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Influence of Environmental Variables on the Diel Movements of the Greenland Shark (*Somniosus microcephalus*) in the St. Lawrence Estuary

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The geographic distribution of the Greenland Shark (*Somniosus microcephalus*) extends from the Arctic Ocean to the North Atlantic Ocean. However, little is known about the habitat of this species, as it is generally found at great depths or in the High Arctic. In the St. Lawrence Estuary, Greenland Sharks undertake diel vertical movements into shallow water (≤ 30 m), but the reasons for these movements are unknown. To test the hypothesis that environmental variables drive the movements of this shark in the St. Lawrence Estuary, eight Greenland Sharks were tagged with acoustic telemetry transmitters during the summer of 2005. Three environmental factors, temperature, light, and tides, were associated with their movements. Movement patterns indicate a preference for deep, cold water during daylight hours and shallow, warmer water during the night. Ascending into shallow water mostly coincided with darkness and high tide. This improved understanding of the spatio-temporal distribution of the Greenland Shark will allow for assessment of the risk to these sharks from commercial fisheries, as occurs in the Greenland Halibut (*Reinhardtius hippoglossoides*) longline fishery. In addition, temperature-driven behavioural patterns may change as the thermal structure of the water column shifts due to global warming.

Key Words: Acoustic telemetry; depth; habitat; light; St. Lawrence River; temperature; tide; shark; Greenland Shark; *Somniosus microcephalus*

Introduction

The Greenland Shark (*Somniosus microcephalus*) is the largest arctic fish, reaching lengths up to 730 cm (Compagno 1984). Despite its size and widespread distribution, extending over the waters adjoining at least six countries in the North Atlantic and Arctic Oceans (Yano *et al.* 2007; Chernova *et al.* 2015), the Greenland Shark remains largely unknown. Little is known about its life cycle, habitat use, and the environmental factors that influence its movements. Most studies have focused on its geographic distribution, diet, and contaminant or parasite loads (MacNeil *et al.* 2012).

Because of the paucity of visual observations in surface waters until recently, the Greenland Shark was long considered a primarily cold water bathybenthic species, found at depths of up to 2200 m (Herdendorf and Berra 1995). In the St. Lawrence Estuary, Greenland Sharks undertake diel vertical movements into shallow depths (≤ 30 m) (Stokesbury *et al.* 2005), but the reasons for these movements are unknown. Although more recent studies indicate that Greenland Sharks show no temperature preference within the narrow range observed in the Arctic Ocean at Svalbard, Norway (Fisk *et al.* 2012), and Baffin Island, Canada (Skomal and Benz 2004), thermal preference may exist in the shallower waters of the St. Lawrence Estuary, where temperatures fluctuate by as much as 23°C (Stokesbury *et al.* 2005; JG, unpublished data).

Sightings of Greenland Sharks at shallow depths are not limited to the St. Lawrence. The species has been harvested by harpoon at the surface on Baffin Island (Beck and Mansfield 1969), and the Inuit from Cumberland Sound, Nunavut, occasionally observe these sharks from the surface as they swim along the sea floor (Idrobo 2008). However, this behaviour is associated with hunting activities when marine mammals are being butchered on the shore, which is not the case in the St. Lawrence since the Beluga (*Delphinapterus leucas*) fishery in Quebec was terminated in 1960. Natural encounters with scuba divers have also taken place in the Saguenay Fjord, Quebec (Harvey-Clark *et al.* 2005), and at Qaanaaq, Greenland (JG, unpublished data).

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The observed diel movements of the Greenland Shark are not unique for a shark of its size and northern distribution. A close relative, the Pacific Sleeper Shark (*Somniosus pacificus*), travels mainly below the photic zone during daylight hours and approaches the surface at night (Hulbert *et al.* 2006). The Sixgill Shark (*Hexanchus griseus*), another benthic species of comparable size found in cold water, has also been associated with nocturnal tides but at greater depths (Andrews *et al.* 2009). It remains to be determined whether Greenland Sharks respond to the same environmental stimuli as these two boreal deepwater species.

Several shark species follow circadian rhythms, remaining in deep water during the day and then ascending through the water column to shallower depths at night: Blue Shark (*Prionace glauca*; Carey and Scharold 1990), Bigeye Thresher (*Alopias superciliosus*; Nakano *et al.* 2003; Weng and Block 2004), Caribbean Reef Shark (*Carcharhinus perezii*; Chapman *et al.* 2007), Mako Shark (*Isurus oxyrinchus*; Klimley *et al.* 2002), Megamouth Shark (*Megachasma pelagios*; Nelson *et al.* 1997), Sixgill Shark (Andrews *et al.* 2009), and the Small-Spotted Catshark (*Scyliorhinus canicula*; Sims *et al.* 2006). However, studies on other shark species, including the Sixgill Shark (Hulbert *et al.* 2006) and the Greenland Shark (Skomal and Benz 2004; Stokesbury *et al.* 2005; Campana *et al.* 2013) point to conflicting diel movement patterns, and Stokesbury *et al.* (2005) observed Greenland Sharks swimming mostly close to the bottom rather than ascending vertically.

