique is universally effective, creating gaps in the data available for certain species (Butler et al. 2004; Treberg et al. 2016). While heartrate telemetry and the doubly labeled water method have proven useful for the estimation of FMR in terrestrial species (Speakman 1997; Green 2011), these techniques are often less effective or completely ineffective when applied to fish (Treberg et al. 2016). Consequently, many studies addressing field metabolism in fish have relied on other methods such as measuring carbon isotopes in excised otoliths (Chung et al. 2019), or developing models using acceleration data from fish equipped with biologger packages (Metcalfe et al. 2016). FMR can be divided into three basic subunits of metabolism: standard metabolic rate (SMR), specific dynamic action (SDA), and activity metabolism (Chung et al. 2019). While previously derived estimates of SMR and SDA can be incorporated into FMR models with reasonable accuracy, activity's contribution is particularly variable and requires knowledge of the mechanical work undergone by an animal's muscle tissues while behaving normally in the wild (Wilson et al. 2006). Directly measuring the muscle contractions of wild fish is not feasible and so proxies, such as acceleration data recorded on biologgers, can be used to derive activity metrics such as overall dynamic body acceleration (ODBA) and tailbeat frequency (TBF) which have been shown to correlate with energy expenditure in many fishes (Ohlberger et al. 2007; Bouyoucos et al. 2017; Karissa O Lear et al. 2017).

In order to accurately model FMR in fish, the effect of environmental temperature on metabolic rate must be accounted for, as this is one of the principal drivers of metabolic rate in ectotherms (Treberg et al. 2016; Lear et al. 2020). Wild fish often experience environmental temperatures that vary spatially (e.g. deep vs shallow; Thums et al. 2013), or temporally (e.g. summer vs winter; Luongo and Lowe 2018), and these differences will generally lead to changes in body temperature which in turn lead to changes in FMR (Lear et al. 2020). Due to the inherent difficulties associated with recording body temperature in free-roaming fish, most studies rely on ambient temperature as a proxy for body temperature, but this can lead to errors when estimating instantaneous FMR in species who behaviourally thermoregulate (Watanabe et al. 2019a; Lear et al. 2020). For example, some sharks maintain relatively stable body temperatures throughout the day despite experiencing highly variable external temperatures by exhibiting a "yo-yo" style of diving where they cycle between warmer surface waters and colder deep waters (Andrzejaczek et al. 2018). In such cases, ambient temperature may lead to an over- or underestimate of FMR at any given time (i.e. instantaneous FMR), but can still be useful at estimating the time-averaged FMR of an individual over a longer period (i.e. hours or days).

Taken a step further, FMR can be used with diet information to estimate prey consumption rates, which allow for the quantitative assessment of trophic interactions within ecosystems where direct measures of prey consumption are often impossible (Nagy 1987). The oceans represent one such place. In fact, the inaccessibility of most marine species during the majority of their lives makes observation-based consumption rates unfeasible, leaving modelled estimates as the best alternative.

Analyses of prey consumption rates can be particularly useful when deciphering the ecological role of a species in the context of the surrounding food web. The consumer links between predators and prey drive community dynamics and, when disturbed, can lead to cascading effects throughout the ecosystem (Heithaus et al. 2008). For example, the collapse of Atlantic cod (*Gadus morhua*) populations in the Northwest Atlantic led to a large-scale restructuring of the local marine community with effects persisting decades later (Frank et al. 2005). Developing an understanding of the prey consumption rates of predators helps quantify their role in a given ecosystem and ultimately informs conservation initiatives through improved ecological predictions (Baum and Worm 2009). Even so, acquiring reliable population-level estimates of prey consumption can be challenging when data for species of interest are limited (Grubbs et al. 2016). Furthermore, even when data are abundant, they may not be representative of the entire population or time frame being studied (Hewitt et al. 2007). For example, many polar species undergo large migrations or experience dramatic seasonal shifts in their habitats, yet data are often collected in the summer because of the lack of year-round accessibility. Consequently, ecological predictions based on these data alone provide an incomplete view of annual ecosystem dynamics.

The estimation of prey consumption rates has become an important tool used to elucidate the ecological impact of marine predators, including sharks whose global numbers are declining rapidly due to overfishing (Williams et al. 2004; Worm et al. 2013; Mourier et al. 2016). That being said, bioenergetics, population and behavioural data for sharks is often limited, making their ecological role as predators difficult to ascertain (Hammerschlag 2019; Lawson et al. 2019). As a result of this data deficiency, many studies have relied on modeled data or data derived from related species when estimating the FMR and predation rate of sharks (Semmens et al. 2013; Barnett et al. 2017). This increases the uncertainty surrounding estimates, but can still be useful when addressing conservation and management objectives (Barnett et al. 2017). Aside from their direct effects on prey populations, there is also mounting evidence that sharks influence their ecosystems through non-lethal behavioural and physiological effects on prey species (Heithaus et al. 2007; Guttridge et al. 2012; Hammerschlag et al. 2017). As such, studying both direct and indirect effects of sharks on their surrounding communities should be a priority.

Very little is currently known about the ecological role of Greenland sharks (*Somniosus microcephalus*), yet their size, abundance and trophic position indicate that they could serve as important top-down regulators of Arctic food webs (MacNeil et al. 2012; Hussey et al. 2014). To date, no FMR or prey consumption rate estimates exist for

Greenland sharks, largely due to the lack of metabolic and behavioural data for the species. Recent respirometer derived estimates of resting and active metabolic rate for Greenland sharks inhabiting Baffin Bay, Nunavut, provide a foundation on which we can now begin exploring the FMR and prey consumption rate of this species (Ste-Marie et al. 2020). Consumer linkages to locally and commercially important species makes studying their role as predators essential to the proper management of Arctic ecosystems (Tyrrell et al. 2011). Quantifying the consumption of prey species such as Greenland halibut (*Reinhardtius hippoglossoides*), for example, could subsequently be used to inform population models used for the management of fisheries targeting this species.

In the present chapter, I will integrate the resting and active metabolic rates presented in Chapter 2 of my thesis with biologged acceleration and temperature data in order to model the FMR of Greenland sharks tagged in the coastal fjord systems of Baffin Island, Nunavut. I will then integrate these FMR estimates with published diet data to estimate the prey consumption rates of this Arctic predator. The basic consumption model will take into account the energetic needs of individuals in the wild, the composition of their diet and the caloric value of each diet item. Building from this, local abundance estimates and population demographics will be used to assess the ecosystem level impact of Greenland sharks. Given their generally lethargic lifestyles, we expect individual sharks to have relatively low field metabolic rates and that this will translate into low prey consumption needs. However, their high abundance in certain parts of the Arctic suggest that local populations of Greenland sharks may play an important role as consumers in Arctic marine ecosystems.

3.2 Methods

3.2.1 Fishing and Tagging

Sharks were captured in Scott Inlet and Tremblay Sound, Nunavut, using baited longlines. In 2015 and 2016, longlines made up of 50 hooks baited with squid were set for 12 hours and subsequently pulled to the surface using a winch system aboard the MV Kiviuq II. In 2017-2019, longlines baited with donated seal, char or narwhal were set for 3-8 hours and then pulled to the surface by hand. Once a shark was at the surface in either location, it was restrained alongside a small zodiac using straps, measured, tissue samples taken, and biologger packages attached. Sharks were initially inverted to expose their ventral side and to facilitate surgical implantation of an acoustic tag into the peritoneal cavity (V16, 69-Hz, Vemco Ltd, Nova Scotia, Canada). Following tag implantation, blood and fin samples were taken for genetics and stable isotope analysis; these procedures provided data independent from this study. Measurements were taken for both total and fork length (TL and FL), as well as inner and outer clasper length if the shark was a male. Sharks were then righted and equipped with an archival biologger package (Figure 3.1), attached to the head region using a cable tie release system (Little Leonardo). Following all tagging procedures, restraining straps were removed and sharks were released. After 1-4 days (i.e. a predetermined time frame set within the Little Leonardo cable tie release system), the cable tie broke allowing the biologger package to float to the surface. The biologger package was then retrieved using satellite (SPOT, Wildlife Computers Inc.) and VHF radio tags (F2000 series, Advanced Telemetry Systems Inc.).

3.2.2 Biologging Data

Activity and temperature data were recorded in wild free-swimming Greenland sharks using animal-borne biologger packages. Activity was monitored through the use of triaxial accelerometers (DTAG-3, Johnson and Tyack 2003; Sonar tag, Goulet et al. 2019; PD3GT, Little Leonardo; Maritime bioLoggers) that recorded at frequencies of at least 16 Hz. Ambient temperature (external) was recorded for all tagged sharks (n=30), while body temperature (internal) was also recorded for a small subset of sharks (n = 2) in 2018 and 2019 (LAT1810, Lotek).

