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RESEARCH ARTICLE

Life in the slow lane: field metabolic rate and prey consumption rate of the Greenland shark (*Somniosus microcephalus*) modelled using archival biologgers

Eric Ste-Marie^{1,*}, Yuuki Y. Watanabe^{2,3}, Jayson M. Semmens⁴, Marianne Marcoux⁵ and Nigel E. Hussey¹

ABSTRACT

Field metabolic rate (FMR) is a holistic measure of metabolism representing the routine energy utilization of a species living within a specific ecological context, thus providing insight into its ecology, fitness and resilience to environmental stressors. For animals that cannot be easily observed in the wild, FMR can also be used in concert with dietary data to quantitatively assess their role as consumers, improving understanding of the trophic linkages that structure food webs and allowing for informed management decisions. Here, we modelled the FMR of Greenland sharks (*Somniosus microcephalus*) equipped with bilogger packages or pop-up archival satellite tags (PSATs) in two coastal inlets of Baffin Island (Nunavut) using metabolic scaling relationships for mass, temperature and activity. We estimated that Greenland sharks had an overall mean ($\pm$ s.d.) FMR of $21.67 \pm 2.30 \text{ mg O}_2 \text{ h}^{-1} \text{ kg}^{-0.84}$ ($n=30$; 1–4 day accelerometer package deployments) while residing inside these cold-water fjord systems in the late summer, and $25.48 \pm 0.47 \text{ mg O}_2 \text{ h}^{-1} \text{ kg}^{-0.84}$ ($n=6$; PSATs) over an entire year. When considering prey consumption rate, an average shark in these systems (224 kg) requires a maintenance ration of 61–193 g of fish or marine mammal prey daily. As Greenland sharks are a lethargic polar species, these low FMR estimates, and corresponding prey consumption estimates, suggest they require very little energy to sustain themselves under natural conditions. These data provide the first characterization of the energetics and consumer role of this vulnerable and understudied species in the wild, which is essential given growing pressures from climate change and expanding commercial fisheries in the Arctic.

KEY WORDS: Biologging, Ecology, Energetics, Metabolism, Food web dynamics

INTRODUCTION

The energy requirements of wild animals are often influenced predictably by their behaviour, physiology and environment (Brown et al., 2004; Metcalfe et al., 2016). As a result, holistic estimates of the energy needed by individuals to support

life-sustaining activities in the wild, referred to as field metabolic rate (FMR), can inform our understanding of their ecology and fitness (Treberg et al., 2016; Wilson et al., 2006). In turn, this can guide conservation and management initiatives through improved knowledge of the costs and benefits of different lifestyles occurring under varying environmental conditions (Metcalfe et al., 2016; Treberg et al., 2016). This has led researchers to estimate FMR across diverse species in terrestrial and aquatic environments, inhabiting polar to tropical latitudes, and encompassing a broad array of locomotory strategies (e.g. walking, swimming and flying). While multiple approaches are available to estimate FMR for terrestrial and air-breathing aquatic species (e.g. doubly labelled water and heart rate methods), the majority of these have proven ineffective when applied to fish (Butler et al., 2004; Green, 2011; Speakman, 1997; Treberg et al., 2016). This has limited our ability to study the energetics of most fish in the wild, but has naturally led to innovative methods such as the combined use of accelerometry and respirometry (Metcalfe et al., 2016; Wilson et al., 2006) and isotopic analyses (e.g. otolith microchemistry; Chung et al., 2019) that are now advancing this field. To date, studies of FMR of fish have allowed prediction of the energetic impacts of changing climate (Lear et al., 2020), highlighted the effect of ecotourism on individual energy demands (Barnett et al., 2016), identified population-level metabolic differences across ecotypes (Chung et al., 2020), and parameterized bioenergetic models (Cooke et al., 2016).

While valuable on its own, if FMR is combined with diet information, species' prey consumption rates can be estimated. Prey consumption rates provide a quantitative assessment of trophic interactions within ecosystems where direct measures of predation are often impractical (Nagy, 1987). The consumer links between predators and prey drive community dynamics and, when disturbed, can lead to cascading effects throughout an ecosystem (Frank et al., 2005; Heithaus et al., 2008). Developing an understanding of the prey consumption rates of predators consequently provides a more quantitative approach to understand their role in a given ecosystem and ultimately can inform conservation initiatives (Baum and Worm, 2009). For example, fish consumption by reef sharks inhabiting an atoll in French Polynesia was estimated to outpace actual fish production in the area, suggesting the resident shark population was relying on seasonal immigration pulses of spawning fish to a greater extent than previously thought (Mourier et al., 2016). These data highlight the importance of applying ecosystem-based conservation strategies in the context of marine predators. Moreover, while prey consumption rates can inform our understanding of predator ecology, they can also be applied to prey-focused objectives. Fisheries stock models that incorporate predation mortality tend to be more effective predictors of population dynamics than those that do not (Tyrrell et al., 2011).

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The use of bioenergetic modelling to estimate prey consumption rates in Arctic marine systems is growing in popularity, stemming from the urgent need to address the impacts of climate change, rapidly shifting species ranges and growing anthropogenic pressure on local food web dynamics (Christiansen et al., 2014; Perry et al., 2005). Prey consumption rates for endothermic predators such as narwhal (*Monodon monoceros*) and killer whales (*Orcinus orca*) have provided insight into the current and evolving food web dynamics of Arctic marine ecosystems, though the logistics of measuring metabolism in such large and difficult to access species prevented the use of empirically derived energetics data, leading to a degree of uncertainty surrounding estimates (Laidre et al., 2004; Lefort et al., 2020). Nevertheless, similar prey consumption rate estimates are lacking for many fish species including the largest ectothermic predator in the Arctic, the Greenland shark (*Somniosus microcephalus*).

While the ecological role of Greenland sharks remains largely unknown, their large size, presumed 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). However, climate change and expanding commercial fisheries for Greenland halibut coupled with historical exploitation have led to an overall decreasing population trend for Greenland sharks and the recently downgraded status of 'Vulnerable' by the International Union for the Conservation of Nature (IUCN 2020). Despite the logistic challenges associated with studying a large Arctic fish, bridging the knowledge gaps surrounding the ecology of Greenland sharks is required to inform management decisions. This is pertinent given the Marine Stewardship Council recently certified the offshore (NAFO 0B region) Greenland halibut (*Reinhardtius hippoglossoides*) fishery with requirements for improved ecological data on the regional population of Greenland sharks, which form a large portion of bycatch (Knapman et al., 2019). Given recent respirometer-derived estimates of resting and active metabolic rate for Greenland sharks inhabiting Baffin Bay, Nunavut, a foundation is now established on which to begin exploring the FMR and prey consumption rate of this species (Ste-Marie et al., 2020). Quantifying the consumption of prey species such as Greenland halibut, for example, could subsequently be used to inform ecosystem models used for the management of developed and developing fisheries targeting this species in both coastal and offshore environments.

Here, we integrated previously derived resting and active metabolic rates of Greenland sharks with biologged acceleration and temperature data in order to model the FMR of individuals tagged in coastal fjord systems of Baffin Island, Nunavut, Canada, during the summer (biologger packages), as well as over an entire year [pop-up archival satellite tags (PSAT) recording temperature and depth only]. We then integrated FMR estimates with published diet and abundance data to estimate the prey consumption rates of this Arctic predator on locally and commercially valuable species at both the individual and local population level. Given their generally lethargic lifestyle (Watanabe et al., 2012), we predicted that individual sharks would have relatively low FMRs and that this would translate into low prey consumption needs, especially when compared with their tropical counterparts or local endothermic predators.

