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RESEARCH ARTICLE

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Ultrasonic tracking of Greenland sharks, *Somniosus microcephalus*, under Arctic ice

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Abstract Six Greenland sharks, *Somniosus microcephalus* (Bloch and Schneider, 1801), 190–355 cm fork length, were tracked under land-fast sea ice off northern Baffin Island (73.2°N; 85.3°W) between 16 and 28 May 1999, using ultrasonic telemetry. The sharks were tracked continuously for periods of 5.5–13.0 h, with the tracks of two individuals lasting 31.4 and 42.8 h, respectively, each with an interval when the track was lost. Several sharks dove after release and moved along the ocean bottom for the duration of the tracking period, while others varied their movements regarding course and depth. Two sharks made repeated visits to within 11 m of the ice–water interface from deeper water. The tracked sharks exhibited no apparent depth or temperature preferences, and pooled data indicated that sharks remained deep during the morning and gradually moved into shallower depths through the afternoon and night. Rates of descent (average = 0.099 m s^{-1}) were significantly greater than rates of ascent (average = 0.058 m s^{-1}) for all sharks, and the average rate of horizontal movement over ground was estimated as 0.215 m s^{-1}. Based on the movements of tracked sharks and information contained in the literature,*S. microcephalus* may prey on seals in areas covered by land-fast sea ice.

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Introduction

The Greenland shark, *Somniosus microcephalus*, inhabits the Atlantic Ocean from the high Arctic southward to at least 32°N latitude (Bigelow and Schroeder 1948; Templeman 1963; Compagno 1984; Francis et al. 1988; Herdendorf and Berra 1995). In the southern portion of its range the species has only been observed at depths of 2200 m (Herdendorf and Berra 1995), but, in north temperate to Arctic regions, Greenland sharks are known from the shallows (see Bigelow and Schroeder 1948; Bruemmer 1969; Reeves 1980). The Greenland shark is the only shark known in Arctic waters (Compagno 1984), where it commonly inhabits areas seasonally covered by sea ice (Jensen 1914; Bigelow and Schroeder 1953; Templeman 1963; Caloyianis 1998). Cloaked by ice within its northern-most range for much of the year, and with its deep-water presence at southern latitudes, *S. microcephalus* is an enigmatic species known mostly from limited and often serendipitous observations made on dead specimens.

The Greenland shark is considered an omnivore and scavenger (Bigelow and Schroeder 1948, 1953; Compagno 1984), and a recent study (Fisk et al. 2002) suggested that seals eaten either as prey or carrion may comprise a significant portion of its diet. Seals are plentiful in the Arctic, and the ringed seal, *Phoca hispida*, is the only seal species that prefers regions of land-fast sea ice, where they are bound to one to several breathing holes for much of the year (Reeves 1998).

The present study was designed to track the vertical and horizontal movements of Greenland sharks below land-fast sea ice in a region inhabited by ringed seals.

Materials and methods

Study area

This study was conducted in and about the confluence of Victor Bay and Strathcona Sound off northern Baffin Island, Nunavut, Canada (Fig. 1) from 16 to 28 May 1999. Victor Bay (Fig. 1) is relatively narrow, 5.2 km wide at its mouth, 12 km long, and approximately 49.3 km^2 in surface area. Water depth in Victor Bay increases rapidly from the shoreline, with only about 38.1% of the bay <100 m and about 20.1% <50 m depth. The maximum depth of 262 m is in the center of the bay, about 3 km from the mouth. Strathcona Sound is approximately 8.7 km wide at its mouth, 54.7 km long, and about six times the surface area of Victor Bay. Depths at the head of Strathcona Sound are <100 m, but near its mouth (i.e. principal study area) water depth increases sharply from the shore to a maximum depth of 320 m. Only about 14% and 8% of the study area in the sound are <100 and 50 m, respectively. The confluence of Victor Bay and Strathcona Sound is bounded by the mouths of each body of water and by an imaginary line extending from Victor Point to Cape Strathcona (Fig. 1). The confluence surface area is about 29.4 km^2, of which only about 15.8% is <100 m depth. Maximum depth within the confluence area is 366 m. The study area extended a short distance beyond the confluence into Admiralty Inlet, a large body of water the bottom slopes of which are from just over 400 m deep in the study area to >600 m nearby. The bathymetry of the study area was obtained from the Canadian Hydrographic Service (1985).

Sunlight persisted 24 h day^{-1}throughout the study, with several hours of reduced light from 2300 to 0100 hours, when the sun was just below the mountainous horizon. Temperature at depth data were periodically collected throughout the study using an expendable bathythermograph (XBT) system (Sippican, Marion, Mass.). Ice conditions within the study area were heterogeneous. Much of the land-fast sea ice covering Victor Bay was flat, 1.5–2.4 m thick, and frosted by a thin layer (<30 cm) of snow, except in localized areas of rough ice where snow accumulation reached about 1 m. The mouths of Victor Bay and Strathcona Sound, and their confluence area were covered by rough, land-fast ice. Snow cover throughout this region seemed related to ice surface conditions, with rougher ice covered by deeper snow. No large chunks of multi-year ice resided within the study area. Evidence of ringed seal presence within the study area included several kills by project guides and periodic location of subnivean breathing holes. These observations corroborated the traditional knowledge of the local Inuits that the study region supported a large population of ringed seals and that areas of rough ice contained the highest density of seal holes (A. Tunraluk and O. Naqitarvik, Arctic Bay Hunters and Trappers Association, personal communication).

