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The slowest fish: Swim speed and tail-beat frequency of Greenland sharks

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ABSTRACT

Locomotory muscle function of ectothermic fishes is generally depressed in cold waters, making them vulnerable to avian and mammalian predators whose body temperature remains high. Paradoxically, Greenland sharks *Somniosus microcephalus* exhibit the reverse of this usual predator–prey thermal pattern by apparently hunting seals in Arctic waters. To examine whether this species possesses cold-adaptations that enhance its swimming performance, we used data-logging tags to measure swim speed and tail-beat frequency (which reflects muscle-shortening speed) of six free-swimming sharks (204–343 kg). For comparison, we compiled these parameters for wild fishes from the literature over a wide body mass range (0.2–3900 kg) and examined the scaling relationships using phylogenetically informed statistics. The sharks cruised at 0.34 $m \cdot s^{-1}$ with a tail-beat frequency of 0.15 Hz, both of which were the lowest values for their size across fish species. The mean and maximum speed (0.74 $m \cdot s^{-1}$) and acceleration during burst swimming (0.008 $m \cdot s^{-2}$) were much lower than those of seals. Our results indicate that the swimming performance of Greenland sharks is limited by cold waters (~2 °C) and insufficient to catch swimming seals. However, Arctic seals sleep in water to avoid predation by polar bears *Ursus maritimus*, which may leave them vulnerable to this cryptic slow-swimming predator.

1. Introduction

Many physiological processes are depressed at low temperatures, including the contraction speed and power output of locomotory muscles in aquatic vertebrates (Bennett, 1984; Rome, 1990; Wardle, 1980). Consequently, both sustained and maximum swim speeds decrease with a decrease in temperature in ectotherms such as fishes and amphibians (Bennett, 1990; Claireaux et al., 2006; Navas et al., 1999). In contrast, swim speed is likely to be independent of ambient temperature in endotherms (e.g., birds and mammals), in which locomotory muscles function at high body temperatures of 30–40 °C. This fundamental difference is thought to impact the global structure of marine vertebrate communities (Cairns et al., 2008). Seabirds and marine mammals can swim fast even in cold water, and hence, they have an advantage when attacking ectothermic fishes; this hypothesis explains the dominance of avian and mammalian aquatic predators at mid to high latitudes. On the other hand, birds and mammals are hunted by sharks in the tropics and subtropics, where warm waters help sharks to chase endothermic prey by enhancing their swimming performance.

Some sleeper sharks (*Somniosus* spp.), including the Greenland shark *Somniosus microcephalus* and Pacific sleeper shark *Somniosus pacificus* (following Murray et al., 2008, although taxonomic relationships have not been resolved) appear to be paradoxical within the general framework of how body temperature affects predator–prey relationships in marine ecosystems. Despite their cold habitats and ectothermic physiology, they are known to consume marine mammals, especially seals, as a significant part of their diets (Fisk et al., 2002; Leclerc et al. 2012; Yano et al., 2007). Judging from the condition of seal remains in shark stomachs (Leclerc et al. 2012; Sigler et al., 2006) and wounds on live or dead stranded seals (Lucas and Natanson, 2010; van den Hoff and Morrice, 2008), sleeper sharks apparently attack live seals. These paradoxical observations are highlighted in the Greenland shark, which is the only elasmobranch that routinely inhabits the Arctic Ocean, where water temperature can fall below zero. These observations indicate the possibility that, although sleeper sharks are often described as “sluggish” (Compagno et al., 2005), they are in fact physiologically adapted to low temperature such that they could catch fast-swimming seals. Physiological adaptations to low temperature are found in the muscle functions of Antarctic teleosts (Johnston et al., 1975). In addition, some teleosts can be experimentally acclimated to low temperature and show improved swimming performances in cold waters (Rome et al., 1985). Although the horizontal swim speed (relative to ground) for Greenland sharks has been crudely estimated by a tracking study (Skomal and Benz, 2004), direct measurements of their swimming performance are still unavailable.

In this study, we used data-logging tags to examine the depth, swim speed (relative to water), tail-beat frequency (which reflects the contraction speed of locomotory muscles), and ambient water temperature of free-ranging Greenland sharks in Svalbard, Norway. The behavioural data allowed us to examine whether their swimming performance is

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(1) limited by cold water and (2) sufficient to catch swimming seals. The first question was addressed by comparing the data on Greenland sharks to those in the literature on other wild fishes at various ambient water temperatures. Given the wide range in body size (0.2–3900 kg) for fish species in the collected literature, the possible effect of body size needed to be considered in inter-specific comparisons. We therefore used a scaling approach, in which the locomotory parameters were regressed against body mass, and the residuals around the regression line were compared. The effect of phylogeny, the tendency of closely related species to resemble each other because of common ancestry (Felsenstein, 1985), was also accounted for in the regression. The second question was addressed by comparing data on Greenland sharks to those on seals in the literature.