MATERIALS AND METHODS

Fishing and tagging

Greenland sharks, *Somniosus microcephalus* (Bloch and J. G. Schneider 1801), were captured in Scott Inlet (2015–2016)

and Tremblay Sound (2017–2019), Nunavut, using baited longlines. Longlines in Scott Inlet consisted of 50 barbed circle hooks (16/18 O; O. Mustad & Son Americas Inc., Miami, FL, USA) baited with squid, set for 12 h at ~900 m depth and subsequently hauled to the surface using a motorized winch aboard the MV *Nulijuk*. Between 2017 and 2019, longlines of a similar design, but with between 5 and 10 hooks, were baited with seal, char or narwhal (donated by local Inuit subsistence hunters) and set at ~100–150 m depth in Tremblay Sound. These lines were set for 3–8 h and then pulled to the surface by hand (see Supplementary Materials and Methods for more details). Once a shark was at the surface at either location, it was restrained alongside a small Zodiac boat using straps secured around the tail and mid-body, measured (total length, TL; and fork length, FL), and tissue samples taken. In order to equip sharks with biologger packages (Fig. 1), a sterilized plastic cable tie was threaded beneath the skin behind each shark's head on the dorsal side and connected to a timed release system (Little Leonardo Ltd, Tokyo, Japan). Following all tagging and sampling procedures, the hook and restraining straps were removed and sharks were released once they resumed consistent tail movements (see Supplementary Materials and Methods for further details regarding handling of animals). After 1–4 days (a predetermined time frame set within the Little Leonardo release system), the cable tie was severed, allowing the biologger package to release from the animal and float to the surface. The biologger package was then retrieved using satellite (SPOT, Wildlife Computers Inc., Redmond, Seattle, WA, USA) and VHF tags (MM100 series, Advanced Telemetry Systems Inc., Isanti, MN, USA).

Similar capture and handling procedures were carried out for sharks equipped with PSATs in Scott Inlet between 2013 and 2015. However, tags were attached to a raised contact point on a circular disc manufactured from a strong plastic polymer mounted on the dorsal fin using three plastic bolts and associated stainless steel washers and lock nuts. Actual tag attachment was undertaken by crimping a ~5 cm leader wire from the base of the PSAT to the raised contact point. This approach was used because of the extremely soft muscle tissue in this species, which makes long-term dart retention difficult; see details of a similar approach in Hussey et al. (2018).



Fig. 1. Biologger attachment. Photo depicting the placement of a biologger package on the superior dorsal region of a Greenland shark (*Somniosus microcephalus*) used to estimate field metabolic rate (FMR) in the current study.

All fishing and tagging protocols adhere to local and federal regulations, and were approved by the University of Windsor's Animal Care Committee (AUPP #18-01 and #17-12).

Biologging data and analysis

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 Ltd; Maritime BioLoggers, Halifax, NS, Canada) that recorded at frequencies of at least 16 Hz depending on the model. Ambient temperature (external) was recorded for all tagged sharks ($n=30$; 1 Hz), while body temperature (internal) was recorded at ~15 cm depth in the dorsal musculature for a subset of sharks ($n=2$; 1 Hz) in 2018 and 2019 (LAT1810, Lotek Inc., Newmarket, ON, Canada; Nakamura et al., 2015).

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 10 h of each deployment were cut from the data to account for post-release recovery (Y. Y. Watanabe, A. N. Barkley, K. J. Hedges and N. E. Hussey, unpublished). Tail-beat frequency (TBF), or the number of complete back-and-forth strokes of the caudal fin per second, was derived from raw acceleration in the lateral (or sway) axis using continuous wavelet transformation and then subsampled to 1 Hz (Sakamoto et al., 2009). TBF was chosen over other common activity metrics such as overall dynamic body acceleration (ODBA) and swim speed because it could be derived for all accelerometer-tagged sharks (unlike swim speed), it is less sensitive to tag position than ODBA (Mori et al., 2015; Wilson et al., 2020), and it was the metric used to record activity levels in a 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 other shark species (e.g. lemon sharks, *Negaprion brevirostris*; Bouyoucos et al., 2017).

Modelling FMR

Following the initial processing of biologged activity and ambient/body temperature data, we constructed a model in R (<http://www.R-project.org/>) to estimate FMR for each tagged Greenland shark using metabolic scaling relationships for mass, temperature and activity:

$$\text{FMR} = (20.22 \times \text{TBF} \times M) + \left[(\text{rRMR} \times M^{0.84}) \times Q_{10}^{\frac{T_2 - T_1}{10}} \right]. \quad (1)$$

Respirometer-derived estimates of resting routine metabolic rate (rRMR) were first scaled according to the estimated mass ($M=1.109 \times 10^{-6} \times \text{FL}^{3.4199}$; Leclerc et al., 2012) of each individual using an interspecific allometric scaling exponent previously derived for sharks (0.84, derived over a mass range of <1 to 126 kg; Ste-Marie et al., 2020). Though no intraspecific exponent currently exists for Greenland sharks, those published for other shark species cover a narrow range of values and encompass the interspecific estimate provided above (i.e. 0.80–0.86; Sims, 1996, 2000; Payne et al., 2015). Following this mass adjustment, rRMR was scaled according to biologged body/ambient temperature data (T_2) using the interspecific Q_{10} for sharks of 2.23 and an initial temperature (T_1) representing the experimental temperature at which rRMR was measured (Ste-Marie et al., 2020). 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 other shark species (2.99 for nurse sharks, *Ginglymostoma cirratum*; Lear et al., 2017; 1.34 for scalloped 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 an individual's biologged activity levels. The effect of TBF on oxygen consumption rate for Greenland sharks was approximated using the mass-specific slope (20.22) of an interpolated linear relationship connecting the active routine metabolic rate for one individual (aRMR at TBF=0.18 Hz) studied in a large circular respirometer to its rRMR (i.e. its oxygen consumption rate at TBF=0 Hz; Ste-Marie et al., 2020). Though activity cost equations for other shark species have been derived using data for multiple individuals across a range of swim speeds, we opted to use one derived from the limited Greenland shark data because of the highly variable effect of activity on the energetics of different species (Lear et al., 2017), as well as the differing fin morphology and swimming behaviour of our focal species (Watanabe et al., 2012; Iosilevskii and Papastamatiou, 2016). Moreover, the shark used to derive our activity scaling slope was closer in body size (126 kg) to the wild sharks for which we were estimating FMR (range 33–367 kg). 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 activity (Byrnes et al., 2021). Despite this, body mass and mean TBF were not correlated across the 30 accelerometer-tagged individuals (Fig. S1), suggesting a mass effect on the relationship between oxygen consumption and TBF may be negligible in our sample of mostly sub-adult animals (Bale et al., 2014; Broell and Taggart, 2015; Sato et al., 2010).