Acceleration and temperature data were processed using the Ethographer extension (Sakamoto et al. 2009) available for Igor Pro (WaveMetrics Inc., Lake Oswego, OR, USA). Prior to conducting analyses, the first ten hours of each deployment were cut from the data to account for post-release recovery (Watanabe et al. unpublished). TBF was derived from raw acceleration in the lateral (or sway) axis using continuous wavelet transformation (Sakamoto et al. 2009). TBF was chosen over other common activity metrics such as ODBA and swim speed because it could be derived for all accelerometer tagged sharks (unlike swim speed), and because it was the metric used to record activity levels in our recent study measuring oxygen consumption rates in Greenland sharks through respirometry (Ste Marie et al. 2020). TBF has also been shown to be an effective predictor of metabolic rate in in other shark species (e.g. lemon sharks [*Negaprion brevirostris*], Bouyoucos et al. 2017).

3.2.3 Modeling FMR

Following the processing of biologged activity and ambient/body temperature data, we constructed a model to estimate FMR for each tagged Greenland shark using metabolic scaling relationships for mass, temperature and activity:

$$FMR = 20.22 \times TBF + [(rRMR \times M^{0.84}) \times Q_{10}^{\frac{T2-T1}{10}}]$$

Respirometer derived estimates of resting routine metabolic rate (rRMR) were first scaled according to the mass (M) of each individual shark using our derived interspecific allometric scaling exponent (0.84; Ste-Marie et al. 2020). Following this, rRMR was scaled according to recorded body/ambient temperature data (T2) using the interspecific Q_{10} for sharks of 2.23 (Ste-Marie et al. 2020) and an initial temperature (T1) representing the experimental temperature at which rRMR was measured. Because no intraspecific Q_{10} value has been derived for Greenland sharks, and because of the wide range of Q_{10} values observed across shark species, we created two additional model variants using the maximum and minimum Q_{10} values published for shark species (2.99 for nurse sharks [*Ginglymostoma cirratum*], Lear et al. 2017; 1.34 for Great hammerhead sharks [*Sphyrna lewini*], Lowe 2001).

Once the effect of mass and temperature were accounted for, TBF was used to scale each estimate according to that individual's biologged activity levels. Rather than adopting an activity-level equation for a different species from a previous study, the effect of TBF on oxygen consumption rate for Greenland sharks was approximated using the slope (20.22) of an interpolated line connecting the active routine metabolic rate (aRMR, at TBF=0.18) of the individual studied in the Tremblay Sound respirometer to its rRMR (i.e. its oxygen consumption rate at TBF= 0). Though more rigorous activity cost equations have been derived for other shark species, we opted to use our value derived from limited Greenland shark data because of the highly variable effect of activity on the energetics of different species (Lear et al. 2017). Moreover, the shark used to derive our activity scaling slope was closer in body size (~126 kg) to the wild sharks whose FMRs we are estimating. This latter point is important considering our methods do not account for possible effects of body mass on the slope of the relationship between oxygen consumption and TBF.

For the individuals whose internal body temperatures were biologged, we plotted instantaneous FMR over the course of each deployment, and calculated overall time-averaged estimates using both body and ambient temperature data. Since metabolic rate does not change instantly according to the behaviour and environment of an animal, a one-minute smoothing window (i.e. rolling mean) was applied to the instantaneous FMR data in order to assure our estimates were physiologically plausible (Williams et al. 2014; Watanabe et al. 2019a). For the individuals whose internal body temperatures were not biologged, we calculated only a single time-averaged estimate of FMR using ambient temperature data. While differences between ambient and body temperature at any given moment could lead to an erroneous instantaneous FMR estimate, over time, averages of both types of temperature are likely similar.

In order to extend our short-term FMR estimates (period of days) to encompass a year in the life of a Greenland shark, we used pop-off archival satellite tags (mk10 and miniPAT, Wildlife Computers) that measured ambient temperature and depth every ten minutes for a 365 day period. A similar method as above was employed to estimate long-term (1-year) FMR in these sharks; however, since the tags did not record acceleration, we used the average TBF observed across all accelerometer tagged individuals as the activity component of our estimates. Since activity levels could have varied seasonally with temperature, we calculated vertical velocity (i.e. change in depth per unit time) as a proxy for activity and performed a linear mixed effect model to test whether activity was influenced by temperature throughout the year (with individual sharks as a random effect).

In Microsoft Excel, Short-term FMR estimates derived from biologger deployments in Scott Inlet and Tremblay Sound were compared with each other using unpaired t-tests. Similarly, short-term FMR estimates were compared with long-term estimates. Finally, differences between FMR estimates derived using the three Q_{10} variants were assessed using paired t-tests. A Shapiro-Wilk normality test was initially conducted for each sample group; all of which demonstrated normal distributions.

3.2.4 Modeling Prey Consumption Rates

To estimate prey consumption rates for Greenland sharks, we integrated our FMR estimates with published stomach content data from studies conducted on Greenland sharks in the Canadian Arctic. Specifically, we extracted information regarding the types of prey consumed, their contribution to the shark's overall diet and their caloric value (S.I. Table 3.1). Focal prey species were selected based on their importance to the diet of Greenland sharks and/or their importance to commercial fisheries and Northern indigenous communities as a resource for hunting and fishing. The following formula was used to estimate the mass of a specific prey type (P_x) consumed daily by a shark:

$$P_x = \frac{E \times pDiet}{U_x}$$

Where E represents the number of kilocalories required daily by an individual shark, U_x represents the caloric density (kcal/g) of the prey species, and pDiet represents the proportional contribution of the prey species to the overall diet of a shark.

Before calculating P_x, we converted our short- and long-term FMR estimates from units of oxygen consumption to units of energy expenditure using a conversion ratio of 1 mol O2 per 103.73 kilocalories (Widdows 1987). We then adjusted these estimates to account for incomplete assimilation of consumed prey by sharks using an assimilation efficiency of 73% which is commonly applied in bioenergetics studies on fish (Brett and Groves 1979). The resulting value was taken to represent the energy requirements (E) of a shark in the above equation. The proportional contributions of different prey items to the overall energy requirements of individual sharks could not be measured directly in the wild. As such, frequency of occurrence (%F), extracted from previous stomach content studies, was used as a proxy in our prey consumption model. This diet metric represents the fraction of non-empty stomachs in which a certain prey item is found. While other metrics such as percent weight and percent number have also been used in previous studies attempting to model prey consumption rates in fish (Barnett et al. 2017), no such values have been published for Greenland sharks living in Canadian waters and diets vary regionally in this species. While %F is generally assumed to correspond well with pDiet, the two can differ under certain conditions. For example, if all sampled predators in a study are found with a specific prey item in their stomachs, the %F for this type of prey would be 100% regardless of whether it is found in small amounts and does not contribute a large portion of ingested calories.

In order to scale from individual consumption rate estimates to population level estimates, we incorporated local abundance and demographic data into our basic consumption model. Together, these two layers of additional data permit the estimation of the total biomass of sharks in local ecosystems and, subsequently, their prey demands at the ecosystem level. Local abundance estimates were taken from recent work by Devine et al. (2018). The authors modeled local abundance (# of individuals per km^2) using data derived from baited remote underwater video systems deployed in five regions surrounding the northern tip of Baffin Island. We used these values to estimate local Greenland shark populations in Tremblay Sound, Scott Inlet (localized ecosystems) and Baffin Bay (large-scale ecosystem) by multiplying them by the areas (A) of each region. Since sharks of different masses require different amounts of food, we used five years of catch data (n=177) from Tremblay Sound and Scott Inlet to estimate the size structure of Greenland shark populations in the region and estimate the average energy needs of a shark in these systems (E_{avg}). Mass-adjusted FMR could then be scaled according to the total biomass of sharks and used to estimate the energy requirements of the localized and large-scale ecosystem populations (E_{pop}) such that:

$$E_{pop} = Local\ Abundance \times A \times E_{avg}$$

Since Greenland sharks spend only part of the summer and autumn months in the coastal inlets of Baffin Island (Edwards et al., in review), we used the mean mass-adjusted FMR, derived from our short-term biologger deployments in Tremblay Sound and Scott Inlet, to estimate the energy requirements (E_{pop}) of sharks in those systems. When estimating the population level consumption rate of sharks across all of Baffin Bay, we instead used the mean mass-adjusted FMR derived from our long-term (1-year) biologger deployments. Only FMR estimates derived using the interspecific Q_{10} of 2.23 were used in our prey consumption model. E_{pop} values were then substituted for E in the prey consumption rate equation.

3.3 Results

3.3.1 Field Metabolic Rate

Over five years we equipped 30 Greenland sharks in Tremblay Sound (2017-2019) and Scott Inlet (2015 and 2016), Nunavut, during the late summer (August-September) with recoverable archival biologging packages that recorded triaxial acceleration and temperature for periods ranging from 12-106 hours (mean= 49.5 ± 27.6 [SD] hours). When using the interspecific Q_{10} of 2.23 derived for sharks, mean mass-adjusted FMR was estimated to be 21.67±2.30 $mgO_2h^{-1}kg^{-0.84}$ across all tagged Greenland sharks over the deployment period (Table 3.1). Using a maximum Q_{10} of 2.99 (*Ginglymostoma cirratum*; Lear et al. 2017), mean mass-adjusted FMR decreased slightly to 19.89±2.63 $mgO_2h^{-1}kg^{-0.84}$ (paired t-test, $p<0.01$, n=30). Additionally, when using the lowest Q_{10} of 1.34 (*Sphyrna lewini*; Lowe 2001), mean mass-adjusted FMR estimates increased significantly to 25.49±1.66 $mgO_2h^{-1}kg^{-0.84}$ ($p<0.01$, n=30). FMR estimates did not vary significantly between Greenland sharks sampled in Tremblay Sound and Scott Inlet (Figure 3.2; two-tailed t-test with unequal variance, $p>0.05$, n=21 and 9 respectively). However, there was a greater spread in the results for Tremblay Sound, with both the maximum and minimum FMR estimate recorded for individual sharks in the system ranging from 16.93 to 31.36 $mgO_2h^{-1}kg^{-0.84}$).