Shark capture and transmitter attachment

Sharks, *Somniosus microcephalus* (Bloch and Schneider, 1801), were caught at two locations (A and B; Fig. 1) by fishing through ice holes with individual braided nylon lines connected to stainless steel leaders crimped to size 3/0 shark hooks. Hooks were baited with pieces of ringed seal (each weighing about 0.5 kg and consisting of portions of fur, blubber, and muscle) and fished on or just above the bottom. Hooked sharks were slowly pulled to the surface and partially removed from the water to facilitate measurement [fork length (FL) to the nearest centimeter], sexing, and tagging. The sexual maturity of male sharks was determined by examining clasper length (relative to the length of the pelvic fin) and hardness (Dunbar and Hildebrand 1952). Each shark was fitted with a 32 kHz coded pressure-sensitive transmitter (Vemco, Shad Bay, Nova Scotia, Canada) that was attached to the anterior margin of either the first or the second dorsal fin using a sharp punch and a single nylon cable tie (Fig. 2). A thin leather band was laced around each transmitter and through the fin to prevent transmitters from swaying on swimming sharks (Fig. 2). As specified by the manufacturer, transmitters had a depth accuracy of ±1 m and transmitted an individually coded signal every 45–75 s. Sharks were also tagged with a Cooperative Shark Tagging Program “M-tag” (National Marine Fisheries Service, Narragansett, R.I.). In all cases, sharks were processed (including hook removal) and returned to the water within about 4 min, and in most cases each

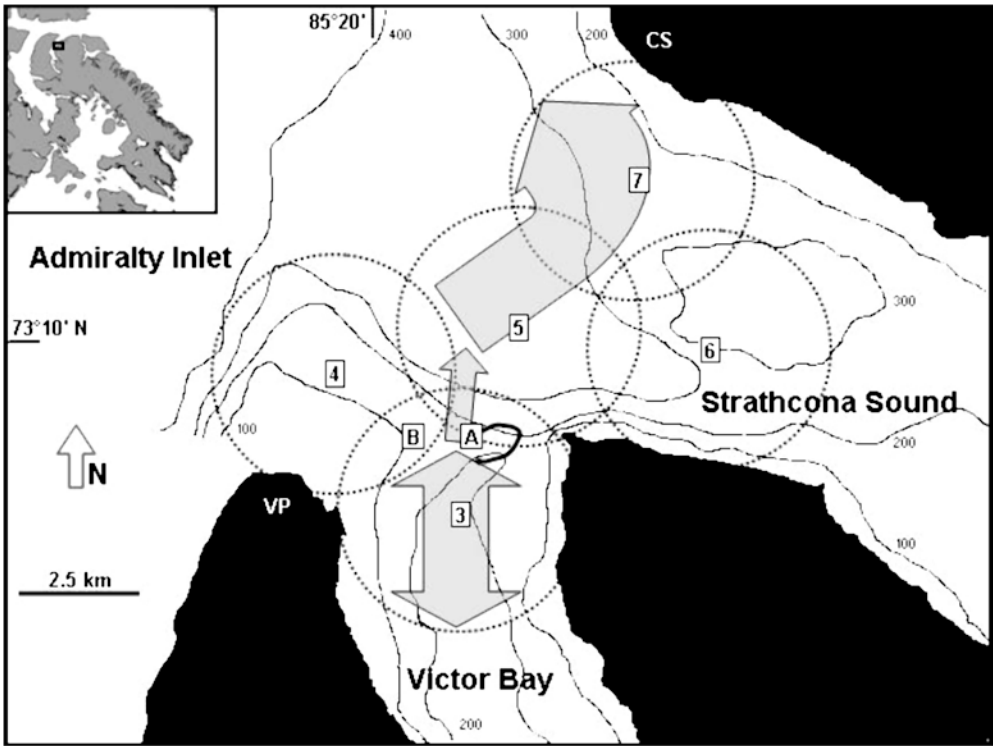

Fig. 1 *Somniosus microcephalus*. Study area and general horizontal movements (*arrows*) of tracked Greenland shark GS3 in and about Victor Bay and Strathcona Sound, Baffin Island, Nunavut, Canada (*VP* Victor Point;*CS* Cape Strathcona; *A*and *B* fishing–release locations; *3–7* remote receiver locations; *dotted circle* about each receiver represents its approximate horizontal detection region; *solid line* depicts shark movements determined by manual tracking; *shaded arrows* depict shark movements determined by remote tracking; *width of shaded arrows*reflects probable range of shark location). Bathymetric contours (m) are from the Canadian Hydrographic Service (1985). Note that receivers 6 and 7 were not in place for the bulk of GS1 and GS2 tracks.*Inset* of Baffin Island indicates location of study area (*box*)

shark's head remained underwater during much or all of this period. In some cases sharks were tethered to a long tail rope and allowed to swim under the ice for up to several hours so that their pre-release movements and behavior could be observed by SCUBA divers and a remotely operated vehicle (ROV) equipped with an underwater camera system (Benthos, North Falmouth, Mass.). In all cases, sharks appeared healthy and behaved normally (i.e. smooth swimming behavior and rhythmic branchial pumping) prior to and at the time they were released.