2. Materials and methods

2.1. Fieldwork and instruments

Fieldwork was conducted in Kongsfjorden (78.9° N, 12.5° E), Svalbard, Norway, in June 2009. Using the research vessel Lance from the Norwegian Polar Institute, a total of 24 sharks were captured using longlines, which were set for <24 h. Seven lively sharks that were hooked only in the mouth were selected, equipped, and released in this study; however, the logger from one individual was lost, and thus the final sample size was six (Table 1). The selected sharks were restrained alongside a 6 m boat using the hook in the mouth and a rope passed around the tail. Body length and girth were measured, and sex was determined for each individual. Body mass was estimated from the body length and girth (K. M. Kovacs and C. Lydersen, unpublished data). The skin on the back of the shark, anterior to the first dorsal fin, was pierced shallowly using a metal probe, and a plastic cable (4 mm in width) was passed through the hole. A W1000-PD2GT data logger (21 mm in diameter, 117 mm in length, 60 g; Little Leonardo Co., Tokyo, Japan) along with an instrument-recovery package (Watanabe et al., 2004) that included a time-scheduled release mechanism (Little Leonardo Co.), float, and VHF transmitter was attached via the cable, before each shark was released. The cable, connected to the release mechanism by an insulated wire, was severed by an electric charge ~24 h after the release of the sharks, so that the whole package was detached. The package subsequently floated to the surface, making the VHF signal detectable. A 24 h deployment period was chosen to keep a feasible search area (<30 km from the shore).

The data logger recorded swim speed at 1/8 s, 1 s, or 2 s intervals (depending on the individual sharks), depth and temperature at a 1 s interval, and acceleration along lateral and longitudinal axes (to detect tail-beat activity and pitch angle, respectively) at a 1/32 s interval. A miniature camera was also attached to sharks C and E; however, the images obtained were too dark to be analysed. The total mass of the packages (data loggers and recovery system) were 188 g (accelerometer only) and 311 g (accelerometer and camera) (0.06–0.15% of the estimated body mass of the sharks). The buoyancies of the two types of packages were 0.53 N and 0.74 N in seawater, respectively. Frontal areas of the packages were 0.7–1.8% of that of the sharks (estimated from the girth measurements, assuming that sharks are circular in cross section). These small values indicate that mass, buoyancy, or hydrodynamic drag of the sharks was changed little by the attached package.

2.2. Behavioural data analyses

Behavioural data were analysed using the software Igor Pro (WaveMetrics Inc., Lake Oswego, OR, USA) with the package Ethographer (Sakamoto et al., 2009). Continuous wavelet transformation was applied to lateral acceleration to determine the tail-beat frequency of the sharks. A single tail beat was defined as the period required for the tail to move from one extreme lateral position back to the original position. The dominant tail-beat frequency over the whole record was calculated for each individual as the peak frequency in the power spectral density analysis of the lateral accelerations (Sato et al., 2007). The pitch angle of the shark (i.e., angle between the long axis of the shark's body and the horizontal) was estimated from the longitudinal acceleration records by filtering out the high-frequency signals. Positive pitch indicates a head-up posture and negative pitch indicates a head-down posture. Because setting the logger exactly parallel to the shark body axis was difficult, the pitch values recorded just before the release, when the shark was held horizontally alongside the boat, were corrected to 0°.

Relative swim speed was recorded as the number of revolutions per second ($\mathrm{rev\cdot s^{-1}}$) of a propeller mounted on the anterior end of the logger. These values were converted to actual swim speeds ($\mathrm{m\cdot s^{-1}}$) by using the equation from a previous calibration experiment (Watanabe et al., 2008). In the experiment, a dead fish was equipped with the logger, and towed vertically (due to difficulty in towing horizontally) in the water column in a bay at several known speeds. Both resolution and accuracy of the swim speed sensor were 0.02 $\mathrm{m\cdot s^{-1}}$.

Burst swimming events were observed in some sharks. Mean forward accelerations during these events were calculated as peak speed minus start speed and then divided by the duration of acceleration. Speed records, rather than acceleration records, were used in the calculations, because (1) forward accelerations of the sharks were below the resolution of the acceleration sensor (0.02 $\mathrm{m\cdot s^{-2}}$), and (2) acceleration records were complicated by other body motions, including changes in pitch angle and tail beats.