As expected, estimates of time-averaged mass-adjusted FMR were very similar when using ambient temperature in lieu of body temperature for the two individuals in which both were recorded simultaneously. Shark 20 had a time-averaged FMR of 22.24 $mgO_2h^{-1}kg^{-0.84}$ when using body temperature and 22.72 $mgO_2h^{-1}kg^{-0.84}$ when using ambient temperature as a proxy. Similarly, shark 27 had a time-averaged FMR of 19.54

$mgO_2h^{-1}kg^{-0.84}$ when using body temperature and 19.78 $mgO_2h^{-1}kg^{-0.84}$ when using ambient temperature. Instantaneous FMR (estimated using body temperature) is plotted over time for these individuals (Figure 3.3). Short periods of elevated FMR can be observed in both individuals, corresponding with bursts of high activity (TBF; Figure 3.3).

Year-long FMR estimates were calculated for six sharks equipped with PSATs in 2013-2015 in Scott Inlet (Table 3.2). The average FMR of these individuals was 25.48±0.47 $mgO_2h^{-1}kg^{-0.84}$ (at Q_{10}=2.23), representing a roughly 18% increase over the short-term estimates presented above for individuals tagged with accelerometer packages (Figure 3.2; two-tailed t-test with unequal variance, $p<0.01$, n=30 [short-term] and n=6 [long-term]). This increase in FMR resulted from the high temperatures experienced by sharks during the winter and spring months (Figure 3.4A). Average winter temperatures of greater than 4ºC were observed in all six sharks indicating that they must have left the cold-water coastal fjord systems of Baffin Island in late autumn. However, the pop-off locations of three sharks indicate that they returned to these areas the following year (Figure 3.4B). As with the short-term accelerometer derived FMR estimates, varying Q_{10} in our FMR model for long-term satellite tagged individuals significantly affected average FMR (paired t-tests, $p<0.05$). The results of a linear mixed effect model suggested no influence of temperature on activity levels throughout the year when using vertical speed as a proxy for activity ($p=0.681$; Figure 3.5).

3.3.2 Prey Consumption Rate

Across all 177 Greenland sharks captured in Scott Inlet and Tremblay Sound over the last five years (mean mass = 224 ± 99 kg, range = 29-692kg), the energy requirements of individuals were estimated on average to be 214.6 ± 80.3 kcal/day during their time inside these coastal inlet ecosystems, and 252.3 ± 94.5 kcal/day for the whole year. Local populations of sharks were calculated using the maximum and minimum abundance density estimates provided for Greenland sharks in the region by Devine et al. (i.e. 0.4-15.5 sharks per km^2, 2018). Combined with upper and lower pDiet (%F) estimates for each prey type, population-level consumption rates varied widely because of the uncertainty surrounding population estimates (Table 3.3). For example, consumption rate estimates of ringed seal ranged from 0.88-161.78 kg/day in Tremblay Sound, 1.51-278.49 kg/day in Scott Inlet, and 1,375.20-253,504.01 kg/day across all of Baffin Bay. Narwhal consumption was predicted to range from 0.36-13.76 kg/day in Tremblay Sound, 0.61-23.68 kg/day in Scott Inlet, and 556.37-21,559.26 kg/day in Baffin Bay. Finally, the population-level consumption rate of Greenland halibut was predicted to be 30.85-1,631.70 kg/day in Scott Inlet, and 28,083.84 – 1,485,284.92 kg/day in Baffin Bay.

3.4 Discussion

3.4.1 Field Metabolic Rate

In the absence of a method to directly measure FMR in fish (Treberg et al. 2016), modelled estimates such as those presented in this chapter can provide important insight into the lives of little understood species such as the Greenland shark. The use of acceleration biologging to model the FMR of fish is a relatively new technique (Metcalfe et al. 2016), with only a handful of studies applying this approach to sharks (e.g. Watanabe et al. 2019a; Lear et al. 2020). Our first estimates for Greenland sharks add to this growing area of research through the inclusion of a large and lethargic cold-water species. Given its polar habitat and low activity levels in the wild, it is no surprise that we estimated such low FMRs for this species; much lower than those estimated for the endothermic white shark (Watanabe et al. 2019a), or the warm-water dwelling bull shark (Lear et al. 2020). These FMR estimates for Greenland sharks also allowed for a preliminary assessment of their consumer role in Arctic ecosystems, though uncertainty surrounding some of the model inputs led to highly variable estimates.

Maintaining a low FMR could be beneficial to Greenland sharks inhabiting areas of the Arctic where prey are scarce, allowing them to survive extended periods of time between feeding events while avoiding competition with endothermic predators such as orcas which require much more food to fuel their rapid metabolisms (Furey et al. 2016; Grady et al. 2019). There has been much debate in the literature over the feeding behaviour of Greenland sharks in the wild, with anecdotal evidence suggesting they rely on both scavenging and active predation (MacNeil et al. 2012). However, many argue the latter method is unlikely to be commonplace given these sharks are slow moving ectotherms feeding on large and often warm blooded prey capable of reaching much higher swim speeds than the sharks themselves (Watanabe et al. 2012). A slow field metabolism could justify a low predation efficiency in Greenland sharks pursuing large energy-rich prey (Norberg 1977). For example, a single successful predation on a seal could provide sufficient energy to fuel an individual shark for several months (Ste-Marie et al. 2020).

Further indirect evidence for active predation can be found in the acceleration profiles presented for Greenland sharks here. Several short bursts (~2-6 minutes) of rapid swimming can be observed in the TBF plots for individuals tagged in Tremblay Sound (Figure 3.3), where thousands of narwhal spend their summer/autumn each year (Heide-

Jørgensen et al. 2002). These spikes in activity could be the result of an attempted predation by the shark, but such patterns in the acceleration profiles of individuals will require validation using secondary data sources before definitive conclusions can be drawn (e.g. video, Watanabe et al. 2019b). Regardless of whether Greenland sharks are opportunistically pursuing live prey, scavenging is likely a major contributor to the diet of Greenland sharks whose powerful olfactory systems can guide them over long distances in search of carcasses from whale falls whether natural or as a result of subsistence hunts (Yopak et al. 2019).

While our modelled FMR estimates represent an important step towards understanding the true metabolic cost of life for these iconic Arctic predators, several assumptions must be acknowledged. Firstly, our model did not explicitly incorporate energetic costs associated with specific dynamic action (SDA), despite the fact that digestion can be a major contributor to the overall metabolic demands of wild fish (Fitzgibbon et al. 2007; Jordan and Steffensen 2007). Because of the limited respirometry data available for Greenland sharks (Ste-Marie et al. 2020), our FMR models were based on the resting metabolic rates of unfasted sharks. These resting metabolic rates could have included some of the costs associated with SDA and are therefore an overestimate of true SMR for this species. As such, we opted not to include SDA as an explicit parameter in our model, similar to the methods employed in a recent study by Lear et al. (2020) to estimate the FMR of bull sharks.

Another important assumption made by our model was that interspecific relationships predicting the scaling of metabolic rate with mass and temperature can serve as proxies for the unknown effects of these variables within Greenland sharks. While intraspecific Q_{10} values are known to vary extensively across shark species (1.34-2.99, Lowe 2001; Lear et al. 2017), the limited research to date addressing intraspecific metabolic allometry in sharks has yielded a relatively narrow range of scaling exponents (0.80-0.86, Sims 1996; Payne et al. 2015) that encompass our estimated interspecific value of 0.84 (Ste-Marie et al. 2020). Consequently, we used the interspecific allometric scaling exponent of 0.84 in our FMR model and created three model variants using the interspecific Q_{10}, as well as the maximum and minimum Q_{10} values published for sharks to account for the uncertainty surrounding our estimates. While we observed a significant difference between FMR estimates calculated using all three Q_{10} values, the estimate derived using the interspecific Q_{10} of 2.23 is likely the closest to reality. In the current literature, all but one species of shark studied at ecologically relevant ambient temperatures have demonstrated metabolic Q_{10} values of greater than two, including a coordinal cousin of Greenland sharks: the spiny dogfish (*Squalus acanthias*) which was found to have a Q_{10} that is similar to the interspecific value for sharks of 2.23 (i.e. Q_{10}=2.59; Giacomin et al. 2017).