Tracking

Movements of most sharks were monitored using both manual (active) and remote (passive) tracking methods. Manual tracking of shark depth (m) and course (compass bearing) was typically limited to several hours post-release, and was executed using a directional hydrophone (V-11, Vemco) interfaced with a surface receiver (VR60, Vemco) and laptop computer. A magnetic compass (Suunto DP 65 Global, Recta, Biel-Bienne, Switzerland) was used to collect compass bearing data. A correction factor of 52°W magnetic variation was used to adjust magnetic compass bearings to true north bearings (National Geophysical Data Center/World Data Center, Boulder, Colo.).

The deployment of five remote data-logging receivers (VR1, Vemco) arranged in a listening array (Fig. 1) facilitated the continuous collection of vertical and horizontal movement data for each tagged shark. Remote receivers were each suspended by a braided steel cable through a 25-cm diameter ice hole to a water depth of 6 m. The detection ranges of these receivers were determined on site to vary from 2.5–3 km, with the variation appearing to be associated with factors such as subsurface ice conditions (as indicated by surface ice conditions) and ambient noise. In addition, it was determined in the field that remote receivers rejected the close range echoes of ultrasonic transmitters, thereby creating a "deaf zone" in the immediate vicinity of each receiver. The size of each deaf zone was estimated to be < 1 km in diameter for one receiver through repeated deployment of a tethered transmitter along a horizontal transect. Receivers were placed 4 km apart in the array to allow some detection overlap (1 km maximum) of adjacent receivers (Fig. 1). The region delimited by the outside boundary of the receiver array was approximately 80.8 km^2. A hand-held Global Positioning System (Garmin model 12, Garmin, Olathe, Kan.) was used to position each receiver. Data (i.e. shark identification code, time, and swimming depth) were downloaded daily from the remote receivers to a laptop computer.

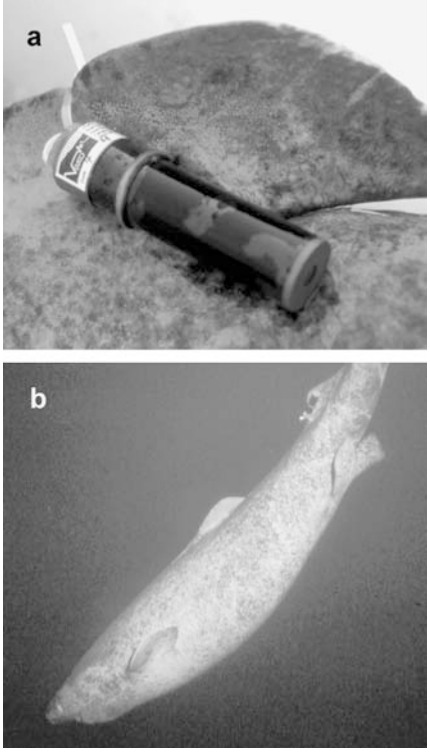

Fig. 2a, b *Somniosus microcephalus*. Tagged Greenland sharks; **a** a coded 32 kHz ultrasonic pressure-sensitive transmitter attached to a dorsal fin; **b** a tagged Greenland shark swimming away under ice after release

Horizontal movement

Horizontal movements of sharks were approximated using compass bearing data, shared data points from receivers with overlapping detection zones, knowledge of the variation in the detection range of receivers, and knowledge of the deaf zone about each receiver. Horizontal speed over ground (m s^{-1}) was calculated for sharks moving along a known course from a known or estimated position to a point that marked the limit of detection along said course for a particular receiver, assuming a standard receiver detection range of 2.5 km. If the direction of movement was unknown, minimum and maximum distances (m) across an area were used to calculate the range of speed over ground for a given shark. These point-to-point horizontal speed estimates were averaged for each individual shark. Rates of shark ascent and descent (m s^{-1}) were calculated using data corresponding to sharks that made continuous ascents or descents ≥20 m. To examine depth distribution, aggregate time (min) at depth was calculated based on 10-m bins as described by Holland et al. (1990). These data were then expressed as a percentage of the total tracking time for each shark, with means (±SE) calculated for all sharks combined. Depth at time of day, expressed as mean hourly depth (m, ±SE), was investigated using pooled data gathered by all remote receivers from all sharks.

Results

Individual tracks

Six Greenland sharks (*Somniosus microcephalus*, two females and four males), ranging from 190 to 355 cm FL, were tracked for total periods of 5.5–72.8 h. At the termination of the study on 28 May 1999, five of the six tagged sharks had moved outside the detection zone (Fig. 3). These five sharks had an average of 160.4 h (±34.99; range = 93.5–277.5 h) after last leaving this zone to return and be detected prior to termination of the study. The eyes of all six sharks were infected by the parasitic copepod *Ommatokoita elongata*.

Greenland shark GS1 (355 cm FL female) was captured at A, released on 16 May 1999 at 1433 hours, and tracked for 5.5 h. Two hours of manual tracking indicated that GS1 initially moved on a northerly course, gradually heading ever more easterly. The shark descended in a step-wise manner to a depth of 200 m during the first 2.5 h, and generally remained well above the bottom. At 1653 hours the shark descended abruptly to 270 m depth, where it remained for the rest of the track (Fig. 3). The shark exited the study area on a northeasterly heading across the mouth of Strathcona Sound.