For individuals whose internal body temperatures were biologged, we plotted instantaneous FMR (i.e. per second) over the course of each deployment. While muscle temperature typically follows ambient temperature closely in ectotherms, some species use behavioural strategies such as yo-yo diving to modulate body temperature, which in turn has implications for their metabolic rate (e.g. Nakamura et al., 2020). Greenland sharks also exhibit yo-yo diving behaviour; consequently, we calculated overall time-averaged FMR estimates using both body and ambient temperature data to check for possible discrepancies between the two estimates. As metabolic rate does not change instantly according to the behaviour and environment of an animal, a 1 min smoothing window (i.e. rolling mean) was applied to the instantaneous FMR data in order to ensure our estimates were physiologically plausible (Watanabe et al., 2019; Williams et al., 2014). For the individuals whose internal body temperature was not biologged, we calculated only a single time-averaged estimate of FMR using ambient temperature data.

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 Ltd) that measured ambient temperature and depth every 10 min for a 365 day period. A similar method as detailed above was employed to estimate long-term (1 year) FMR in these sharks; however, as the tags did not record acceleration, we used the average TBF observed across all accelerometer-tagged individuals as the activity component of our estimates. As activity levels could vary seasonally with temperature, we calculated vertical velocity (i.e.

change in depth per unit time; 10 min sampling rate) as a proxy for activity and performed a linear mixed effects model to test whether activity was influenced by temperature throughout the year. Individual sharks were included as a random effect.

Short-term FMR estimates derived from biologger deployments in Scott Inlet and Tremblay Sound were compared using unpaired *t*-tests in Microsoft Excel. 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 with the exception of two outlying sharks (IDs: 18 and 30).

Modelling prey consumption rates

In order to estimate prey consumption at the individual level, short- and long-term FMR estimates were first converted 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% that is commonly applied in bioenergetics studies on fish (Brett and Groves, 1979). These energy requirements were subsequently interpreted in terms of specific prey requirements using literature-derived caloric densities (kcal g⁻¹) for focal species (Table S1). Greenland halibut, ringed seal and narwhal were

selected as key prey based on their importance to the diet of Greenland sharks in the Eastern Canadian Arctic (McMeans et al., 2015), and/or their importance to commercial fisheries and Northern indigenous communities as a subsistence resource. Given the preliminary nature of these prey consumption estimates, only FMR estimates derived using the interspecific Q_{10} of 2.23 were used in our prey consumption model. Mean individual-level prey consumption rates are presented for Greenland sharks inhabiting Scott Inlet or Tremblay Sound (mean±s.d. body mass 224±99 kg), estimated from the mass-scaled energy requirements of 177 sharks representing 5 years of catch data.

In order to transition from individual-level prey requirements to local population-level consumption rates, we constructed the following model to estimate the mass of a specific prey type (P_x) consumed by a population of Greenland sharks:

$$P_x = \frac{BM \times E \times p_{\text{diet}}}{U_x}, \quad (2)$$

where BM represents the biomass of sharks in a specific region, E represents their energy requirements per unit mass, U_x represents the caloric density (kcal g⁻¹) of a prey species, and p_{diet} represents the proportional contribution of that prey species to the overall diet of a shark.

While population estimates for Greenland sharks are lacking in the literature, a recent study estimated local abundance and biomass

Table 1. Summary of field metabolic rate estimates for individual Greenland sharks (*Somniosus microcephalus*)

Location and year	ID	Sex	FL (cm)	TL (cm)	Mass (kg)	Mass adjusted FMR (mg O ₂ h ⁻¹ kg ^{-0.84})			Deployment duration (h)	TBF (Hz)	Temperature (°C)
						$Q_{10}=2.23$	$Q_{10}=2.99$	$Q_{10}=1.34$			
Scott Inlet (2015)	1	M	241	256	155.1	21.34±0.44	19.74±0.47	24.57±0.40	22.3	0.13±0.01	0.9±0.14
	2	F	278	300	253.1	22.24±1.95	20.55±2.34	25.8±1.02	16.9	0.15±0.01	0.3±1.48
	3	M	215	222	105.1	20.74±0.44	19.13±0.44	23.99±0.42	38.2	0.12±0.01	0.9±0.12
	4	F	310	330	367.4	22.76±0.81	21.11±0.91	26.12±0.61	38.9	0.14±0.01	0.7±0.57
	5	M	280	300	259.4	21.97±0.90	20.33±0.95	25.3±0.83	100.5	0.14±0.02	0.8±0.44
Scott Inlet (2016)	6	M	294	312	305.1	23.67±1.32	22.07±1.56	26.95±0.82	106.1	0.16±0.01	0.8±0.90
	7	M	269	286	226.6	23.12±0.95	21.5±1.05	26.41±0.77	105.6	0.16±0.02	0.8±0.64
	8	M	153	163	33.1	23.09±1.37	21.55±1.57	26.19±1.00	44.6	0.21±0.02	1.1±0.71
	9	M	210	223	96.8	23.37±0.71	21.79±0.74	26.56±0.65	23.7	0.19±0.01	1±0.18
Tremblay Sound (2017)	10	F	273	292	237.9	20.66±0.42	18.6±0.42	25.23±0.43	45.9	0.16±0.01	-1.3±0.04
	11	M	284	313	272.3	21.32±0.73	19.32±0.73	25.68±0.73	68	0.16±0.01	-0.9±0.06
	12	M	277	290	250	20.62±0.41	18.54±0.42	25.2±0.41	70.6	0.16±0.01	-1.3±0.05
	13	M	269	286	226.2	19.6±0.75	17.57±0.85	24.06±0.52	85.9	0.13±0.01	-1.1±0.47
	14	M	295	320	310.1	19.89±0.99	17.95±1.12	24.05±0.64	86.1	0.12±0.01	-0.6±0.68
Tremblay Sound (2018)	15	F	251	265	178.5	21.73±1.11	19.78±1.28	25.94±0.67	62.9	0.17±0.01	-0.7±0.84
	16	M	260	276	201.3	21.25±0.81	19.39±0.92	25.21±0.50	28.3	0.15±0.01	-0.2±0.59
	17	M	257	279	193.5	20.77±0.69	18.68±0.76	25.43±0.47	32.5	0.17±0.01	-1.5±0.53
	18	F	294	320	306.5	16.93±0.47	14.87±0.53	21.45±0.31	31.7	0.08±0.00	-1.2±0.34
	19	F	231	238	134.4	20.32±0.48	18.3±0.49	24.72±0.47	57.3	0.16±0.01	-0.9±0.13
	20 ^a	M	279	288	256.2	22.72±0.62	21.01±0.73	26.26±0.44	83.3	0.16±0.01	0.5±0.68
	21	M	247	257	168.9	22.11±0.90	20.17±0.99	26.28±0.66	61.1	0.18±0.01	-0.6±0.61
Tremblay Sound (2019)	22	F	305	322	347.5	21.58±0.98	19.67±1.12	25.67±0.61	42.4	0.15±0.01	-0.4±0.71
	23	M	285	305	275.6	20.84±1.01	18.93±1.15	24.94±0.67	41.7	0.14±0.01	-0.4±0.68
	24	F	280	305	259.4	21.05±1.49	19.21±1.71	24.95±0.89	29.6	0.14±0.01	-0.2±1.02
	25	M	246	270	166.6	20.14±0.73	18.2±0.85	24.34±0.44	33.1	0.14±0.01	-0.6±0.63
	26	M	271	285	232	20.71±0.31	18.65±0.31	25.22±0.31	12.2	0.16±0.01	-1.2±0.03
	27 ^a	F	229	248	130.4	19.78±0.57	17.77±0.64	24.15±0.41	39.3	0.15±0.01	-0.9±0.38
	28	M	261	281	204	22.74±1.82	21.16±2.19	25.97±0.94	38.8	0.15±0.01	0.8±1.29
	29	M	280	297	259.4	21.76±1.50	19.87±1.76	25.79±0.87	37.3	0.16±0.01	-0.4±0.97
	30	M	295	324	310.1	31.36±6.78	31.21±8.92	32.2±3.09	14.6	0.24±0.02	3±3.78
Mean			264	282	224	21.67±2.30	19.89±2.63	25.49±1.66	50	0.15±0.03	-0.1±1.02