2.3. Comparative analysis

We collected data from the literature on the mean swim speed (relative to water) and mean tail-beat frequency, or fin-beat frequency for non-axial swimmers (e.g., ocean sunfish *Mola mola*; Watanabe and Sato, 2008), for as many species of fishes as possible (Table 2). All values were for wild fishes swimming under natural conditions,

Table 1
Descriptive information and swimming behaviour of Greenland sharks.

Shark ID	Date of release	Deployment duration (h)	Sex	Total length (m)	Girth (m)	Estimated body mass (kg)	Swimming depth (m)		Swim speed (m s^{-1})		Tail-beat frequency (Hz)	Water temp. (°C)	
							Mean	Max.	Mean	Max.		Mean	Range
A	16 June, 2009	23.5	M	3.00	1.75	312	96	226	–	–	0.14	2.6	1.3–3.2
B	16 June, 2009	23.5	M	3.10	1.56	283	106	189	–	–	0.16	2.2	1.0–3.4
C	22 June, 2009	23.4	M	2.85	1.38	207	72	143	0.31[a]	0.54	0.13	2.6	2.1–3.2
D	22 June, 2009	23.3	F	3.05	1.25	204	32	58	0.34[a]	0.54	0.14	2.5	1.3–3.2
E	24 June, 2009	23.1	F	3.10	1.80	343	142	273	0.32[a]	0.58	0.14	1.9	−1.2–2.8
F	24 June, 2009	23.4	M	2.80	1.52	228	68	148	0.37	0.73	0.16	2.1	−0.9–3.2
Mean		23.4		2.98	1.54	263	86	173	0.37	0.60	0.15	2.3	

[a] About half the records were below the stall speed of the sensor.

Table 2
Mean swim speed and tail-beat frequency of fishes recorded in the field.

Species	ID[a]	N	Body length (m)[b]	Body mass (kg)	Swim speed (m s^{-1})	Method[c]	Tail-beat frequency (Hz)[d]	Method[e]	Water temp. (°C.)	Reynolds number	Reference
Atlantic cod *Gadus morhua*	1	4	0.40	0.8	0.29	Tracking	–	–	5	7.4×10^4	Fernö et al. (2011)
Atlantic herring *Clupea harengus*	2	–	0.31	0.2	–	–	1.40	Sonar	7	–	Handegard et al. (2009)
Basking shark *Cetorhinus maximus*[f]	3	2	4.0	390	1.08	Boat	–	–	13	3.5×10^6	Sims (2000)
		1	9.5	3900	–	–	0.20	Observation	10	–	Harden Jones (1973)
Blacktip reef shark *Carcharhinus melanopterus*	4	1	1.6	30	–	–	0.60	Acoustic	28	–	Meyer et al. (2007)
Blue marlin *Makaira nigricans*	5	3	2.2	85	0.50	Speedometer	–	–	28	1.2×10^6	Block et al. (1992)
Blue shark *Prionace glauca*	6	2	2.66	125	0.42	Speedometer	–	–	22	1.1×10^6	Carey and Scharold (1990)
Brown trout *Salmo trutta*	7	1	0.30	0.8	–	–	1.75	EMG	7	–	Ross et al. (1981)
Chinese sturgeon *Acipenser sinensis*	8	8 and 9[g]	2.99	198	1.10	Speedometer	0.77	Accelerometer	20	3.3×10^6	Watanabe et al. (2012)
Chinook salmon *Oncorhynchus tshawytscha*	9	–	1.0	11.7	–	–	1.50	Sonar	10	–	Mueller et al. (2010)
Chum salmon *Oncorhynchus keta*	10	7 and 2[g]	0.65	3.4	0.75	Speedometer	1.80	Accelerometer	18	5.3×10^5	Tanaka et al. (2001)
Greenland shark *Somniosus microcephalus*	11	4 and 6[g]	2.98	263	0.34	Speedometer	0.15	Accelerometer	2	5.9×10^5	This study
Japanese flounder *Paralichthys olivaceus*	12	2	0.52	2.2	0.31	Speedometer	1.48	Accelerometer	14	1.3×10^5	Kawabe et al. (2004)
Lemon shark *Negaprion brevirostris*[f]	13	3	1.7	27	0.63	Speedometer	–	–	22	1.1×10^6	Sundström and Gruber (1998)
		2	1.7	27	–	–	0.73	Accelerometer	25	–	Gleiss et al. (2009a)
Nurse shark *Ginglymostoma cirratum*	14	1	2.5	86	–	–	0.40	Accelerometer	27	–	Whitney et al. (2010)
Ocean sunfish *Mola mola*	15	3	1.15	87	0.60	Speedometer	0.46	Accelerometer	16	6.0×10^5	Watanabe and Sato (2008)
Pink salmon *Oncorhynchus gorbuscha*	16	12	0.52	1.6	1.14	Tail beat	2.23	EMG	15	5.2×10^5	Standen et al. (2002)
Scalloped hammerhead shark *Sphyrna lewini pups*	17	5	0.57	0.76	0.46	Tail beat	1.17	Magnetic	26	2.8×10^5	Lowe (2002)
Shortfin mako shark *Isurus oxyrinchus*[f]	18	1	1.8	63	0.90	Speedometer	–	–	–	–	Block et al. (1992)
		4	1.0	8.0	–	–	1.03	Observation	19	–	Sepulveda et al. (2007)
Sockeye salmon *Oncorhynchus nerka*[f]	19	15	0.56	2.0	1.00	Tail beat	–	–	18	5.3×10^5	Hinch and Rand (1998)
		–	0.70	3.1	–	–	2.40	Sonar	10	–	Mueller et al. (2010)
Tiger shark *Galeocerdo cuvier*	20	4	3.57	266	0.69	Speedometer	0.51	Accelerometer	26	2.7×10^6	Nakamura et al. (2011)
Whale shark *Rhincodon typus*[f]	21	9	6.0	2200	0.85	Pitch	–	–	25	5.4×10^6	Gleiss et al. (2011)
		2	6.0	2200	–	–	0.21	Accelerometer	25	–	Gleiss et al. (2009b)
Whitetip reef shark *Triaenodon obesus*	22	1	1.3	15.0	–	–	0.89	Accelerometer	25	–	Whitney et al. (2007)

