Journal of Experimental Marine Biology and Ecology 426–427 (2012) 5–11

Contents lists available at SciVerse ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

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

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ARTICLE INFO

Article history:
Received 20 November 2011
Received in revised form 11 April 2012
Accepted 19 April 2012
Available online 8 June 2012

Keywords:
Cold adaptation
Ectotherm
Phylogenetically independent contrast
Scaling
Swimming performance

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 $0.34\ \mathrm{m \cdot s^{-1}}$ 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 ($0.74\ \mathrm{m \cdot s^{-1}}$) and acceleration during burst swimming ($0.008\ \mathrm{m \cdot s^{-2}}$) 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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doi:10.1016/j.jembe.2012.04.021

(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 ($\mathrm{m\ s^{-1}}$)		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.