Sharks were equipped with accelerometers and temperature loggers in Tremblay Sound and Scott Inlet, Nunavut, Canada ($n=30$). Mass-adjusted field metabolic rate (FMR), mean tail-beat frequency (TBF) and temperature for each deployment are presented (means±s.d.), along with fork length (FL), total length (TL) and the durations of each deployment. ^aIndividual for which both ambient and body temperature were recorded.

for several inshore regions of the eastern Canadian Arctic using data derived from baited remote underwater video surveys (Devine et al., 2018). We multiplied the authors' biomass density estimate for Scott Inlet ($1210.6 \text{ kg km}^{-2}$) by the area of the system (890 km^2), estimated using a polygon of the region created in QGIS; for details, see Supplementary Materials and Methods) in order to approximate overall Greenland shark biomass (BM) in the above equation. Frequency of occurrence (%F) data, extracted from a previous diet study undertaken in another coastal inlet of Baffin Island (Cumberland Sound; McMeans et al., 2015), was used as a proxy for true p_{diet} in our model as the latter could not be measured directly in the wild (Table S1). Derived from stomach content analysis, %F represents the fraction of non-empty stomachs in which a certain prey item is found. While other diet metrics such as percentage mass (%M) and percentage number (%N) have also been used in previous studies attempting to model prey consumption rate in fish (Barnett et al., 2017), no such values have been published for Greenland sharks in coastal Eastern Canadian waters. Although these data are available for other regions such as Western/Eastern Greenland, diet varies regionally in this species, negating the applicability of those data in the present context. Only the mean short-term FMR derived for biollogger-equipped sharks in Scott Inlet was used to estimate the energy requirements (E) of sharks in that system. Without abundance or biomass estimates for Greenland sharks inhabiting Tremblay Sound and the greater Baffin Bay area, we could not estimate local population-level prey consumption rates for sharks in these systems.

RESULTS

FMR

Over 5 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 biollogging packages that recorded triaxial acceleration and temperature for periods ranging from 12 to 106 h (mean $\pm$ s.d. 49.5 ± 27.6 h). When using the interspecific Q_{10} of 2.23 derived for sharks, mean mass-adjusted FMR was estimated to be $21.67 \pm 2.30 \text{ mg O}_2 \text{ h}^{-1} \text{ kg}^{-0.84}$ (95% CI 20.85 – $22.49 \text{ mg O}_2 \text{ h}^{-1} \text{ kg}^{-0.84}$) across all tagged Greenland sharks over the deployment period (Table 1). Using a maximum Q_{10} of 2.99 (*Ginglymostoma cirratum*; Lear et al., 2017), mean mass-adjusted FMR decreased slightly to $19.89 \pm 2.63 \text{ mg O}_2 \text{ h}^{-1} \text{ kg}^{-0.84}$ (95% CI 18.95 – $20.83 \text{ mg O}_2 \text{ h}^{-1} \text{ kg}^{-0.84}$, 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 to $25.49 \pm 1.66 \text{ mg O}_2 \text{ h}^{-1} \text{ kg}^{-0.84}$ (95% CI 24.90 – $26.08 \text{ mg O}_2 \text{ h}^{-1} \text{ kg}^{-0.84}$, $P < 0.01$, $n = 30$). FMR estimates did not vary significantly between Greenland sharks sampled in Tremblay Sound and Scott Inlet (Fig. 2; two-tailed t -test with unequal variance, $P > 0.05$, $n = 21$ and 9, respectively). However, results were more variable across sharks tagged in Tremblay Sound, with both the maximum and minimum FMR estimates recorded for individual sharks in this system (i.e. ranging from 16.93 to $31.36 \text{ mg O}_2 \text{ h}^{-1} \text{ kg}^{-0.84}$, at mean temperatures and TBF of -1.2 to 3.0°C and 0.08 to 0.24 Hz , respectively).

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 $22.24 \pm 0.62 \text{ mg O}_2 \text{ h}^{-1} \text{ kg}^{-0.84}$ when using body temperature and $22.72 \pm 0.62 \text{ mg O}_2 \text{ h}^{-1} \text{ kg}^{-0.84}$ when using ambient temperature as a proxy. Similarly, shark 27 had a time-averaged FMR of $19.54 \pm 0.74 \text{ mg O}_2 \text{ h}^{-1} \text{ kg}^{-0.84}$ when using body temperature and

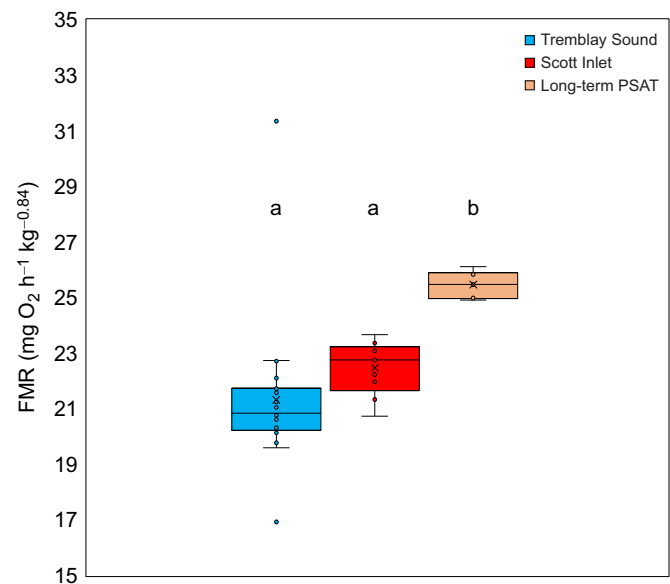


Fig. 2. Comparison of mass-adjusted FMR for individual Greenland sharks. Sharks were tagged with short-term biollogger packages in Scott Inlet ($n = 9$) and Tremblay Sound ($n = 21$), Nunavut, and with long-term pop-up archival satellite tags (PSATs; 1 year deployments) in Scott Inlet ($n = 6$). Only sharks tagged with long-term PSATs had FMRs that were significantly different from those of the other cohorts (two-tailed t -test with unequal variance, $P < 0.01$, $n = 30$ short-term and $n = 6$ long-term). Circles represent individual Greenland shark FMR estimates, crosses and middle line indicate the mean and median estimate, respectively, the bottom and top edges of each box represent the first and third quartile, and whiskers indicate the maximum and minimum FMR estimate for each cohort, excluding outliers (i.e. points beyond 1.5 times the interquartile range).

$19.78 \pm 0.57 \text{ mg O}_2 \text{ h}^{-1} \text{ kg}^{-0.84}$ when using ambient temperature. When considering instantaneous FMR (estimated using body temperature) plotted over time, short periods of elevated FMR were observed in both individuals, corresponding with bursts of elevated activity (TBF; Fig. 3).