[a] Corresponds to species ID numbers in Fig. 2.

[b] Total length or fork length, except for blue marlin for which lower-jaw fork length was estimated from the body mass reported using the equation in Wilson et al. (1991).

[c] Methods to record swim speed include 'Tail beat', from tail-beat frequency detected by magnetic sensor or electromyogram, 'Tracking', from high-resolution acoustic tracking, 'Speedometer', from speed sensor attached to fish, 'Boat', from flow-speed measurements taken on a boat driven alongside surface-swimming fish, and 'Pitch', from the vertical speed divided by the sine of the pitch angle of the fish.

[d] 'Tail-beat frequency' is not a relevant term for ocean sunfish, which swim with their dorsal and anal fins (Watanabe and Sato, 2008).

[e] Methods to record tail-beat frequency include 'Sonar', from remote monitoring of echograms, 'EMG', from electromyogram radiotelemetry, 'Observation', from direct observations in the field, and several types of animal-attached sensors ('Magnetic', 'Accelerometer', and 'Acoustic').

[f] Species for which swim speed and tail-beat frequency was reported in separate papers.

[g] Sample size for swim speed and tail-beat frequency, respectively.

except for blacktip reef sharks *Carcharhinus melanopterus* (Meyer et al., 2007), whitetip reef sharks *Triaenodon obesus* Whiteney et al., 2007, and lemon sharks *Negaprion brevirostris* (Gleiss et al., 2009a), which were studied in semi-natural conditions. Mean swim speed, rather than median or mode, was collected, because it is a commonly reported swimming parameter in the literature. When it was not reported, we used the mode value (blue marlin *Makaira nigricans*). In this compilation, swim speed data were obtained (1) by direct measurement using a speedometer with a propeller or paddle wheel sensor attached to the fish (Watanabe and Sato, 2008), (2) by high-resolution acoustic tracking (Fernö et al., 2011), (3) from vertical speed detected by depth sensors and divided by the sine of the pitch angle estimated from acceleration records (Gleiss et al., 2011), (4) from the tail-beat frequency detected by magnetic sensors (Lowe, 2002) or electromyograms (EMGs) (Standen et al., 2002), or (5) from flow-speed measurements taken on a boat driven alongside surface-swimming fish (Sims, 2000). Tail-beat frequency data were obtained by (1) accelerometers (Watanabe and Sato, 2008), acoustic loggers (Meyer et al., 2007), or magnetic sensors (Lowe, 2002) attached to fish, (2) remote monitoring with echosounders (Handegard et al., 2009), (3) EMG radiotelemety (Standen et al., 2002), or (4) visual observations in the field (Harden Jones, 1973). We also collected data on the ambient water temperature for each species. When it was not reported in the paper, we contacted authors (nurse sharks *Ginglymostoma cirratum*, blacktip reef sharks, and whitetip reef sharks), used water temperature maps at various depths provided by the National Oceanic and Atmospheric Administration (NOAA) (basking sharks *Cetorhinus maximus*, whale sharks *Rhincodon typus*, lemon sharks, and Atlantic herring *Clupea harengus*), or used water temperature of the river provided by local stations (Chinook salmon *Oncorhynchus tshawytscha* and sockeye salmon *Oncorhynchus nerka*). Unlike other fishes in the data compilation, shortfin mako sharks *Isurus oxyrinchus* maintain higher core body temperature than ambient water temperature (Carey and Teal, 1969); hence this species was excluded in analysis involving water temperature. For species in which swim speed and water temperature were collected, Reynolds number, a dimensionless number that characterizes the scale effect of flow (Vogel, 1994), was calculated as $L \cdot U \cdot \nu^{-1}$, where L is the body length (m), U is the swim speed ($\mathrm{m \cdot s^{-1}}$), and ν is the kinematic viscosity of water at the temperature ($\mathrm{m^2 \cdot s^{-1}}$).