Most of the FMR estimates presented in this chapter were derived using biologged ambient temperature instead of body temperature, yet time-averaged estimates were nearly identical in the individuals where both were recorded simultaneously. This finding, although based on a small sample of sharks, suggests that time averaged FMR can be accurately modeled using ambient temperature in this species and lends credibility to our estimates for the twenty-eight sharks in which body temperature was not recorded. While ambient temperature cannot be directly used to estimate instantaneous FMR since an animal's size and the thermal conductance of its tissues delay the transfer of heat between its body and its surroundings (Carey et al. 1982; Vogel 2005), knowledge of the relationship between these two measures of temperature could eventually allow us to estimate body temperature from ambient temperature in Greenland sharks.

Instantaneous FMR estimates over time can be used to estimate the energetic investments of an individual towards specific activities (Williams et al. 2014; Watanabe et al. 2019a). For example, if Greenland sharks are using bursts of elevated swim speed to pursue prey (as discussed above), then it is possible to estimate the relative cost of these predation attempts using the instantaneous FMR estimates derived over that period. Ultimately, this information could be used to assess the energetic trade-offs associated with different foraging strategies in this species (Williams et al. 2014). In other words: Does the energy reward offered by the successful capture of a prey item outweigh the costs associated with its pursuit and previous failed pursuits? For this question to be answered, the identification of prey captures using acceleration data would need to be validated for Greenland sharks. Previous studies on other marine taxa have validated prey capture acceleration signatures using animal-borne cameras alongside acceleration biologgers (Watanabe and Takahashi 2013), but stomach temperature tags may also be effective at corroborating assumed prey captures by sharks (Jorgensen et al. 2015).

Estimates of FMR based on long-term behavioural and environmental datasets are essential to developing an accurate understanding of a species' energetics (Cooke et al. 2016). The biologged data used in many studies to model FMR in fish is often collected over short time periods consisting of days or weeks instead of years (e.g. Brodie et al. 2016). These snapshots can be useful when describing the role of a species in a specific habitat or ecological context but can lead to the over- or underestimation of energy requirements for species that migrate and/or who undergo large seasonal shifts in their habitat (e.g. Sinclair et al. 2013). This is the case for many Arctic species, including the Greenland shark which is known to move long distances and occupy a range of habitats varying in depth, temperature, and prey availability, among other factors (MacNeil et al. 2012; Hussey et al. 2018).

Our short-term FMR estimates were based on data collected in two coastal fjord systems during the ice-free Arctic summers of 2015-2019. The conditions experienced by the sharks while in these fjords differs from those experienced by the sharks outside of these areas. This was evident when assessing the temperature profiles of sharks equipped with satellite tags for an entire year (Figure 3.4). Many sharks overwintered in waters that were several degrees warmer than the summer temperatures experienced in Scott Inlet and Tremblay Sound, resulting in yearly FMRs that were approximately 18% higher than our short-term estimates. In reality, we might expect a larger discrepancy between these estimates had we also been able to measure activity over the course of the year. Activity levels generally increase with temperature in ectothermic fish (Payne et al. 2016), thus higher winter temperatures could have been accompanied by a higher average TBF. However, vertical velocity (calculated from biologged depth data) remained relatively constant throughout the year and across temperatures indicating average activity levels may not have changed significantly (Gleiss et al. 2013). Nevertheless, the higher energetic demands predicted for Greenland sharks overwintering in warm waters has implications for their prey consumption rate and ultimately their overall impact on Arctic food webs.

3.4.2 Prey Consumption Rate

We estimated that an average shark weighing 224 kg requires approximately 215 kilocalories per day when inhabiting the coastal inlets of Baffin Island, or 252 kcal/day over the course of a full year in the Baffin Bay region. This is equivalent to only 164-192g of halibut, 61-71g of seal, or 86-101g of narwhal. Considering that a typical halibut weighs approximately one kilogram, A Greenland shark could theoretically survive 5 or 6 days without feeding after consuming a single fish. That number increases dramatically when considering the energy that would be provided by the consumption of a large meal of energy dense prey such as seal or narwhal. For example, a 25kg meal of narwhal could provide enough energy to fuel a shark for 248-291 days and the same amount of seal could fuel a shark for 351-412 days. This further supports the idea that opportunistic binge feeding by Greenland sharks on either live or dead marine mammal prey could allow them to inhabit regions of the Arctic where preferred prey is only available seasonally (Armstrong and Schindler 2011; Furey et al. 2016), encountered sporadically, or where successful predation events are rare. It is important to note, however, that we lack knowledge as to what extent Greenland sharks are able to store energy in their tissues or as undigested food in their stomachs. Furthermore, our estimated energy requirements for this species do not take into account energy investment into growth or reproduction, both of which could increase the FMR values presented here (Barnett et al. 2017; Nielsen et al. 2020). In support of the reliability of the presented FMR estimates, available data in the literature for Greenland sharks suggests they have an incredibly slow growth rate (~0.5 cm/year, Hansen 1963), while sharks inhabiting Scott Inlet and Tremblay Sound are mostly sexually immature and thus should not incur high reproductive costs (Nielsen et al. 2020).

Using the limited diet and population (size/demographics) data available for Greenland sharks, we extrapolated individual-level energy requirements to estimate localized population-level prey consumption of ringed seal, narwhal and halibut. However, due to the high degree of uncertainty surrounding abundance estimates and the range of published %F values for each focal prey species, consumption rate estimates were highly variable (two orders of magnitude between upper and lower estimates). This large discrepancy echoes the need for improved population data across the entire geographic range of Greenland sharks, as well as more extensive diet data for sharks inhabiting Canadian waters, and particularly coastal inlet systems such as Tremblay Sound and Scott Inlet (MacNeil et al. 2012; Edwards et al. 2019).

All three stomach content papers used to determine the proportional contribution of prey items to the diets of Greenland sharks used data collected from Cumberland Sound, a large inlet of Baffin Island to the south of Scott Inlet and Tremblay Sound (Fisk et al. 2002; McMeans et al. 2012; McMeans et al. 2015). While Cumberland Sound may share many of the same prey resources as nearby coastal systems of Baffin Island, there are a few key differences that could influence the relative importance of prey items within these systems. For example, though the stomach contents of sharks in Cumberland Sound point to a high reliance on halibut and a low reliance on narwhal, Greenland halibut are not present in the immediate vicinity of Tremblay sound (though they do occur in neighbouring Eclipse Sound) and there is a large seasonal population of narwhal (Heide-Jørgensen et al. 2002). This may indicate that sharks in Tremblay Sound rely on narwhal to a greater extent than what we predicted here. As noted above, however, more stomach content data across diverse coastal environments of the Canadian Arctic will be necessary in order to improve the accuracy of prey consumption estimates at these locations (Edwards et al. 2019).

While we covered a wide range of potential population estimates in our consumption rate models for Tremblay Sound, Scott Inlet and Baffin Bay, not all possibilities are equally likely. The literature derived abundance estimates used to estimate populations in all three systems were based on data collected in coastal regions of Baffin Bay where Greenland sharks are known to aggregate during the ice-free Arctic summer (July-September, Edwards et al, in review; Devine et al. 2018). Sharks may be much more dispersed during the winter after they leave the coastal inlet ecosystems and move into Baffin Bay (Edwards et al, in review). As such, we speculate that our lower prey consumption rate estimates for the Baffin Bay region are likely closer to reality. Additionally, abundance estimates were highly variable between the locations assessed in Devine et al.'s study, indicating a preference by sharks for certain areas (2018). Estimating prey consumption rates for sharks in areas where local abundance is known would drastically reduce the uncertainty surrounding estimates. Therefore, acquiring better population data for Greenland sharks throughout Baffin Bay should be a research priority going forward (MacNeil et al. 2012; Devine et al. 2018; Edwards et al. 2019).

The prey consumption rates estimated here for Greenland sharks, though coarse, provide a preliminary examination of the ecological role of Greenland sharks in Arctic ecosystems. These results can be used to improve our understanding of the food web dynamics in arctic marine ecosystems (Myers et al. 2007; Darnis et al. 2012; Coll et al. 2013). To date, most food web models have ignored Greenland sharks despite the fact that, as the largest ectothermic consumer in the Arctic, they may play a unique role as regulators of lower trophic levels (Darnis et al. 2012; Hussey et al. 2014). Greenland sharks also make-up a large proportion of the bycatch in growing commercial fisheries for Greenland Halibut (Davis et al. 2013; DFO 2013). Understanding their role in arctic ecosystems is therefore essential to the proper management of fisheries and to maintaining a healthy population of sharks moving forward (Edwards et al. 2019). Predation rates by Greenland sharks can also be used to improve natural mortality estimates in stock assessment models for Greenland halibut, as models that incorporate predation mortality tend to be better predictors of the population dynamics of targeted fish (Tyrrell et al. 2011).

3.4.3 Conclusion

Overall, our assessment of the field metabolism and prey consumption rates of Greenland sharks inhabiting the Eastern Canadian Arctic has provided novel insight into the ecology of this species. Their predicted low metabolic demands in the wild suggest that individuals require very little food to sustain themselves, but population level estimates indicate that they could play a significant role as consumers in Arctic food webs. However, further research is needed into the population dynamics and diet of local populations of Greenland sharks before definitive conclusions can be drawn. These simple prey consumption estimates also fail to differentiate between active predation and scavenging, which could significantly affect how we perceive the ecological role of these sharks. Regardless, climate change is affecting both the physical environment and biological communities of the Arctic, emphasizing the importance of continued long-term monitoring of the behaviour and energetics of Greenland sharks.