Year-long FMR estimates were calculated for six sharks equipped with PSATs in 2013–2015 in Scott Inlet (Table 2). The average FMR of these individuals was $25.48 \pm 0.47 \text{ mg O}_2 \text{ h}^{-1} \text{ kg}^{-0.84}$ (95% CI 25.10 – $25.85 \text{ mg O}_2 \text{ h}^{-1} \text{ kg}^{-0.84}$, at $Q_{10} = 2.23$), representing an approximate 18% increase over the short-term estimates presented above for individuals tagged with accelerometer packages (Fig. 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 higher temperatures experienced by sharks during the winter and spring months (Fig. 4A). Average winter temperatures of $>4^\circ\text{C}$ were observed in all six sharks, indicating that these individuals left the cold-water coastal fjord systems of Baffin Island in late autumn. The pop-off locations of three sharks, however, indicated that they returned to these areas the following year (Fig. 4B). As with the short-term accelerometer-derived FMR estimates, varying Q_{10} in our FMR model for long-term satellite tagged individuals resulted in significantly different average FMR values (paired t -tests, $P < 0.05$; Table 2). 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 ($P = 0.681$; Fig. S2).

Prey consumption rate

The mean energy requirement of Greenland sharks in the study system, estimated from 177 Greenland sharks captured and

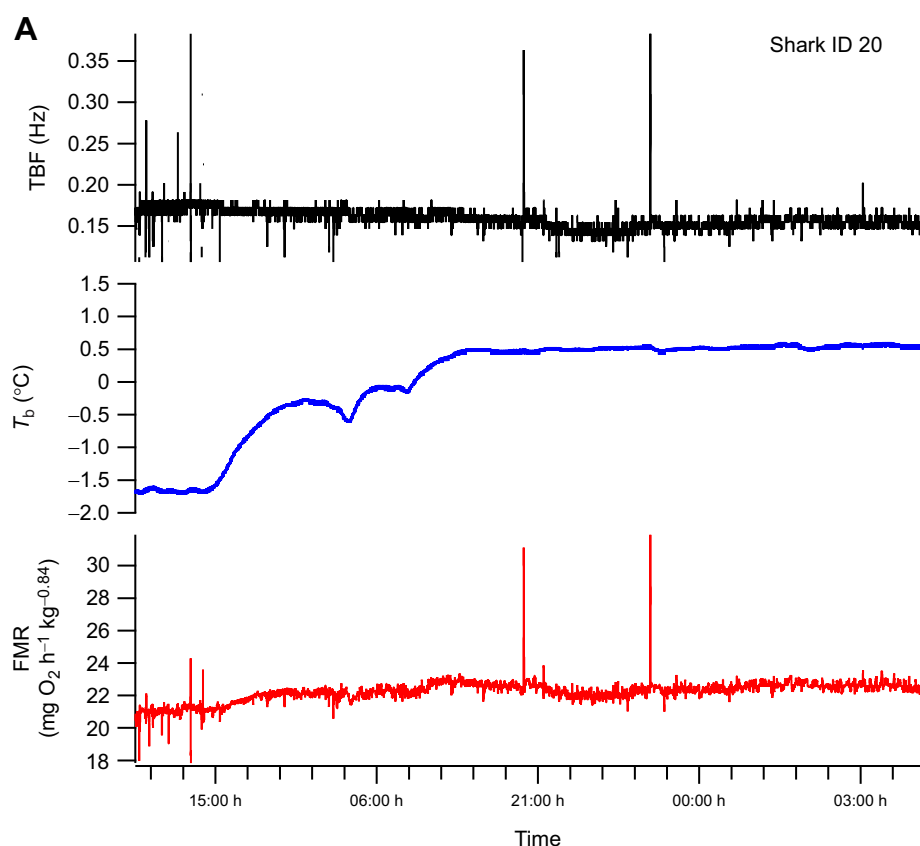


Fig. 3. Instantaneous FMR estimates for individual Greenland sharks. Data are shown for the two sharks whose body temperature was recorded alongside triaxial acceleration by biollogger packages (A, shark ID 20, recorded 19–21 August 2018; B, shark ID 27, recorded 18–19 August 2019). FMR traces are presented below the traces for acceleration derived tail-beat frequency (TBF) and body temperature (T_b).

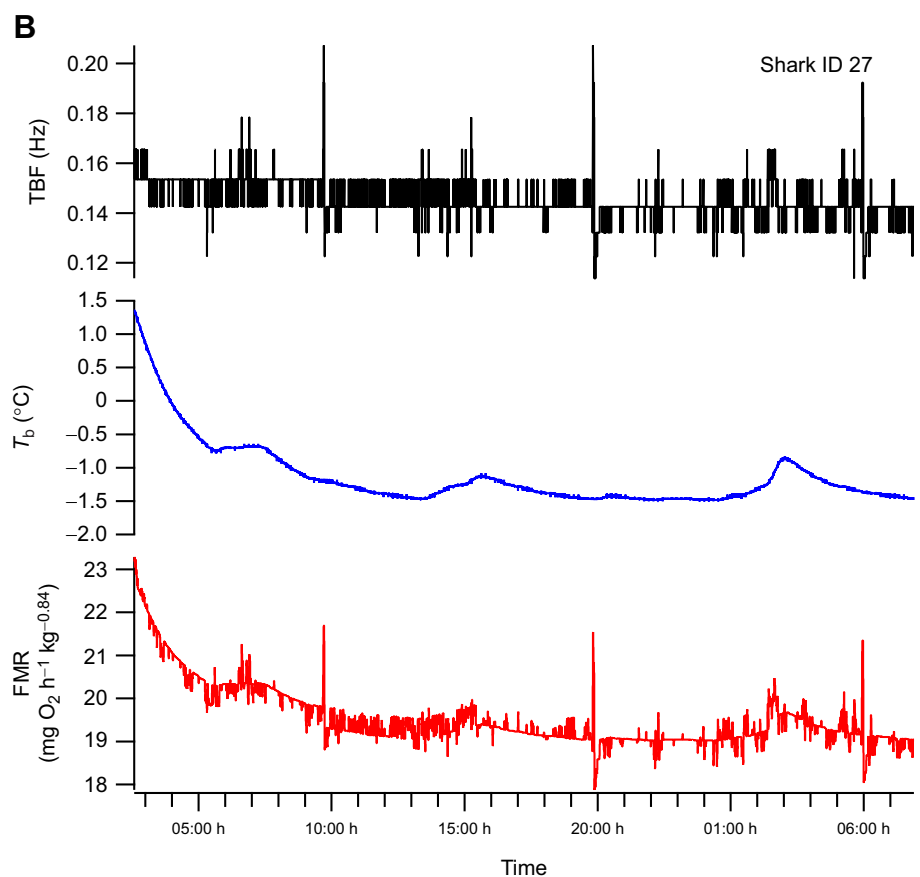


Table 2. Summary of FMR estimates for individual Greenland sharks tagged with long-term pop-up archival satellite tags (PSATs)