Although body length is easier to measure and more frequently reported, body mass was used as a measure of body size. This is because fishes in our dataset vary greatly in body shape (e.g., ocean sunfish), presumably making body length a poor predictor of swim speed (see Fisher and Wilson, 2004 for the case of reef fish larvae). Body mass is likely a better predictor of the amount of locomotory muscle and hence swimming performance. When body mass was not reported, it was estimated from body length using published length–mass relationships for the individual species [nurse sharks (Castro, 2000), blacktip reef sharks (Stevens, 1984), lemon sharks (Sundström and Gruber, 1998), shortfin mako sharks (Kohler et al., 1995), blue sharks *Prionace glauca* (Kohler et al., 1995), whitetip reef sharks (Randall, 1977), Atlantic herring (Cardinale and Arrhenius, 2000), Atlantic cod *Gadus morhua* (Svåsand et al., 1996), brown trout *Salmo trutta* (Hyatt and Hubert, 2001), and Chinook salmon (Schneider et al., 2000)] or that of a close relative [sockeye salmon (Schneider et al., 2000)]. The mass of a large individual blacktip reef shark had to be extrapolated. Length–mass relationships have not been published for basking or whale sharks, which are very large. The mass for these sharks was set on the basis of catch records for individuals of similar lengths [2.2 tons for a 5.7-m whale shark (Doiphode, 1986), 385 kg for a 3.75-m basking shark (Kruska, 1988), and 3909 kg for a 9.1-m basking shark (Bigelow and Schroeder, 1948; as cited by Sims, 2008)].

Individual species do not represent evolutionarily independent data points, and phylogenetic information was incorporated in the calculation of allometric equations (slopes and intercepts) to alleviate this issue (Felsenstein, 1985; Garland et al., 2005). A phylogenetic tree of our study animals was created using published phylogenetic relationship among species (Miya et al., 2001, 2003; Oohara et al., 1997; Vélez-Zuazo and Agnarsson, 2011). When available, branch lengths should be set by divergence time estimated from molecular or fossil data, but such estimates were unavailable for the majority of our branches. We therefore tested an arbitrary proportional branch length (Grafen, 1989), where the depth of each node is set equal to one less than the number of tip species that descend from it (Fig. S1). Data were log transformed, and phylogenetically independent contrasts (Felsenstein, 1985) were calculated using the PDAP package (Midford et al., 2003) with the software Mesquite (Maddison and Maddison, 2010). The suitability of our arbitrary branch length was then tested by plotting the absolute values of the contrasts against their standard deviations (Garland et al., 1992), with the value for statistical significance set at $P<0.05$. These two parameters were not significantly correlated for body mass ($t=-1.55$, $N=15$ contrasts, $P=0.15$) or swim speed ($t=-1.97$, $N=15$ contrasts, $P=0.07$) in the swim speed dataset or for body mass ($t=-1.40$, $N=18$ contrasts, $P=0.18$) or tail-beat frequency ($t=-1.31$, $N=18$ contrasts, $P=0.21$) in the tail-beat frequency dataset. This lack of significance indicated that the assumed proportional branch length adequately standardized the contrasts (Garland et al., 1992). Phylogenetically independent contrasts only give the slope of the scaling line; therefore, the intercept was determined by forcing the line through the value estimated for the root node of the phylogenetic tree, which is equivalent to the overall mean value weighted by phylogeny (Garland et al., 1993). The PDAP package also allowed us to calculate phylogenetically informed 95% confidence intervals around the regression (Garland and Ives, 2000).