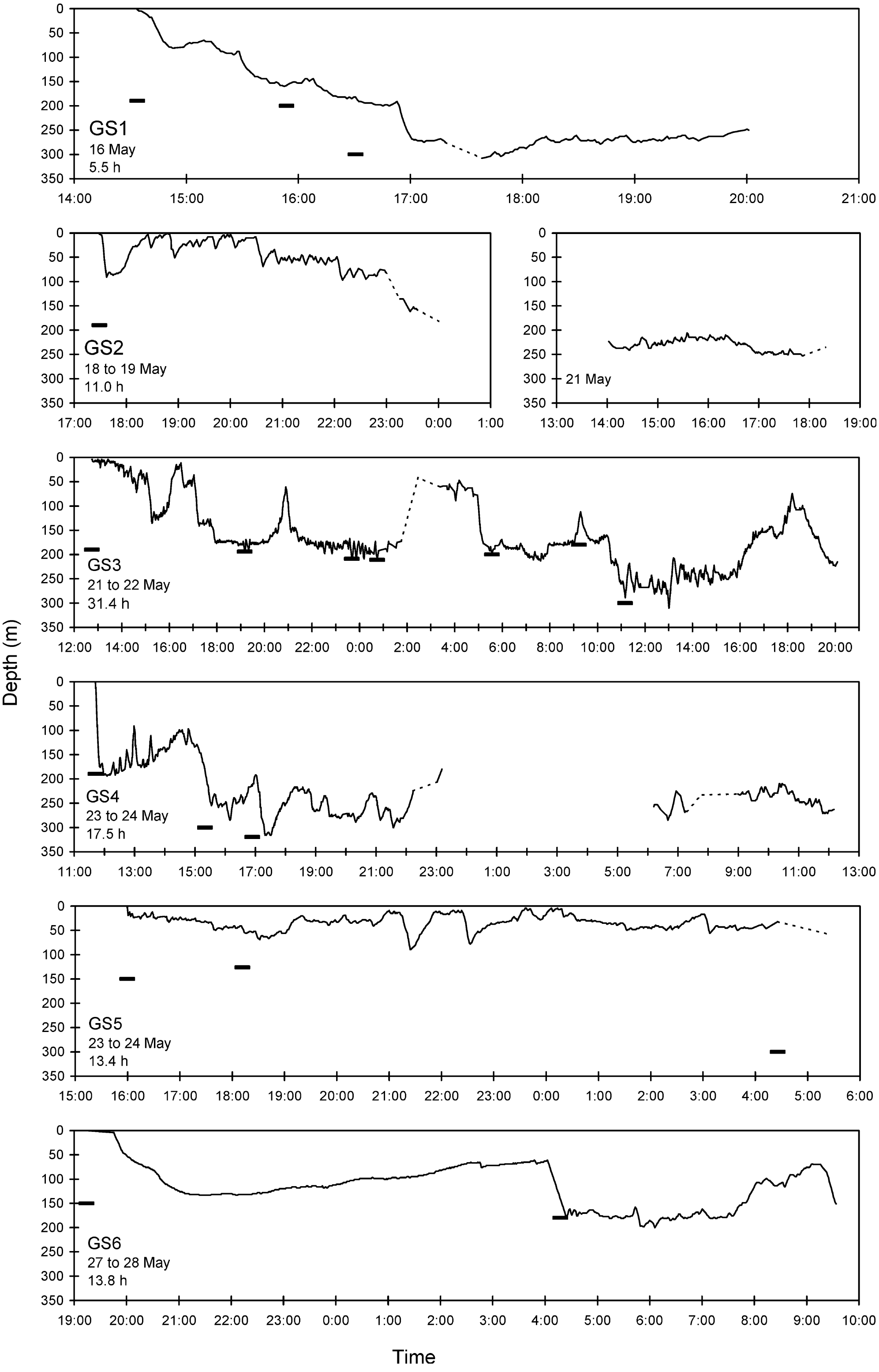

Fig. 3 *Somniosus microcephalus*. Vertical movements in and about Victor Bay and Strathcona Sound, Baffin Island, Nunavut, Canada, of six Greenland sharks tracked between 16 and 28 May 1999 using ultrasonic telemetry. *Dashed lines* indicate breaks in data, *horizontal bars* indicate bottom depths at various track points (see "Results"). Surface of study area was covered by land-fast sea ice

Total time-at-depth data indicated that GS1 spent 39% of the 5.5-h track at depths of 260–280 m.

Greenland shark GS2 (241 cm FL male) was captured at A and released on 18 May at 1729 hours. This shark was not manually tracked due to temporary equipment failure. Following its release, GS2 was tracked for 6.5 h on 18–19 May, after which it moved outside the study area. Once receivers 6 and 7 were established at the mouth of Strathcona Sound, GS2 was tracked for an additional 4.5 h on 21 May (Fig. 3). Thus, although the total tracking period for GS2 spanned 72.8 h, the cumulative time that this shark was closely monitored totaled 11 h. GS2 remained < 100 m deep for 85% of the first segment of the tracking period (i.e. 6.5 h) and then gradually descended. On several occasions during its shallow residence, the shark ascended to within a few meters of the sea ice (Fig. 3). During the first segment of the track, GS2 moved eastwards into Strathcona Sound and out of the receiver array, re-entering the study area on the north side of Strathcona Sound after 2.5 days. During the 4 h that it was tracked on 21 May, GS2 was close to the bottom. Time-at-depth analysis indicated that GS2 resided in the top 100 m of the water column for 58% of the track, even though it swam in relatively deep sections of Victor Bay and Strathcona Sound for much of the tracking period.