ID	Sex	TL (cm)	FL (cm)	Mass (kg)	Year	Deployment duration (days)	Mass adjusted FMR (mg O ₂ h ⁻¹ kg ^{-0.84})			Ambient temperature (°C)
							Q ₁₀ =2.23	Q ₁₀ =1.34	Q ₁₀ =2.99	
31	F	186	174	51.4	2013	366	24.92±3.04	25.99±1.20	24.42±3.99	3.4 (−0.5–6)
32	F	150	141	24.7	2013	366	25.84±1.74	25.98±0.67	25.80±2.32	4.5 (−1.1–5.8)
33	M	146	137	22.5	2013	364	25.49±2.11	25.79±0.83	25.36±2.77	4.3 (−1.3–5.8)
34	M	234	219	113	2014	366	25.48±2.81	26.70±1.10	24.89±3.68	3.2 (−1.7–6)
35	F	193	181	58.4	2014	364	24.99±2.74	26.10±1.09	24.45±3.57	3.4 (−1.6–5.7)
36	M	300	281	264	2015	355	26.12±1.79	27.57±0.71	25.36±2.32	3.1 (−1.5–5.7)
Mean		202	189	88.9		364	25.48±0.47	26.35±0.67	25.05±0.55	3.6 (−1.7–6)

Sharks were equipped with PSATs (to record depth and temperature time series data) in Scott Inlet, Nunavut, Canada (*n*=6). The mean ambient temperature recorded in each deployment is included (with the range in parentheses).

measured in Scott Inlet and Tremblay Sound over the last 5 years (mean mass 224±99 kg, range 29–692 kg), was 214.6±80.3 kcal day⁻¹ during their late summer/autumn residency within these coastal systems, and 252.3±94.5 kcal day⁻¹ averaged for the whole year (Table 3). This is equivalent to a daily maintenance ration of only 164 g (95% CI 155–173 g) of Greenland halibut, 61 g (95% CI 57–64 g) of ringed seal or 86 g (95% CI 81–91 g) of narwhal while the sharks are resident in the fjords during the late summer/autumn, or 193 g (95% CI 182–203 g), 71 g (95% CI 67–75 g) or 101 g (95% CI 95–107 g), respectively, when considering their mean energy needs for the entire year. Accounting for the relative contributions of each prey type and the estimated shark biomass (1210.6 kg km⁻², Devine et al., 2018) in Scott Inlet during the ice-free Arctic summer when sharks are known to be resident (Edwards et al., 2021), daily population-level prey consumption rates for this system were estimated to be 8.7 kg (95% CI 7.3–10 kg) of narwhal, 91 kg (95% CI 76–105 kg) of ringed seal and 440 kg (95% CI 370–511 kg) of Greenland halibut (Table 4).

DISCUSSION
FMR

In the absence of a method to directly measure FMR in fish (Treberg et al., 2016), modelled estimates such as those presented here can provide important insight into the lives of little-known and difficult to study species such as the Greenland shark. The use of acceleration biologging to model the FMR of fish is a relatively new technique (as reviewed in Metcalfe et al., 2016), with few studies to date applying this approach in sharks (e.g. Watanabe et al., 2019; Lear et al., 2020). As expected given the Greenland shark’s polar habitat and low activity levels in the wild, our estimates of FMR were much lower than those previously reported for the regionally endothermic white shark (*Carcharodon carcharias*; Watanabe et al., 2019) and the warm water dwelling bull shark (*Carcharhinus leucas*; Lear et al., 2020). These FMR estimates for Greenland sharks also allowed for an assessment of their consumer role in coastal Arctic ecosystems through the estimation of individual and local population-level prey consumption rates. While uncertainty surrounding several of the model inputs remains, these preliminary consumption rate estimates indicate a relatively low biomass of prey is required to sustain Greenland sharks inhabiting the coastal regions of Baffin Island, Nunavut, Canada.

The maintenance of a low FMR in Greenland sharks may provide an adaptive advantage to the polar environments they inhabit where resource distribution is often patchy and highly seasonal. While endothermic predators in the Arctic such as many marine mammals benefit from their ability to exhibit higher swim speeds than their ectothermic prey (Grady et al., 2019), their much higher energy demands also restrict them to areas with high prey densities for most

of the year (Bluhm and Gradinger, 2008). Conversely, a large and slow moving ectothermic predator such as the Greenland shark, requiring much less energy to fuel its metabolism, may be able to survive extended periods of time between feeding events (Furey et al., 2016), allowing it to thrive in areas with scarce or unpredictable resource availability, and possibly accounting for a presumably much lower success rate in cases of active predation (Norberg, 1977). While scavenging is generally considered the primary foraging strategy for Greenland sharks consuming large mobile prey, anecdotal accounts from indigenous harvesters, evidence from closely related pacific sleeper sharks, and the biologged burst-swimming events lasting several minutes recorded here (Fig. 3, assessed by TBF) suggest active predation may also represent an important foraging strategy (MacNeil et al., 2012; Watanabe et al., 2012; Horning and Mellish, 2014).

Instantaneous FMR estimates over time can be used to estimate the energetic investments of an animal towards specific activities (Watanabe et al., 2019; Williams et al., 2014). For example, if Greenland sharks are in fact using bursts of elevated swim speed to pursue prey (as suggested above), then it should eventually be possible to estimate the relative aerobic cost of these predation attempts using instantaneous FMR estimates derived over that period, assuming activity cost equations for burst swimming were first derived through respirometry. Ultimately, this information could be used to assess the energetic trade-offs associated with different foraging strategies in this species (Williams et al., 2014). However, 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 these ectothermic sharks when feeding on endothermic prey (Jorgensen et al., 2015; Meyer and Holland, 2012; Sepulveda et al., 2004). Additionally, one of the greatest challenges associated with estimating the energetics of individual prey pursuits will be determining anaerobic costs associated with bursts of rapid swimming, as these are not accounted for in classic activity–oxygen consumption relationships and can significantly increase overall energy requirements in some fish (Nelson, 2016).

Most of the FMR estimates presented here 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 is likely because of the slow swim speeds exhibited by Greenland sharks in the wild and the much smaller temperature gradients present in the Arctic compared with those observed across depths at southern latitudes (Carey et al., 1990; Watanabe et al., 2012; Nakamura et al., 2015). This finding, although based on a small sample of sharks, suggests