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TABLES AND FIGURES

Table 3.1: Summarized FMR estimates for individual Greenland sharks (*Somniosus microcephalus*) equipped with accelerometers and temperature tags in Tremblay Sound and Scott Inlet, Nunavut, Canada (n=30).

ID	**Location**	**Sex**	**FL**	**TL**	**Mass**	**Year**		**Mass adjusted FMR ($mgO2h^{-1}kg^{-0.84}$)**			**Length (hours)**	**TBF (Hz)**	**Temp (°C)**
							Q_{10}=	**2.23**	**2.99**	**1.34**			
1	Scott Inlet	M	241	256	155	2015		21.34	19.74	24.57	22.3	0.13	0.9
2	Scott Inlet	F	278	300	253	2015		22.24	20.55	25.80	16.9	0.15	0.3
3	Scott Inlet	M	215	222	105	2015		20.74	19.13	23.99	38.2	0.12	0.9
4	Scott Inlet	F	310	330	367	2015		22.76	21.11	26.12	38.9	0.14	0.7
5	Scott Inlet	M	280	300	259	2015		21.97	20.33	25.30	101	0.14	0.8
6	Scott Inlet	M	294	312	305	2016		23.67	22.07	26.95	106	0.16	0.8
7	Scott Inlet	M	269	286	226	2016		23.12	21.50	26.41	106	0.16	0.8
8	Scott Inlet	M	153	163	33.1	2016		23.09	21.55	26.19	44.6	0.21	1.1
9	Scott Inlet	M	210	223	96.8	2016		23.37	21.79	26.56	23.7	0.19	1.0
10	Tremblay	F	273	292	238	2017		20.66	18.60	25.23	45.9	0.16	-1.3
11	Tremblay	M	284	313	272	2017		21.32	19.32	25.68	68.0	0.16	-0.9
12	Tremblay	M	277	290	250	2017		20.62	18.54	25.20	70.6	0.16	-1.3
13	Tremblay	M	269	286	226	2017		19.60	17.57	24.06	85.9	0.13	-1.1
14	Tremblay	M	295	320	310	2017		19.89	17.95	24.05	86.1	0.12	-0.6
15	Tremblay	F	251	265	179	2017		21.73	19.78	25.94	62.9	0.17	-0.7
16	Tremblay	M	260	276	201	2018		21.25	19.39	25.21	28.3	0.15	-0.2
17	Tremblay	M	257	279	194	2018		20.77	18.68	25.43	32.5	0.17	-1.5
18	Tremblay	F	294	320	307	2018		16.93	14.87	21.45	31.7	0.08	-1.2
19	Tremblay	F	231	238	134	2018		20.32	18.30	24.72	57.3	0.16	-0.9
20[a]	Tremblay	M	279	288	256	2018		22.72	21.01	26.26	83.3	0.16	0.5

21	Tremblay	M	247	257	169	2018	22.11	20.17	26.28	61.1	0.18	-0.6
22	Tremblay	F	305	322	348	2019	21.58	19.67	25.67	42.4	0.15	-0.4
23	Tremblay	M	285	305	276	2019	20.84	18.93	24.94	41.7	0.14	-0.4
24	Tremblay	F	280	305	259	2019	21.05	19.21	24.95	29.6	0.14	-0.2
25	Tremblay	M	246	270	167	2019	20.14	18.20	24.34	33.1	0.14	-0.6
26	Tremblay	M	271	285	232	2019	20.71	18.65	25.22	12.2	0.16	-1.2
27[a]	Tremblay	F	229	248	130	2019	19.78	17.77	24.15	39.3	0.15	-0.9
28	Tremblay	M	261	281	204	2019	22.74	21.16	25.97	38.8	0.15	0.8
29	Tremblay	M	280	297	259	2019	21.76	19.87	25.79	37.3	0.16	-0.4
30	Tremblay	M	295	324	310	2019	31.36	31.21	32.20	14.6	0.24	3.0
Mean	-	-	264	282	224	-	21.67	19.89	25.49	50.0	0.15	-0.1

[a] Individual for which we used body temperature instead of ambient temperature in our FMR model

Table 3.2: Summarized FMR estimates for individual Greenland sharks (*Somniosus microcephalus*) tagged with long-term pop up archival satellite tags (PSATs - depth and temperature time series data) in Tremblay Sound and Scott Inlet, Nunavut, Canada (n=6).

ID	Sex	TL	FL	Mass	Year	Days		Mass adjusted FMR (mgO2h^{-1}kg$^{-0.84}$)			Temp (°C)
							Q$_{10}$=	2.23	1.34	2.99	
31	F	186	174	51.4	2013	366		24.92	25.99	24.42	3.4
32	F	150	141	24.7	2013	366		25.84	25.98	25.80	4.5
33	M	146	137	22.5	2013	364		25.49	25.79	25.36	4.3
34	M	234	219	113	2014	366		25.48	26.70	24.89	3.2
35	F	193	181	58.4	2014	364		24.99	26.10	24.45	3.4
36	M	300	281	264	2015	355		26.12	27.57	25.36	3.1
Mean	-	202	189	88.9	-	364		25.48	26.35	25.05	3.6

Table 3.3: Population level prey consumption estimates for Greenland sharks in two coastal fjord systems (Tremblay Sound and Scott Inlet, Nunavut), and across all of Baffin Bay, Nunavut. Consumption rates are presented as the mass of prey consumed daily by the entire population of Greenland sharks using the minimum population estimate (left) and the maximum (right). Additionally, estimates are provided using the minimum (top) and maximum (bottom) pDiet values derived from published stomach content studies on Greenland sharks.

Location	**Area (km^2)**	**Population**	**Greenland Halibut**			**Ringed Seal**			**Narwhal**		
			pDiet (%)	**Mass consumed (kg/day)**		**pDiet (%F)**	**Mass consumed (kg/day)**		**pDiet (%)**	**Mass consumed (kg/day)**	
Tremblay Sound[a]	517	207-8,014	-	-	-	7.0	0.88	34.01	0.02	0.36	13.76
			-	-	-	33.3	4.17	161.78	-	-	-
Scott Inlet	890	356-13,795	52.9	30.85	1195.52	7.0	1.51	58.54	0.02	0.61	23.68
			72.2	42.11	1631.70	33.3	7.19	278.49	-	-	-
Baffin Bay	689000	275,600-10,679,500	52.9	28083.84	1088248.92	7.0	1375.20	53289.13	0.02	556.37	21559.26
			72.2	38329.93	1485284.92	33.3	6542.04	253504.01	-	-	-

[a] Greenland halibut are not present in Tremblay Sound, so consumption estimates for this prey species were excluded.