Greenland shark GS3 (250 cm FL mature male) was captured at A, released on 21 May at 1244 hours, and continuously tracked for 31.4 h. Upon its release, GS3 was manually tracked for approximately 3 h. The vertical behavior of this shark was characterized by a series of descents and ascents with periods of deeper residence. The shark punctuated the latter with several roundtrip excursions to < 60 m, including a prolonged visit to a depth of 60 m between 0200 and 0500 hours on 22 May (Fig. 3). Manual tracking indicated that GS3 remained about its release area for several hours before moving south into Victor Bay, where it remained over the next 17 h (Fig. 1). At 0913 hours on 22 May, GS3 moved to the mouth of Victor Bay and then northeast across the mouth of Strathcona Sound before leaving the study area to the northwest into Admiralty Inlet (Fig. 1). During this latter part of the track, GS3 was initially deeper than 200 m followed by a gradual ascent to 74 m, and then a descent to 200 m as it exited the study area (Fig. 3). Despite the fact that the vertical track of GS3 was punctuated by several steep ascents and descents, time-at-depth data indicated that this shark spent most of the tracking period (i.e. 83%) below 100 m (Fig. 3).

Greenland shark GS4 (246 cm FL mature male) was captured at A and released on 23 May at 1142 hours. GS4 was manually tracked for 5 h after its release and was detected by the remote array for 17.5 h over a total period of 24.5 h (Fig. 3). Upon its release, GS4 descended to 190 m and was probably at or close to the bottom, and then slowly returned to 100 m during the following 3 h via a series of ascents and descents (Fig. 3). Throughout this period, GS4 remained in the general vicinity of its release, making a slow southeast loop before turning northeast as it gradually moved out of Victor Bay. GS4 descended to depths > 200 m shortly after 1500 hours on 23 May and resided there for most of the remaining track (Fig. 3). During this period GS4 moved on a northeasterly heading across the mouth of Strathcona Sound as it left the receiver array. Seven hours later, on 24 May, the shark re-entered the study area on the northeastern side of Strathcona Sound, remaining in this area for the last 3 h of the track. Bathymetry data and depth observations suggested that GS4 swam close to the bottom during this period, exiting the study area on a northwesterly course into Admiralty Inlet. GS4 inhabited depths of ≥200 m for ~70% of the tracking period, probably close to the bottom for much of this time.

Greenland shark GS5 (190 cm FL female) was captured at B and released on 23 May 1999 at 1558 hours. It was tracked for 13.4 h and compass bearing data were collected for only 1 h immediately after its release. GS5 remained in the upper 90 m of the water column throughout the entire tracking period, spending 90% of this time at depths < 50 m. The vertical behavior of this shark comprised a number of ascents and descents between the surface and 60 m (Fig. 3). After release, GS5 moved in a southwesterly direction into Victor Bay, where it remained for most of the night before exiting the study area at 0524 hours on 24 May along a northerly course. Throughout much of the track GS5 moved along the western side of Victor Bay at depths ranging from close to the surface to near the bottom.

Greenland shark GS6 (207 cm FL male) was captured at B and released on 27 May 1999 at 1945 hours. This shark was tracked for 13.8 h before the track was terminated by removal of the receiver array. After its release, GS6 gradually descended to a depth of 133 m at 0.024 m s^{-1}, the slowest estimated rate of descent for any of the sharks (Table 1). GS6 then slowly ascended to 61 m over the next 6.5 h, before it descended relatively rapidly to depths of 160–197 m for the next 3 h, most likely close to the bottom. At 0736 hours it slowly ascended to 70 m, and, as the track was terminated, it was descending again (Fig. 3). Upon its release, GS6 moved easterly across the mouth of Victor Bay before turning northeast. Time-at-depth data indicated that GS6 spent the entire track at depths < 200 m, ranging from 60 to 140 m for 72% of the time.

Aggregate time at depth

The six Greenland sharks spent all of their time at depths ≤ 320 m, even though the study area included regions of deeper water. The sharks exhibited no apparent depth or temperature preference, although 97% of the depth observations were < 280 m (Fig. 4). During about 31%, 26%, and 42% of the total aggregate tracking time, the sharks were 0–70 m, 70–170 m, and 170–280 m deep, respectively (Fig. 4). Pooled data for the six sharks seemed to indicate nocturnal movement into shallower depths of < 100 m between midnight and 0300 hours (Fig. 5). This was followed by relatively deeper residence during the morning hours, followed by a gradually shallower residence as the day progressed (Fig. 5).