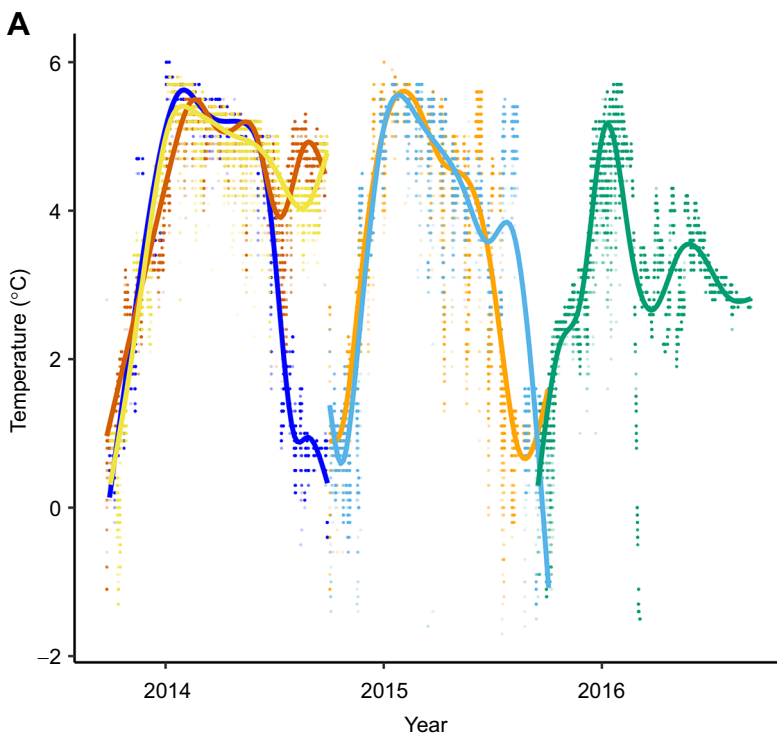
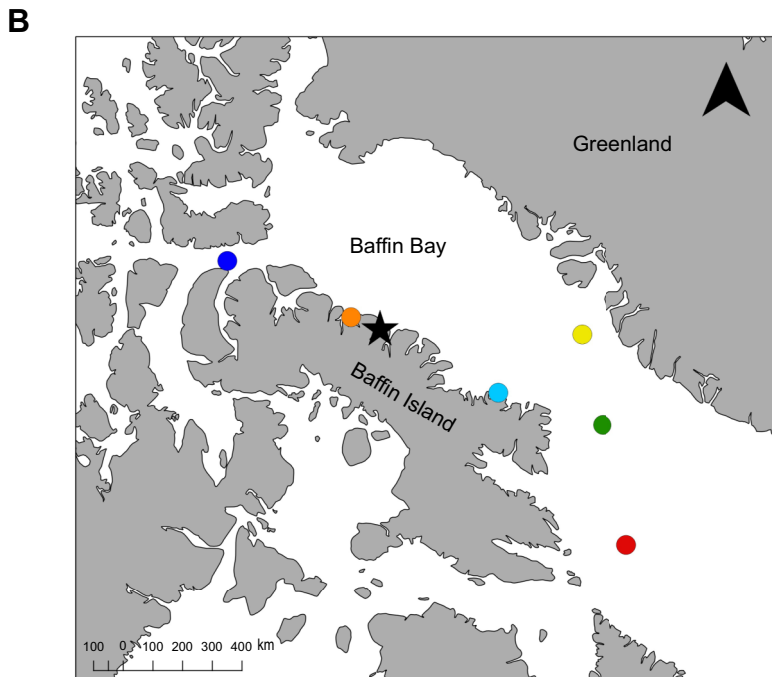


Fig. 4. Ambient temperature profiles and pop-up locations for PSAT tagged Greenland sharks. (A) Ambient temperature recorded by PSATs from individual Greenland sharks ($n=6$) over a 1 year duration. (B) Map showing the tagging location (black star; Scott Inlet) and pop-off locations (circles) of all six individuals equipped with long-term PSATs. Locations were not transmitted by the tags during the course of each deployment, and track reconstruction was not possible because of seasonal daylight cycles; consequently, only initial (tagging) and final (tag pop-off) locations are known.



that time-averaged FMR can be accurately modelled using ambient temperature in this slow swimming species and lends credibility to the estimates provided for the 28 sharks for which body temperature was not recorded. While ambient temperature cannot be directly used to estimate instantaneous FMR, as 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 the estimation of heat-transfer coefficients for Greenland sharks and improve on current energetic models (Nakamura et al., 2015, 2020).

Estimates of FMR based on long-term behavioural and environmental datasets are essential for developing an accurate understanding of a species' energetics under natural conditions (Cooke et al., 2016). The biologged data used in many studies to model FMR in fish are often collected over short time periods consisting of days or weeks instead of years because of battery or memory limitations and the need to recover tags (Metcalf et al., 2016; Treberg 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 overestimation or underestimation of energy requirements for species that migrate and/or undergo

Table 3. Average daily energy requirement for individual Greenland sharks and corresponding maintenance rations of prey

FMR	Energy requirement (kcal day ⁻¹)	Daily prey requirement (g)		
		Greenland halibut	Narwhal	Ringed seal
Short-term	215±80.3	164 (155–173)	86 (81–91)	61 (57–64)
Long-term	252±94.5	193 (182–203)	101 (95–107)	71 (67–75)

Energy requirements for sharks (mass 224±99 kg, $n=177$) were estimated from catch data for Scott Inlet and Tremblay Sound (see Materials and Methods). Prey consumption estimates (i.e. minimum mass of prey required to meet energy needs) were derived using both short-term (i.e. 1–4 days) and long-term (i.e. 365 days) FMR estimates (with 95% confidence intervals in parentheses).

large seasonal shifts in habitat (Lear et al., 2020; 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 summer. The conditions experienced by the sharks while in these fjords differ from those experienced by the sharks outside of these areas and at different times of the year. This was evident when assessing the temperature profiles of sharks equipped with satellite tags for an entire year (Fig. 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 FMR estimates that were approximately 18% higher than our short-term estimates. Moreover, we might expect a larger discrepancy between these estimates if we were 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 would be predicted to drive higher average activity levels. However, vertical velocity (calculated from PSAT depth data) remained relatively constant throughout the year across temperatures. As vertical velocity is determined in part by swim speed (Sato et al., 2003), this finding suggests average activity levels may not have changed dramatically between winter and summer, though definitive conclusions cannot be drawn without direct measurements of activity or corresponding body angles for sharks during dives. Nevertheless, the higher energetic demands predicted for Greenland sharks overwintering in warm waters have implications for their long-term prey consumption rates and ultimately their overall impact on Arctic food webs.

While our modelled FMR estimates represent an important step towards understanding the true metabolic cost of life for this iconic Arctic predator, a couple assumptions must be acknowledged. First, 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 therefore could be 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.

Second, an important assumption of 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 the 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 small but 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 to be the closest to reality. In the current literature, the majority of sharks studied at ecologically relevant experimental temperatures have demonstrated metabolic Q_{10} values of >2, including a cordal cousin of Greenland sharks, the spiny dogfish (*Squalus acanthias*), which was found to have a Q_{10} of 2.59 (Giacomin et al., 2017), which is also similar to the interspecific value for sharks.

Prey consumption rate

The low predicted energy requirements for Greenland sharks tagged in this study suggest these animals can meet their energy demands

Table 4. Local population-level prey consumption estimates for Greenland sharks in Scott Inlet, Nunavut

Species	p_{diet} (%F)	U (kcal g ⁻¹)	Predicted consumption (kg)	
			Daily	90 days
Greenland halibut	52.9	1.31	440 (370–511)	39,632 (33,312–45,951)
<i>Reinhardtius hippoglossoides</i>				
Ringed seal	29.4	3.54	91 (76–105)	8151 (6851–9451)
<i>Pusa hispida</i>				
Narwhal	2	2.5	8.7 (7.3–10)	785 (660–910)
<i>Monodon monoceros</i>				

p_{diet} represents the proportional contribution of the prey species to the overall diet of a shark (%F, frequency of occurrence). U represents the caloric density of the prey species. Consumption rates are presented as the predicted mass of prey consumed daily and over their 3 month (~90 days) summer residency period (Edwards et al., 2021) (with 95% confidence intervals in parentheses). Shark biomass was extrapolated from local abundance estimates presented in Devine et al. (2018).

with minimal prey consumption rates. To put this into context, a typical Greenland shark's daily caloric requirement is predicted to be at least 45 times less per kilogram than that of the average killer whale in the system, a more active endothermic predator known to feed on similar prey species (Lefort et al., 2020; Williams et al., 2004). Given these energy requirements, we found that an average shark (224 ± 99 kg) could potentially sustain itself for 5–6 days with the consumption of a single adult Greenland halibut (1 kg), or for several months following a larger meal (15 kg) of marine mammal prey (Fig. 5). 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) or 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 in growth or reproduction, both of which could increase the energy requirements presented here (Barnett et al., 2017; Nielsen et al., 2020). However, available data in the literature for Greenland sharks suggest a very slow growth rate (~ 0.5 cm per year, estimated from a recaptured individual that grew from 262 to 270 cm over a 16 year period; Hansen, 1963), while sharks inhabiting Scott Inlet and Tremblay Sound are mostly sexually immature and consequently should not incur high reproductive costs (Nielsen et al., 2020).