3. Results

The sharks swam at a wide range of depths (<273 m) with up-and-down movements, and the grand mean swimming depth was 86 m (Table 1, e.g., Fig. 1A). Swim speed was not recorded for the first two sharks (A and B), probably because the sampling interval set (1/8 s) was too short for the swim speed of the sharks (i.e., propeller did not move enough between samples to make an accurate recording). It was recorded for the other four sharks (C–F) with the sampling intervals of 1 or 2 s, and the grand mean value was $0.34\ \mathrm{m \cdot s^{-1}}$ (Table 1, Fig. 1A). However, the recorded values were below the stall speed of the propeller sensor ($0.17\ \mathrm{m \cdot s^{-1}}$) during 57%, 60%, and 55% of the records for sharks C, D, and E, respectively. Swim speed tended to gradually decrease over the records (Fig. 1A), which may represent a fishing and handling effect. Tail beats were continuous throughout the records, except for minor gliding behaviour during descent in sharks A, B, and F (accounting for 5.2%, 12.0%, and 0.2% of their descent time, respectively), and increased during burst swimming (Fig. 1). The dominant tail-beat frequencies over the whole records were 0.14–0.16 Hz (Table 1). A single burst-swimming event was observed in each of two sharks (C and F), with speeds up to 0.54 and $0.73\ \mathrm{m \cdot s^{-1}}$, tail-beat frequencies up to 0.27 and 0.26 Hz, and positive (i.e., upward) pitch angles up to 28° and 18°, respectively (e.g., Fig. 1B). Mean forward accelerations during these events were 0.0067 and $0.0086\ \mathrm{m \cdot s^{-2}}$ for sharks C and F, respectively. The sharks experienced a grand mean water temperature of 2.3 °C, and minimum sub-zero values of −0.9 °C and −1.2 °C were recorded for sharks E and F, respectively (Table 1).

Swim speed of 16 fish species over a body mass range of 0.8–2200 kg ranged from 0.3 to $1.1\ \mathrm{m \cdot s^{-1}}$ (Table 2, Fig. 2A). Despite considerable variations around the scaling line, swim speed increased significantly with body mass ($t=2.29$, $N=15$ contrasts, $P<0.05$). Greenland sharks had the lowest swim speed for a given size. Tail-beat frequency of 19 fish species over a body mass range of 0.2–3900 kg ranged from 0.15 to 2.4 Hz, and decreased significantly with body mass ($t=-9.50$, $N=18$ contrasts, $P<0.0001$; Table 2, Fig. 2B). Greenland sharks had the lowest tail-beat frequency, regardless of whether body size was accounted for or not. Water temperature was not significantly correlated

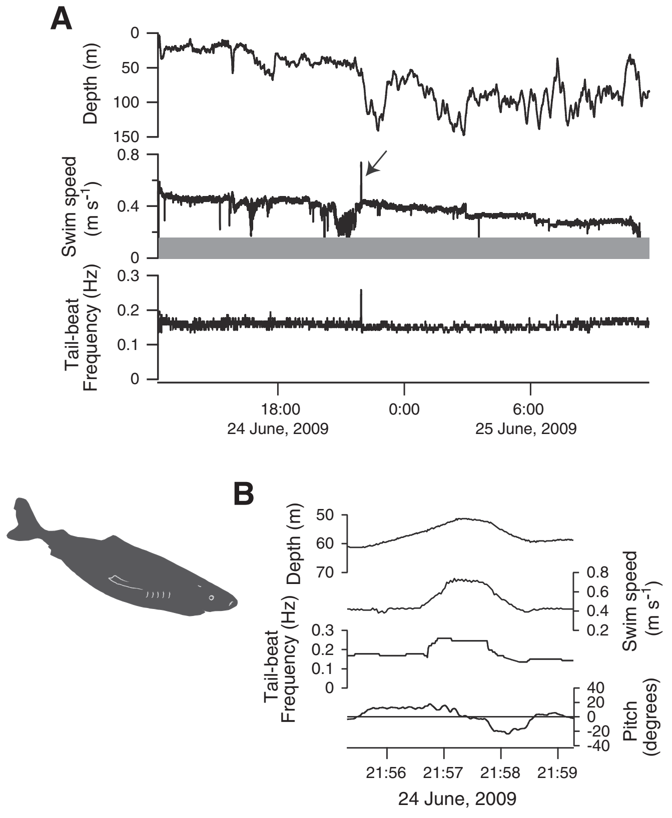

Fig. 1. Swimming behaviour of a Greenland shark. (A) The whole ~24 h records of depth, swim speed, and tail-beat frequency for shark F. Arrow indicates burst swimming event, and grey horizontal bar represents the stall speed of the speed sensor ($0.17\ \mathrm{m \cdot s^{-1}}$). (B) Depth, swim speed, tail-beat frequency, and pitch (i.e., angle between the long axis of the shark's body and the horizontal, with positive values indicating ascent and negative values indicating descent) during the burst swimming event indicated by arrow in (A).