Rate of movement

Rates of descent ($n = 66$) for the six sharks were significantly higher (t-test, $P < 0.01$) than rates of ascent

Table 1 *Somniosus microcephalus*. Rates of descent and ascent calculated from straight-line movements of 20 m or more; average rates calculated from means for each shark

Shark	Descent ($m\ s^{-1}$)					Ascent ($m\ s^{-1}$)				
	n	Mean	SE	Min.	Max.	*n*	Mean	SE	Min.	Max.
GS1	4	0.083	0.021	0.050	0.145	1	0.028	0.000	0.028	0.028
GS2	9	0.116	0.014	0.025	0.177	8	0.051	0.004	0.033	0.073
GS3	28	0.102	0.007	0.036	0.180	29	0.103	0.006	0.052	0.200
GS4	18	0.111	0.015	0.030	0.309	15	0.092	0.014	0.035	0.208
GS5	3	0.112	0.002	0.108	0.115	7	0.041	0.003	0.030	0.048
GS6	4	0.072	0.017	0.024	0.099	5	0.036	0.010	0.007	0.069
Pooled	66	0.104	0.006	0.024	0.309	65	0.081	0.005	0.007	0.208
Average	6	0.099	0.007	0.072	0.116	6	0.058	0.013	0.028	0.103

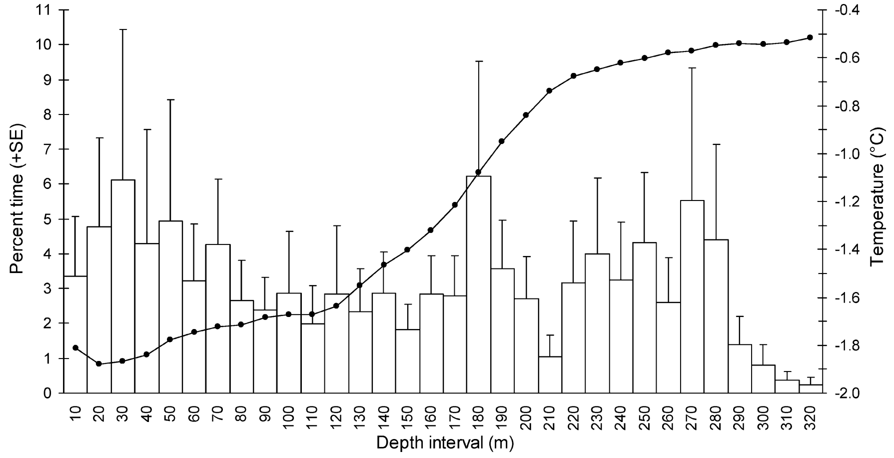

Fig. 4 *Somniosus microcephalus*. Vertical distribution of six tracked Greenland sharks expressed as percentage (mean + SE) of time logged at various depth intervals (m) in and about Victor Bay and Strathcona Sound, Baffin Island, Nunavut, Canada between 16 and 28 May 1999. *Line* depicts mean water temperature at depth

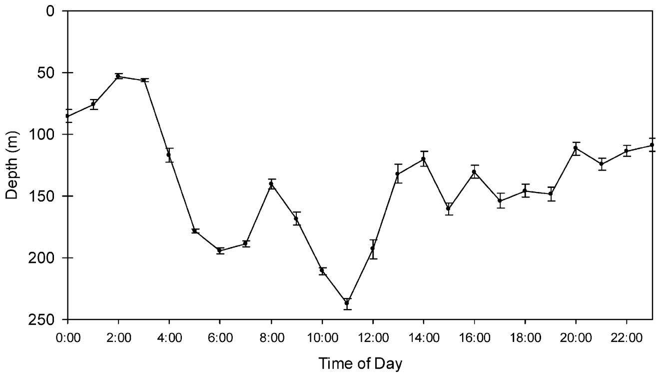

Fig. 5 *Somniosus microcephalus*. Diel behavior of six tracked Greenland sharks depicted by the mean (±SE) residence depth (m) for all sharks combined during hourly intervals

($n = 65$) (Table 1). Rates of horizontal movement were estimated from 27 point-to-point shark positions and ranged from 0.015 to 0.463 $m\ s^{-1}$ (mean = 0.217 $m\ s^{-1}$) for all sharks pooled (Table 2).

Discussion and conclusions

This is the first documentation of shark movements under sea ice using ultrasonic telemetry. Most ultrasonic telemetry studies of sharks have used tracking vessels, and, as noted by Carey and Scharold (1990), sometimes such tracking can influence shark behavior. In the present study, the use of remote and fixed-position manual receivers deployed through a thick layer of sea ice seemed to eliminate the possibility of such biases. In addition, the extremely docile nature of *Somniosus microcephalus* facilitated handling such that sharks did not seem to overly exert themselves during capture and tagging, and they did not speed off from the release site as if fleeing from a negative stimulus.

Results of this study indicate that the Greenland shark is not strictly a benthic or deep-water species while living under land-fast sea ice. All six sharks spent some time well above the ocean bottom, all but one exhibited vertical movements to depths < 100 m, and three made ascents to depths < 25 m. Vertical movements of many shark species are generally thought to be driven by foraging behaviors (reviewed by Sundström et al. 2001). For example, Carey and Scharold (1990) hypothesized that the rhythmic diving of blue sharks, *Prionace glauca*, to depths of several hundred meters facilitated searching for pelagic prey. A megamouth shark, *Megachasma pelagios*, exhibited diel diving behavior that Nelson et al. (1997) attributed to foraging activity. Carey et al. (1982) hypothesized that the brief excursions of a tracked white shark, *Carcharodon carcharias*, to the bottom were associated with scavenging of whale carcasses. The

Table 2 *Somniosus microcephalus*. Estimated rates of horizontal speed over ground (m s^{-1}) of sharks derived from remote receiver data and magnetic compass bearings (*n* number of point-to-point estimates)