In order to better understand the potential impact of such low individual-level prey consumption rates on the broader ecosystem, we further estimated prey consumption at the local population level for Scott Inlet using published biomass estimates for the system and proportional diet contributions derived for another nearby coastal inlet, Cumberland Sound (McMeans et al., 2015; Devine et al., 2018). Despite the high abundance of sharks (15.5 individuals km^{-2}) in Scott Inlet relative to the other areas surveyed in Devine et al.'s (2018), prey consumption estimates for

the system were low. For example, we estimated that over the entire ~ 90 day period in which Greenland sharks inhabit Scott Inlet (Edwards et al., 2021), the local population of sharks consumes 40,000 kg of Greenland halibut, 8000 kg of ringed seal and <1000 kg of narwhal (i.e. less than the mass of an average adult narwhal; Heide-Jørgensen, 2018). By comparison, sub-populations of narwhal overwintering in two regions of Baffin Bay have previously been predicted to consume between 90,000 and 700,000 kg of Greenland halibut daily (Laidre et al., 2004), far outpacing halibut consumption by Greenland sharks in Scott Inlet, even when adjusting for the larger geographic areas covered in the narwhal study (i.e. $\sim 11,000$ and $26,000$ km^2 ; Laidre et al., 2004).

These preliminary estimates rely on the assumption that focal prey species are being consumed by Greenland sharks in similar proportions in Scott Inlet to those in Cumberland Sound where the stomach content data used to estimate p_{diet} in our model were collected (McMeans et al., 2015). While Cumberland Sound may share many of the same prey resources as Scott Inlet, small differences in the relative contributions of focal prey species could affect the prey consumption rates presented here, as well as future estimates for other coastal regions of Baffin Island such as Tremblay Sound. For example, although 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; Marcoux et al., 2019). This may indicate that sharks in Tremblay Sound rely on narwhal to a greater extent than would be predicted using a p_{diet} derived from the Cumberland Sound stomach content data in prey consumption rate models for the region. Therefore, before population-level prey consumption rates can be reliably estimated across the geographic range of Greenland sharks, spatial and temporal uncertainty surrounding the diet of Greenland sharks will need to be resolved.

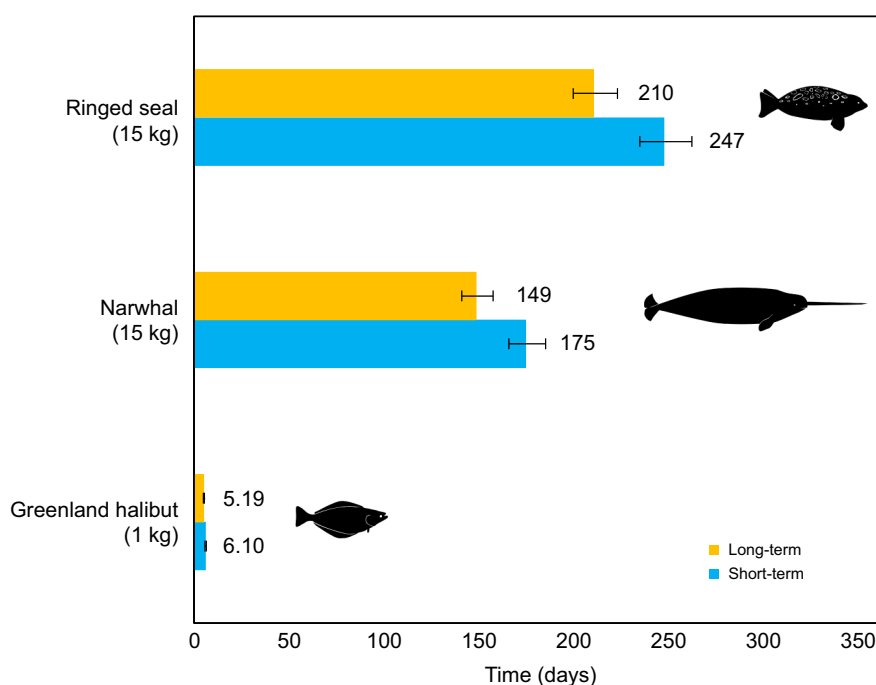


Fig. 5. Energy requirements of Greenland sharks. Predicted number of days that a Greenland shark (average size for Scott Inlet and Tremblay Sound, 224 ± 99 kg) could meet its estimated energy requirements from a meal of Greenland halibut (*Reinhardtius hippoglossoides*), ringed seal (*Pusa hispida*) or narwhal (*Monodon monoceros*). Orange bars represent estimates derived using the 1 year mean FMR (long-term; PSATs). Blue bars represent estimates derived using the mean FMR derived from short-term bilogger deployments in the late summer/autumn. The 95% confidence intervals appear as black whiskers around each bar. Prey icons are not drawn to scale.

The prey consumption rates estimated here for Greenland sharks, though coarse, provide an initial quantitative assessment of the ecological role of Greenland sharks in the Arctic. To date, most food web models have ignored the impact of 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). While the population size of Greenland sharks is unknown across most of the Arctic, localized estimates indicate Greenland sharks can be regionally abundant despite their large size and slow sexual maturation (Devine et al., 2018; Nielsen et al., 2020), perhaps in part as a consequence of the low energy requirements, resulting in high carrying capacities for these areas (Brown et al., 2004). Understanding their consumer role in Arctic ecosystems is therefore essential to the proper management of fisheries and to maintaining healthy shark populations in the future (Edwards et al., 2019; Tyrrell et al., 2011).

Conclusion

Overall, these data provide a preliminary understanding of the field metabolism and prey consumption rates of Greenland sharks inhabiting the Eastern Canadian Arctic. Their predicted low metabolic demands in the wild suggest that both individuals and localized populations of sharks, such as those that occur in the summer in Scott Inlet, Tremblay Sound and likely other fjord systems, require very little food to sustain themselves. However, further research is needed into the population dynamics and diet of localized populations of Greenland sharks to refine the estimates provided. It is also important to consider that these prey consumption estimates do not differentiate between active predation and scavenging, which could significantly affect how we perceive the ecological role of these sharks and remains a key point to address in future work. Regardless, climate change is affecting both the physical environment and biological communities of the Arctic, emphasizing the importance of deriving these types of data on the behaviour and energetics of species such as the Greenland shark.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: E.S., Y.Y.W., J.M.S., N.E.H.; Methodology: E.S., Y.Y.W., J.M.S., N.E.H.; Formal analysis: E.S.; Investigation: E.S., Y.Y.W., M.M., N.E.H.; Resources: N.E.H.; Data curation: E.S., Y.Y.W., N.E.H.; Writing - original draft: E.S., N.E.H.; Writing - review & editing: E.S., Y.Y.W., J.M.S., M.M., N.E.H.; Visualization: E.S.; Supervision: Y.Y.W., N.E.H.; Project administration: E.S., N.E.H.; Funding acquisition: E.S., Y.Y.W., N.E.H.

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