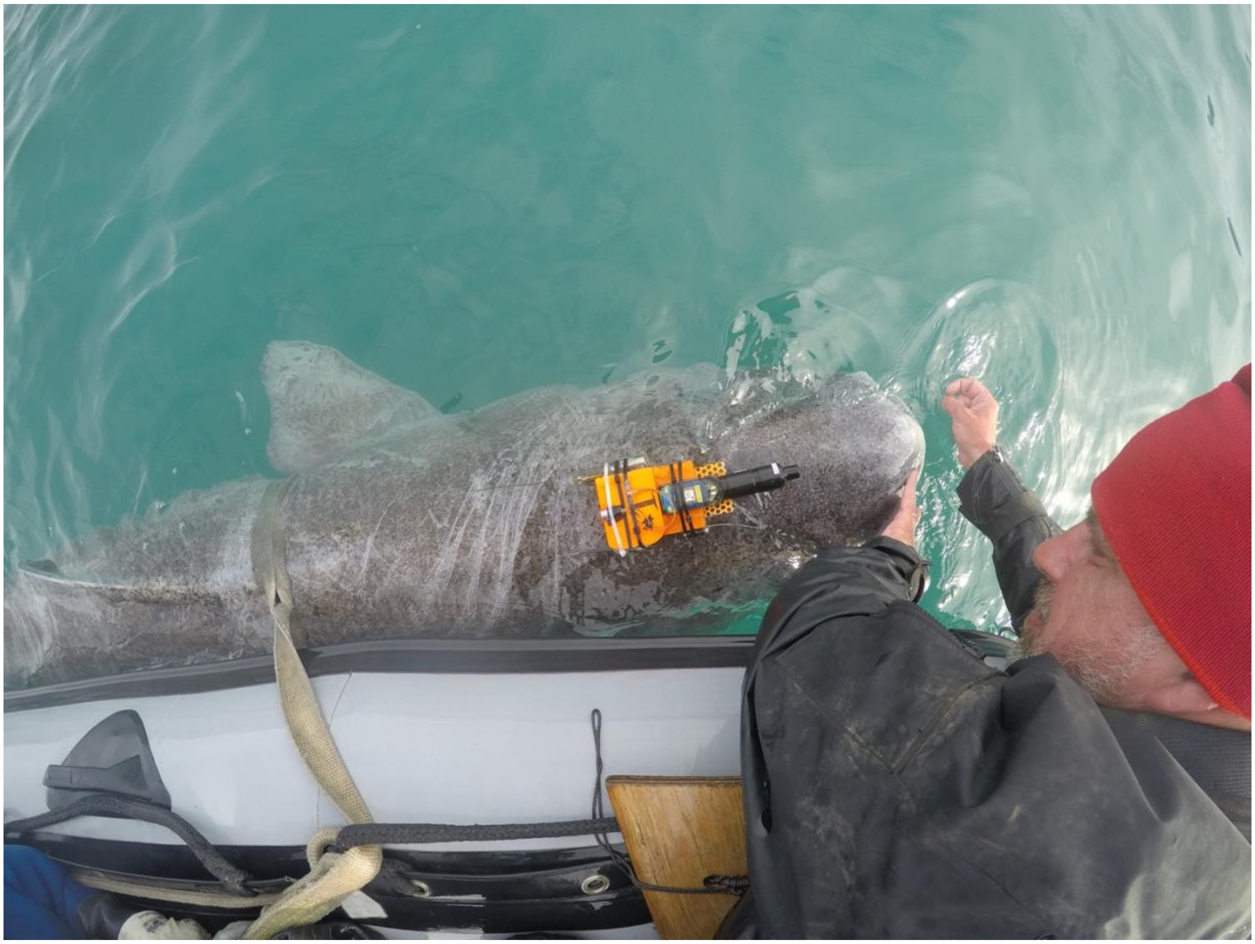

Figure 3.1: Photo depicting the placement of a biologger package on the superior dorsal region of a shark.

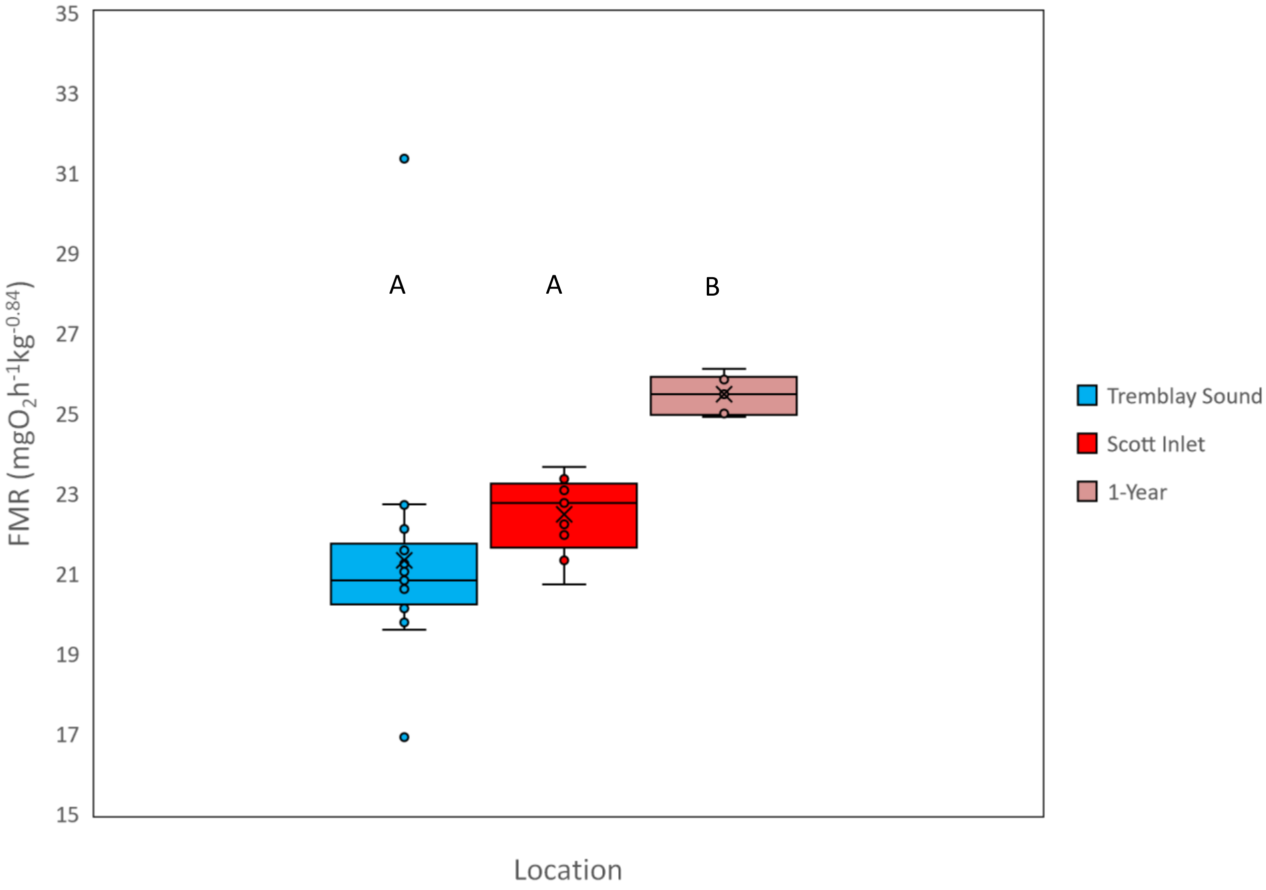

Figure 3.2: Comparison of mass-adjusted FMR for individual Greenland sharks tagged with short-term biologger packages in Scott Inlet (n=9) and Tremblay Sound (n=21), Nunavut, as well as sharks tagged in Scott Inlet with long-term pop up archival satellite tags (PSATs i.e. 1-year, n=6). Only sharks tagged with long-term satellite tags had FMRs that were significantly different from the other cohorts ($p<0.05$).

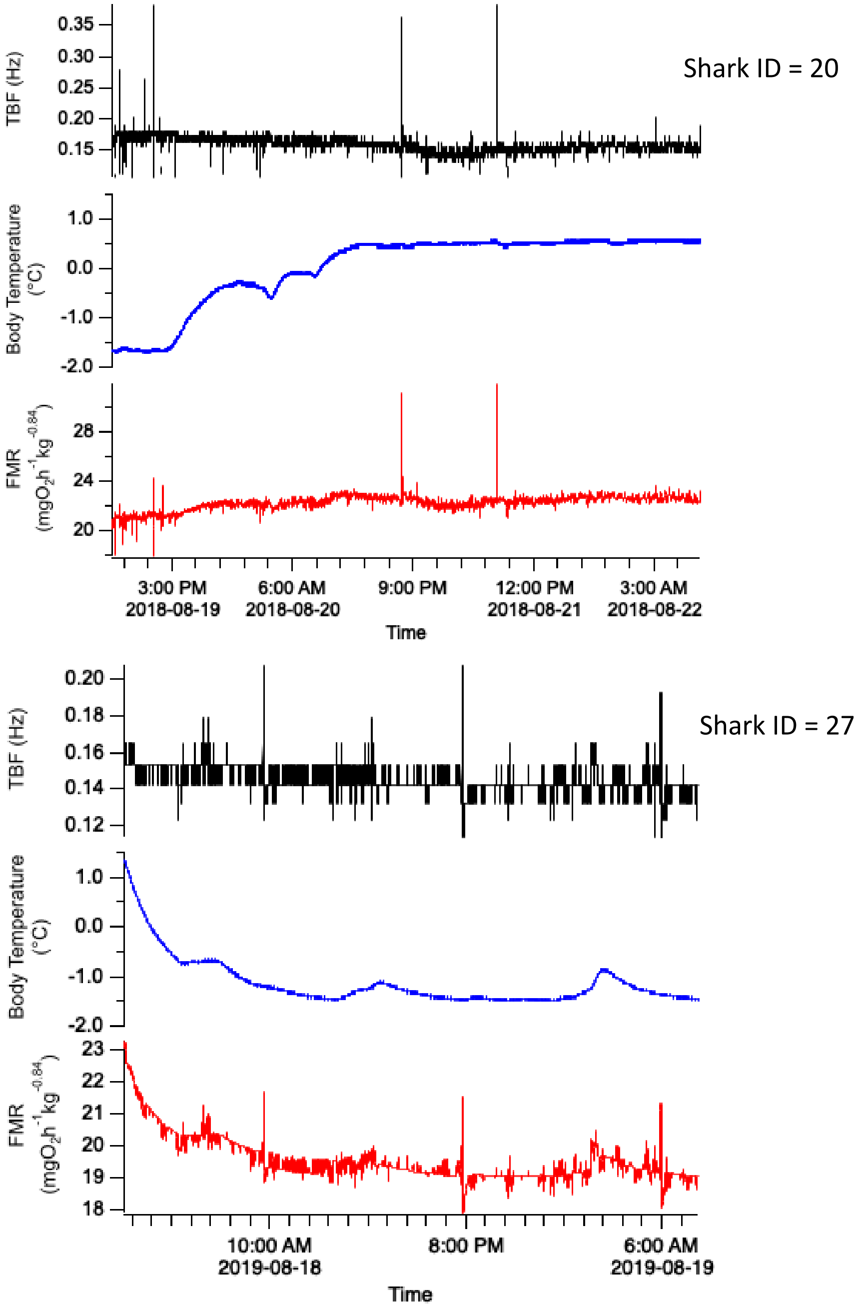

Figure 3.3: The above plots depict instantaneous FMR estimates for the two individual sharks whose body temperatures were recorded alongside triaxial acceleration by biologger packages. FMR traces are presented below the traces for acceleration derived tailbeat frequency (TBF) and body temperature.