Shark	*n*	Mean	SE	Min.	Max.
GS1	3	0.208	0.017	0.179	0.239
GS2	4	0.127	0.030	0.060	0.202
GS3	5	0.351	0.036	0.244	0.463
GS4	4	0.378	0.032	0.292	0.436
GS5	7	0.188	0.033	0.059	0.308
GS6	4	0.037	0.009	0.015	0.055
Pooled	27	0.217	0.026	0.015	0.463
Average	6	0.215	0.053	0.037	0.378

vertical behavior of Greenland sharks reported here is unusual for a species that is typically considered demersal. Based on limited reports, individuals of such species are generally thought to stay closely associated with the bottom and not exhibit wide ranges of vertical movement. For example, Carey and Clark (1995) found that two bluntnose sixgill sharks, *Hexanchus griseus*, tracked off Bermuda remained close to the bottom, at depths of 600–1100 m. Similarly, Yano and Tanaka (1986) reported that a needle dogfish, *Centrophorus acus*, remained within 50 m of the seabed, at 220–680 m during a 21-h track.

Site fidelity has been shown for several species of sharks (e.g. see McKibben and Nelson 1986; Gruber et al. 1988; Klimley et al. 1988, 2001; Holland et al. 1993; Economakis and Lobel 1998; Goldman and Anderson 1999; Sundström et al. 2001). Regarding deep-water species, two bluntnose sixgill sharks that were tracked off Bermuda remained in a limited area of < 10 km for up to 4 days (Carey and Clark 1995). However, none of the tracked Greenland sharks reported herein were within the receiver array (an area of approximately 80.8 km^2) for > 31.4 h. After leaving the area, five of the sharks had 4–12 days (average = 6.7 days) to return to the detection zone prior to the termination of the study, and the only shark (GS4) that left and returned to this zone spent 7 h away before returning for 6 h. Similar results have been reported for tiger sharks, *Galeocerdo cuvier*, tracked off the Hawaiian Islands, and it was hypothesized that those sharks moved within large home ranges (Holland et al. 1999). Large home ranges and site fidelity are suggested for some Greenland sharks based on limited tagging data. From 1936 to 1949, Hansen (1963) tagged 411 Greenland sharks off western Greenland. Of the 28 sharks recaptured over a 16-year period, six were caught within 16 km of their tagging site; these fish were at liberty for up to 7 years. In up to 14 years after being tagged, seven sharks traveled 16–160 km, while the rest traveled 160–1100 km after 2–16 years at liberty. The longest distance traveled during the shortest liberty period (2 years) was 370 km. However, it should be noted that the lack of a seasonal interpretation of Hansen's results (Hansen 1963) precludes a robust assessment of home range size and site fidelity for individual Greenland sharks.

In the present study, horizontal ROM estimates were calculated from estimated positions of Greenland sharks and were based on assumptions of straight-line movement and constant receiver range. These estimates (Table 2) are conservative and must be considered minimum estimates, because the detection range of some remote receivers was slightly > 2.5 km and the vertical movements of sharks were not taken into account in calculating the estimates. Moreover, the assumption of straight-line movement could not be assessed, because data collected from receivers did not pinpoint the position and course of tracked sharks. In general, however, the average horizontal ROM estimate obtained in this study (0.22 m s^{-1}) is similar to that reported by Yano and Tanaka (1986) for the deep-water squaliform *Centrophorus acus*(i.e. 0.25 m s^{-1}, daytime estimate). Although the range of speeds estimated for Greenland sharks (Table 2) shows considerable overlap with other shark species (see Table 1 in Sundström et al. 2001), it contains values that are considerably slower than speeds estimated for known pinniped predators such as the white shark (0.89 m s^{-1}; Carey et al. 1982; Strong et al. 1992) and tiger shark (1.07 m s^{-1}; Lowe et al. 1996; Holland et al. 1999).

Greenland sharks tracked in this study displayed rates of vertical ascent and descent that seem typical of sharks that are slowly cruising. Strong et al. (1992) found that white sharks in Spencer Gulf moved slowly and steadily between the surface and the bottom at an average rate of 0.07 m s^{-1}. This rate is similar to the average ascent rate (0.058 m s^{-1}), but somewhat slower than the average descent rate (0.099 m s^{-1}) estimated for Greenland sharks in the present study. The ascent and descent rates reported for a gulper shark by Yano and Tanaka (1986) (0.23 and 0.20 m s^{-1}, respectively) were similar to one another; however, this fish remained close to or on the bottom (i.e. it displayed relatively limited vertical movement) for most of the tracking period.

Greenland sharks have been described as ravenous, and they eat a wide variety of food, including small invertebrates, fishes, birds, and mammals (Collett 1905; Bigelow and Schroeder 1948, 1953; Compagno 1984; Scott and Scott 1988; Fisk et al. 2002). Carrion, animals incapacitated by nets or traps, and animals recently killed by humans have been readily consumed by Greenland sharks (Dunbar and Hildebrand 1952; Bigelow and Schroeder 1948, 1953; Williamson 1963; Beck and Mansfield 1969; Compagno 1984; Scott and Scott 1988). However, swift-swimming prey such as Atlantic salmon (*Salmo salar*), Arctic char (*Salvelinus alpinus*), and seals (Phocidae) guessed to have been alive when eaten have also been reported from the stomachs of some individuals (Bigelow and Schroeder 1948, 1953; Dunbar and Hildebrand 1952; Berland 1961; Ridoux et al. 1998). Although Greenland sharks are not widely considered to be predators of ringed seals (Reeves 1998), a recent report (Fisk et al. 2002), based on stable isotopes and anthropogenic contaminants, suggested that scavenging or preying on seals does occur.