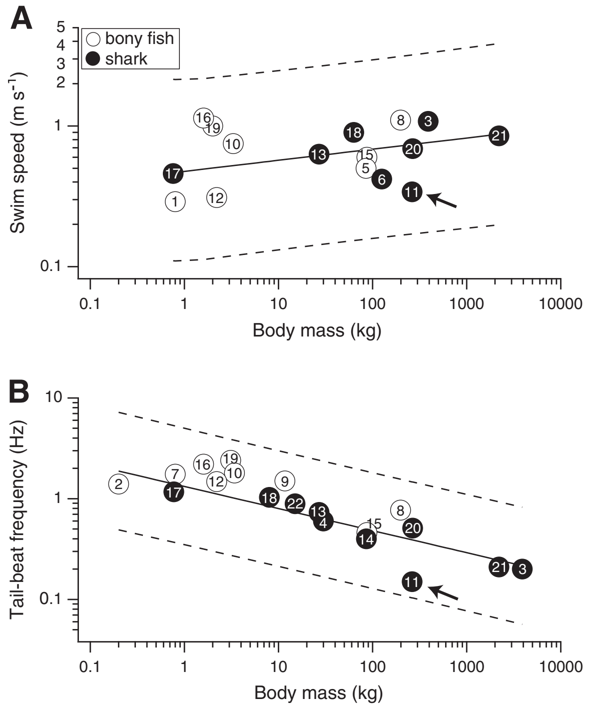

Fig. 2. (A) The mean swim speed ($\mathrm{m \cdot s^{-1}}$) and (B) mean tail-beat frequency (or fin-beat frequency for ocean sunfish) (Hz) of wild fishes in the field, plotted against body mass (kg). Open circles represent bony fishes, including teleosts and a sturgeon, and closed circles represent sharks, with the numbers on the circles corresponding to species ID in Table 2. Arrows indicate Greenland sharks. The thick lines show the scaling relationships calculated using phylogenetically informed statistics.

$$\mathrm{speed} = 0.48 \times \mathrm{mass}^{0.08} \left(R^2 = 0.27\right).$$

$$\mathrm{tailbeat} = 1.32 \times \mathrm{mass}^{-0.22} \left(R^2 = 0.84\right).$$

The dashed lines represent 95% confidence intervals.

with the residuals of log-transformed swim speed ($t = 1.17$, $N = 14$ contrasts, $P = 0.26$) or tail-beat frequency ($t = 1.28$, $N = 18$ contrasts, $P = 0.22$) about the scaling line.

4. Discussion

The combination of field measurements on Greenland sharks, data compilation for a wide range of fishes from the literature, and data analysis using phylogenetically informed statistics showed that this species swims at the lowest speed for their size among fishes studied to date. This is highlighted by the fact that our speed measurements might be at the upper end of the normal range for the species, because about half the records for three of four individuals were below the stall speed of the sensor. The horizontal swim speed (relative to ground) of Greenland sharks estimated by acoustic tracking was $0.2\ \mathrm{m\ s^{-1}}$ (Skomal and Benz, 2004), which is close to the actual swim speed (relative to water) measured in this study. Our comparative analysis indicates that the slow cruising speed of Greenland sharks is a direct result of tail-beat frequency, which was also the lowest among fishes regardless of whether body size was accounted for or not. The low tail-beat frequency, in turn, could be attributed to the low ambient temperatures experienced by the sharks. In general, fishes appear to use optimal muscle-shortening speed (maximizing mechanical power production and efficiency) during steady swimming (Rome et al., 1988), and this shortening speed decreases with decreasing temperature (Bennett, 1984; Rome, 1990). The effect of low temperature on muscle function can be partially compensated for by recruiting more muscle fibres (Rome et al., 1984) or having cold-adapted muscle fibres (Johnston et al., 1975). Indeed, in our comparative analysis, water temperature was not significantly correlated with the residual of swim speed or tail-beat frequency about the scaling line, suggesting that such compensations occur in some species. Unfortunately, we cannot make definitive conclusions, because we had to roughly estimate water temperature for some species in our analyses (see Materials and methods). Nevertheless, our finding that Greenland sharks sustain very low swim speed and tail-beat frequency despite their pelagic lifestyle suggests that the depressing effect of cold polar waters on muscle function is not fully compensated for via adaptation or acclimatization in this species.