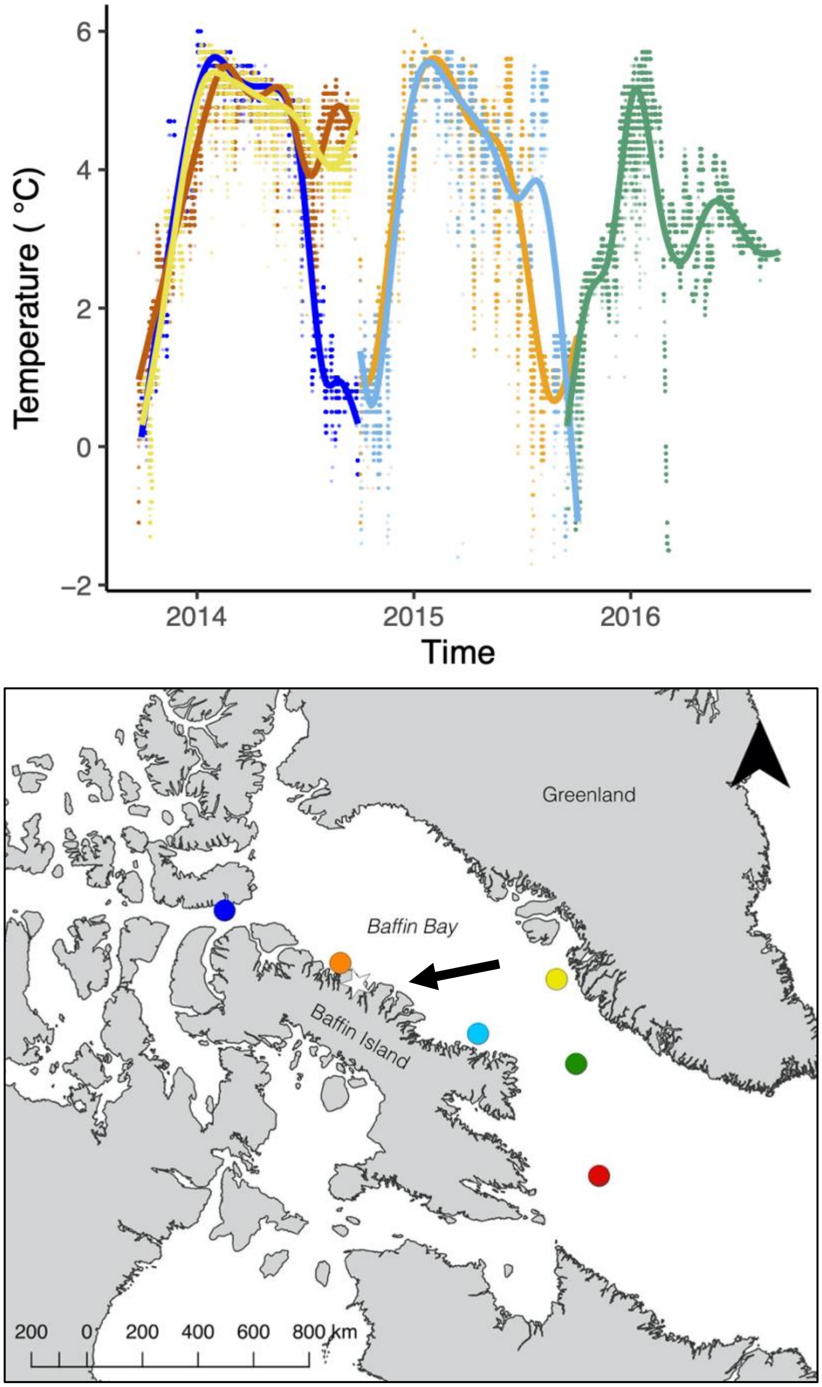

Figure 3.4: The top panel depicts ambient temperature recorded by individual sharks (n=6) equipped with pop up archival satellite tags (PSATs) for a year. The lower panel is a map showing the tagging location (black arrow) and pop-off locations of all six individuals. Locations were not transmitted by the tags during the course of each deployment, so only initial (tagging) and final (tag pop-off) locations are known.

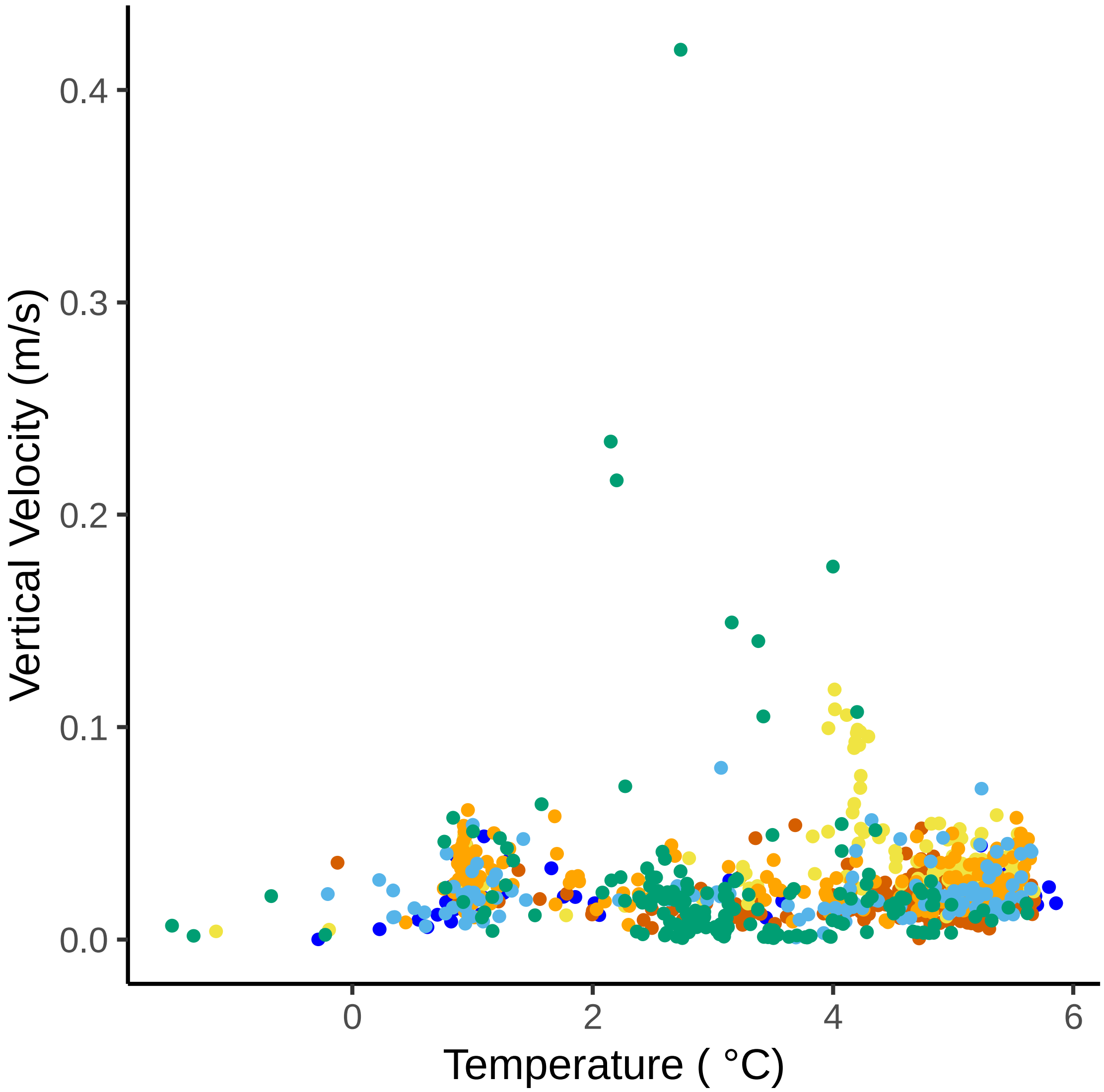

Figure 3.5: Vertical velocity against ambient temperature for the individual sharks (n=6) equipped with pop-up archival satellite tags (PSATs) in Scott Inlet, Nunavut, for one year deployments.

SUPPLEMENTARY INFORMATION

SI Table 3.1: Proportional contributions of narwhal, ringed seal and Greenland halibut to the diet of Greenland sharks sampled in previous stomach content studies in Cumberland Sound, Nunavut, Canada. The caloric densities used to estimate prey consumption rates for each prey species are also provided.