Evidence that Greenland sharks prey on unencumbered seals is perplexing, because the Greenland shark is well known for its extremely lethargic behavior (Jensen 1914; Bigelow and Schroeder 1948, 1953; Lineaweaver and Backus 1969; Compagno 1984). Furthermore, the eyes of many Greenland sharks are infected by *O. elongata*, a large parasite that can compromise vision (Berland 1961; Beck and Mansfield 1969; Benz et al. 1998, 2002; Borucinska et al. 1998). Borucinska et al. (1998) and Benz et al. (2002) proposed that the sleeper sharks *S. microcephalus* and *S. pacificus* do not need to rely on keen vision to survive. They noted that these species probably evolved from deep-water squaliforms (see Shirai 1992) that depended more on other senses such as olfaction, mechanoreception, and electroreception. Bolstering this hypothesis was the observation that the retinas of *S. pacificus* appeared typical for elasmobranchs living in low-light environments, which seemingly possess low visual acuity (Benz et al. 2002). However, Borucinska et al. (1998) and Benz et al. (2002) did not consider the eyes of infected sleeper sharks to be completely nonfunctional, proposing that they might function as light sensors rather than as image-forming cameras.

Although Greenland sharks may prey on seals in open water (Ridoux et al. 1998), seasonally ice-bound seals such as the ringed seal would seem to provide particularly favorable seasonal hunting opportunities for Arctic sharks. For one, an ice-bound seal would annually be inextricably associated with one to several seal holes, which would seasonally establish fixed dive departure and return locations for long periods (Lydersen and Hammill 1993; Reeves 1998). Secondly, a Greenland shark might be attracted to a seal hole by a suite of olfactory, acoustic, and visual cues that are continuously or rhythmically transmitted into the water by seal activity (e.g. seal vocalizations, ice scraping to maintain holes, excretion; Reeves 1998) or environmental phenomena (e.g. increased sunlight penetration through seal holes during some calendar periods). It is interesting to note in this context that Greenland sharks have been attracted to ice holes by fishermen using light, seal blood, or seal offal (Jensen 1914; Lineaweaver and Backus 1969).

Vertical excursions of Greenland sharks swimming just beneath land-fast sea ice in an area inhabited by ringed seals may indicate active seal hunting by these sharks. In regions inhabited by numerous seals, active seal hunting may be an important routine activity for *S. microcephalus*, especially in consideration of the amount of energy that could be obtained from a single meal of seal (Stirling and McEwan 1975). Klimley et al. (2001) found that white sharks expended considerable effort to search for pinnipeds, but the potential caloric harvest associated with a successful hunt theoretically made such long hunts worthwhile. Carey et al. (1982) hypothesized that a 30-kg meal of whale fat could sustain a white shark for 1.5 months, and Klimley et al. (2001) estimated that a 140-kg northern elephant seal (*Mirounga angustirostris*) could sustain two white sharks for that same period. Such a fat-rich meal might provide sustenance for a Greenland shark for an extremely long period and thus promote the evolution of a feeding strategy involving the alternation of hunting seals just below the ice and foraging along the ocean bottom on carrion and living fishes and invertebrates. Carey et al. (1982) used a similar argument to hypothesize that the frequent diving behavior of a white shark in the northwest Atlantic Ocean involved active searching for dead whales on the ocean bottom.

In areas where pinnipeds are highly concentrated, such as the South Farallon and Año Nuevo Islands off California, white sharks have demonstrated site fidelity (Klimley et al. 1992, 2001; Goldman and Anderson 1999). However, the wide-ranging cruising patterns described by Strong et al. (1992) for white sharks in Spencer Gulf off South Australia were also suggestive of seal hunting behavior. The movements of these sharks, which were punctuated by occasional sorties towards islands, were thought to be evidence that white sharks were searching for odor corridors signaling the presence of pinniped colonies (Strong et al. 1992). Unlike the community haul-out areas that characterize seal populations in many regions where white sharks roam, ringed seals in areas of land-fast sea ice typically distribute themselves in a much less concentrated manner [a recent review by Reeves (1998) listed ringed seal densities of 0.08–3.5 seals km^{-2}]. Such a prey distribution would generally require a Greenland shark to wander more widely than a white shark in search of seals. In some respects these movements would be analogous to the inter-island movements of white sharks noted by Strong et al. (1992) and to the movements of polar bears searching for ringed seals in areas of land-fast sea ice (Gjertz and Lydersen 1986; Furgal et al. 1996; Ferguson et al. 1999, 2000). To capture ringed seals, polar bears utilize a roaming style of hunting that relies heavily on olfaction, stealth, and camouflage and an attack style that relies heavily on surprise (Stirling 1974, 1977; Stirling and Archibald 1977; Gjertz and Lydersen 1986; Furgal et al. 1996). Greenland sharks may share many of these same attributes in hunting ice-bound seals.

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