In microbes (Beveridge et al., 2010) and fish larvae (Fuiman and Batty, 1997), decreased swim speed at low temperature is not only due to physiological effects on the animals, but also due to a physical effect of the media (i.e., increased water viscosity). However, the effect of viscosity is probably negligible for relatively large fishes in our comparative analysis, because at their high Reynolds numbers (7.4×10^4–5.4×10^6, Table 2), hydrodynamic drag is often dominated by pressure drag, which is affected by viscosity only indirectly (Vogel, 1994).

The slow speed of Greenland sharks is remarkable, because this species is known to consume ringed seals *Pusa hispida*, harbour seals *Phoca vitulina*, hooded seals *Cystophora cristata*, and bearded seals *Erignathus barbatus* (Fisk et al., 2002; Leclerc et al. 2012; Yano et al., 2007). The mean and maximum (or burst) swim speeds ($0.34\ \mathrm{m \cdot s^{-1}}$ and $0.73\ \mathrm{m \cdot s^{-1}}$, respectively) recorded in this study are much lower than those of adult seals. Harbour and bearded seals swim at $0.9\ \mathrm{m \cdot s^{-1}}$ (Lesage et al., 1999) and $1.2\ \mathrm{m \cdot s^{-1}}$ (Krafft et al., 2000) on average, respectively. All seal species studied to date have mean swim speeds of 0.9–$1.7\ \mathrm{m\ s^{-1}}$, depending mainly on body size (Watanabe et al., 2011).

During burst swimming, Baikal seals *Pusa sibirica*, a close relative of ringed seals, can accelerate up to 2.5 $\mathrm{m \cdot s^{-1}}$ (Watanabe et al., 2004). In contrast, newborn bearded seals (age, 0 days) swim at 0.5 $\mathrm{m \cdot s^{-1}}$ (Watanabe et al., 2009), which is lower than the burst speed of Greenland sharks. However, these pups have mean and maximum speeds of 0.7–0.9 and 1.8 $\mathrm{m \cdot s^{-1}}$, respectively, by the time they are only a few days old (Watanabe et al., 2009). Acceleration may be more important than speed per se for predators (Alexander, 2003), but the mean acceleration during burst swimming by Greenland sharks (0.008 $\mathrm{m \cdot s^{-2}}$) is also much lower than acceleration recorded for Baikal seals (0.15 $\mathrm{m \cdot s^{-2}}$; Y. Y. W., unpublished data). It is possible that the burst-swimming events observed in this study underrepresent their maximum locomotory performance, because our measurements were only for a single day just after the fish were caught on a longline. However, fishes typically show burst swim speed that is approximately double the sustained swim speed (Table 4 in Videler and Wardle, 1991), a ratio observed in this study. Overall, the comparisons above suggest that Greenland sharks are too slow to catch swimming seals, except for maybe very young pups.

The question is how Greenland sharks catch live seals. We hypothesize that this cryptic predator targets sleeping seals. Phocid seals can sleep underwater or at the surface (Ridgway et al., 1975), and while asleep, they are often immobile with a bilaterally symmetrical sleeping pattern similar to that of terrestrial animals (Lyamin, 1993). This pattern contrasts with cetaceans and otariids that show unihemispheric sleep and are thought to be alert while resting one side of the brain (Lyamin et al., 2008a, 2008b). Although parameters indicating sleep (e.g., eye closure or brain wave patterns from electroencephalogram) have never been recorded in the field, bearded seals in Svalbard have repeatedly been observed to be motionless at the surface, presumably sleeping so soundly that they could be approached by boat. In one case, we were able to even touch a seal at the surface before it awoke (Y. Y. W., C. L, and K. M. K; personal observations). By sleeping in the water, Arctic seals would avoid their main predator, polar bears *Ursus maritimus*, which hunt seals primarily on the sea ice.

In conclusion, we showed that Greenland sharks swim at the slowest speed for their size among fishes studied to date, presumably because of the depressing effect of cold polar waters on locomotor muscle functions. Nevertheless, they apparently attack live seals, a fact that makes the species remarkable. This may be accomplished by attacking seals sleeping in the water using cryptic approaches, a hypothesis that needs to be examined in future studies.

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