Species	Common name	pDiet (%F)			Caloric Density	
		McMeans et al. 2015	McMeans et al. 2012	Fisk et al. 2002	kcal/g	Source
Reinhardtius hippoglossoides	Greenland Halibut	52.9	72.2	71	1.31	Lawson et al. 1998
Pusa hispida	Ringed seal	29.4	33.3	7	3.54	Stirling and McEwan 1975
Monodon monoceros	Narwhal	2	-	-	2.5	Lefort et al. 2020

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CHAPTER 4

General Discussion

4.1 Summary

As the largest ectotherm in the Arctic and the oldest living vertebrate species on the planet, the Greenland shark is undeniably unique. However, many aspects of its behaviour, physiology and ecological role in Arctic ecosystems remain shrouded in mystery. Because metabolism relates to virtually all aspects of an organism's biology (either directly or indirectly; Brown et al. 2004), this thesis' exploration of metabolic rate in Greenland sharks lays the groundwork for testing a broad range of ecological hypotheses through the lens of energetics.

Determining the basic maintenance costs needed for an individual to remain alive is at the core of most animal energetics studies (Chabot et al. 2016). Referred to as standard metabolic rate in ectotherms, it forms the basis for the comparison of other common measures of metabolism; all of which, by definition, are themselves inclusive of SMR (e.g. FMR, maximum metabolic rate, routine metabolic rate, etc.; Chung et al. 2019). In chapter 2, we estimated the metabolic rates of resting Greenland sharks for the first time using custom-built field respirometers. We also estimated active metabolic rate in one individual while it swam at a known tailbeat frequency. This allowed us to construct a rudimentary activity-cost equation which was ultimately used to estimate activity's contribution to the field metabolic rates of tagged individuals in Chapter 3.

By using relatively large-bodied individuals in our respirometry trials, we more than doubled the previous size record for respirometry in sharks (Payne et al. 2015). In doing so, we were able to combine our resting metabolic rate data for Greenland sharks with those published for other species in order to derive an interspecific scaling relationship for mass and temperature across sharks. The resulting coefficients describing the links between mass and temperature were found to be quite similar to those derived for teleost fish. Additionally, we found that the Greenland sharks studied in our respirometers did not have mass and temperature adjusted metabolic rates that were unique when compared to other shark species, though our resting estimates (recorded under difficult field conditions) could be overestimating SMR for the species. Finally, since the resting metabolic rates of Greenland sharks measured at ecologically relevant temperatures were not higher than expected, we suggested that metabolic cold adaptation has not led to higher metabolic rates in this species.

In Chapter 3, we modeled the FMR of Greenland sharks equipped with biologger packages recording activity and temperature. Our models used metabolic scaling relationships to transform our respirometer-derived resting metabolic rates into FMR. Because of their frigid habitats and slow cruising speeds, Greenland sharks were predicted to have particularly low FMRs. Due to seasonal differences in the habitat use of individuals, short-term estimates derived for sharks inhabiting the coastal inlets of Baffin Island differed from our long-term (1-year) estimates encompassing both their time in the inlets and their time in the greater Baffin Bay area. These FMR estimates were then combined with literature data describing the diet and abundance of Greenland sharks in the Arctic in order to estimate their prey consumption rates of culturally and commercially relevant species. Given their limited energy requirements, individual Greenland sharks were predicted to consume very little prey. However, local populations of sharks could represent an important consumer link in Arctic marine ecosystems, but further research into the population dynamics and regional diets of Greenland sharks is needed to increase the accuracy of our estimates and to reduce the uncertainty surrounding them.

4.2 Implications and Future Directions

The economy of life functions through the exchange of energy within an ecosystem. Energy – usually from the sun – is captured, transformed, expended and traded up the food chain, allowing all organisms from plankton to whales to survive and interact on our planet. Understanding the flow of energy through ecosystems allows us to better grasp the dynamics of food webs and ultimately predict how they may be affected by environmental or community level changes (O'Connor et al. 2009; Ullah et al. 2018). However, in order to understand energy flow at the food web level, one must first understand it at the species level (O'Connor 2009). While this thesis does not provide a complete assessment of the energetics of Greenland sharks, it does provide key estimates of both resting and field metabolic rate for the species, allowing for an initial description of its consumer role in several regions of the Canadian Arctic.

As climate change warms the Arctic and the loss of sea ice continues to allow for the expansion of commercial fisheries (Christiansen et al. 2014), bridging the knowledge gaps in our understanding of Greenland shark metabolic ecology is an important way by which we can inform the conservation and management of Northern marine ecosystems (Edwards et al. 2019). With this goal in mind, research efforts should be focused on improving and refining the metabolic rate estimates presented here, deriving additional measures of metabolism, and finally linking these to other aspects of Greenland shark biology in order to predict how climate change and commercial fisheries may impact Greenland shark populations moving forward.

The field respirometry protocols employed to estimate metabolic rate in this thesis did not allow for the estimation of a true SMR for Greenland sharks. Instead, the short acclimation periods (~2.5 hours) and lack of pre-trial fasting meant that we could only estimate resting routine metabolic rate as a proxy for SMR. While it may not be feasible to fast a Greenland shark under field conditions for the entirety of its gastric evacuation time (i.e. assuring it is in a post-absorptive state; Chabot et al. 2016), future studies could accelerate the process through stomach flushing prior to conducting respirometry trials. This would shorten the overall duration of captivity and lower the probability that SMR estimates include digestive costs (Sandblom et al. 2012). Assuming good weather, it may also be possible to reduce the energetic cost of stress during trials by allowing sharks to acclimate to the respirometer for longer periods (e.g. 24 hours) prior to estimating SMR (Chabot et al. 2016). Measuring oxygen consumption throughout the acclimation period could also provide insight into the stress metabolism of the species (Schreck et al. 2016). Finally, while the estimates presented here for Greenland sharks cover a much larger range of body masses than any other previous study on fish, the small sample size and lack of temperature variation during respirometry trials prevented the derivation of intraspecific scaling relationships for mass and temperature for this species. As such, acquiring additional data points would greatly benefit our understanding of the dynamics of metabolism in Greenland sharks.

In addition to deriving intraspecific relationships for mass and temperature’s effect on metabolic rate in Greenland sharks, future studies should focus on improving the relationship between activity and metabolic rate, as this would improve the accuracy of the FMR estimates (and prey consumption rates) presented in Chapter 3. Ideally, individual sharks would undergo respirometry trials in which they swam for prolonged periods at various swim speeds, allowing for the derivation of a relationship between activity level and metabolic rate. While using a circular static respirometer would provide a more realistic activity-cost relationship than a flume-style respirometer where swimming is forced (Lear et al. 2018), recording oxygen consumption over a range of volitional swim speeds is not always possible since many species have a preferred/optimal cruising speed and only deviate from it in short bursts (Whitney et al. 2016; Lear et al. 2018). One possible solution would be to equip the sharks with accelerometers during respirometry trials and then correlate dynamic body acceleration with oxygen consumption (Lear et al. 2017). This calibration could then be used when estimating FMR in tagged sharks in the wild.

SMR and FMR are not the only ecologically valuable measures of metabolism. Aerobic scope (i.e. the difference between maximum and minimum metabolic rate) is also a useful metric for predicting the resilience of species faced with different climate change scenarios (Clark et al. 2013). Measuring aerobic scope at various temperatures can help identify under which conditions it is optimized, and ultimately, the likelihood that a species will thrive or not in a changing environment (Clark et al. 2013). For example, the temperature at which aerobic scope is optimized was proposed as a physiological explanation for why two cooccurring species of salmon in British Columbia were being differentially affected by climate change, and why one seemed to have a competitive advantage over the other (Clark et al. 2011). As climate change is expected to disproportionately increase temperatures in the Arctic relative to the global average (Johannessen et al. 2004), estimating aerobic scope for polar species such as Greenland sharks could provide valuable insight regarding their ability to cope with these changes while strengthening predictions about shifting food webs.

While metabolism can be very informative on its own, it is also useful when assessed in the context of other important biological processes such as reproduction. Relatives of the Greenland shark invest huge amounts of energy into reproduction (Nielsen et al. 2020), with gravid females often carrying ova weighing 7.5-22% of their total body mass (Yano 1995; Clarke et al. 2001). Sharks must therefore divest a large proportion of energy from their own metabolism towards the production of ova (Harshman and Zera 2007). However, reproduction can also lead to increases in energetic demand that are not directly related to ova production (Angilletta and Sears 2000). Therefore, assessing the metabolic rates of both gravid and non-gravid Greenland sharks would greatly improve our understanding of the energetics and consumer impact of these sharks in Arctic ecosystems. While previously unknown, recent research by Nielsen et al. determined the size at maturity of both male and female Greenland sharks (2020). Future studies could therefore measure the metabolic rates of both sexually mature and immature sharks, allowing for the estimation of reproductive costs in this species.

4.3 Conclusion

As a slow yet highly mobile species inhabiting one of the most rapidly changing ecosystems on the planet, Greenland sharks are increasingly the focus of research initiatives within the broad fields of ecology, physiology and conservation biology. While recent work on the species has shed light on several longstanding mysteries regarding their biology (diet and trophic position [McMeans et al. 2013; Hussey et al. 2014], contaminant loads [Fisk et al. 2002], life history parameters [Nielsen et al. 2016; Nielsen et al. 2020], and movements [Edwards et al., in review]), a majority of questions remain unanswered. It is the author's hope that the research presented in this thesis will provide a valuable basis for the continuing study of Greenland shark metabolism.

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