In the present study, we tested the hypothesis that environmental variables drive the movements of Greenland Shark in the St. Lawrence Estuary. To this end, we tagged eight Greenland Sharks with acoustic transmitters equipped with depth and temperature sensors and tracked their movements by telemetry during the summer of 2005.

Study Area

Greenland Sharks frequent four bays on the north shore of the St. Lawrence Estuary in the region of Baie-Comeau, Quebec, Canada (Figure 1). These boreal bays are characterized by a seasonally dynamic littoral environment offering a wide variety of known prey species of the Greenland Shark including fish, crustaceans, molluscs, and marine mammals. Baie des Anglais (station 1; 49.268°N, 68.127°W), the largest of the four bays, is 4.4 km long and 4.0 km wide with a maximum depth of 90 m. Baie du Garde-Feu (station 2; 49.281°N, 68.051°W) is 1.0 km long by 0.5 km wide with a maximum depth of 70 m. Baie-Saint-Pancrace (station 3; 49.287°N, 68.046°W) has the second largest

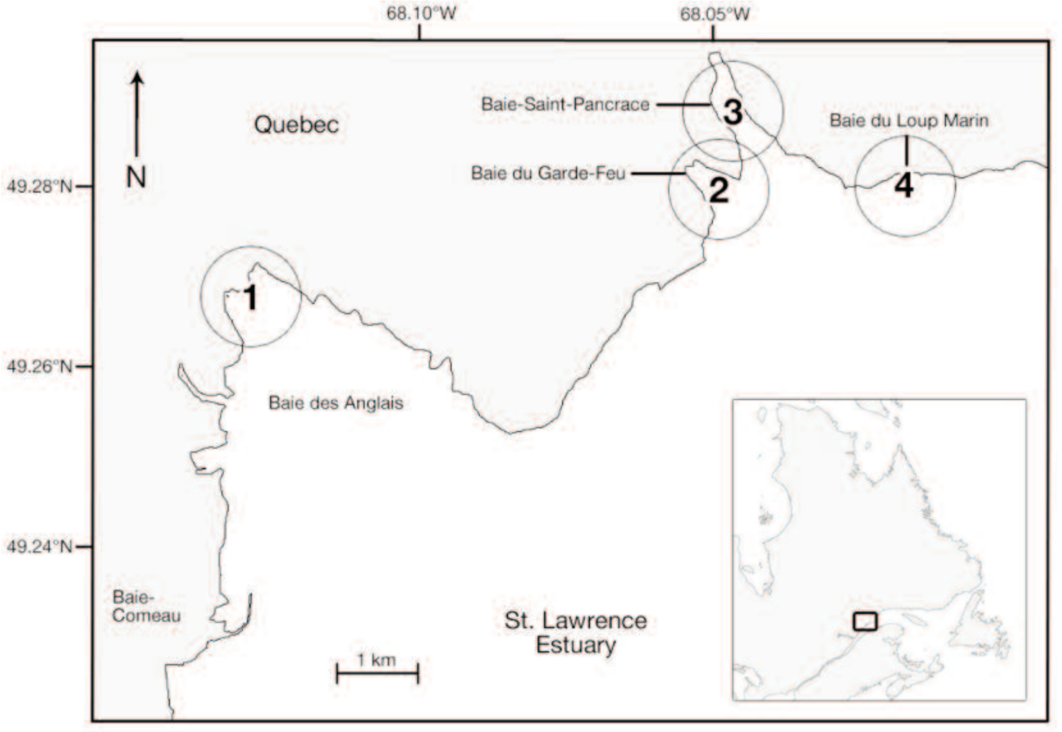

FIGURE 1. Location of acoustic sampling stations in the St. Lawrence Estuary near Baie-Comeau, Quebec. Circles indicate maximum range (600 m) of each receiver.

surface area and is also the narrowest bay (approximately 1.5 km long by 0.25 km wide); its maximum depth is also 70 m. Baie du Loup Marin (station 4; 49.280°N, 68.009°W) is only 0.03 km long by 0.2 km wide. Baie du Loup Marin is different from the other bays because of its steep incline (≥ 40°) and depth (> 150 m). The three other bays are characterized by a more gradual incline (≤ 25°). All four bays open on the St. Lawrence Estuary, which is approximately 56 km wide at the city of Baie-Comeau. The maximum depth of the Laurentian Channel, which lies at the centre of the estuary, is 350 m.

Methods

Acoustic Telemetry

To record the movements of Greenland Sharks, we deployed acoustic transmitter tags on eight sharks (unknown sex, mean length 3 m) at station 3 on 18 and 19 June 2005. To reduce the risk of injury to the sharks and divers, no shark was captured or restrained. Acoustic coded tags (V16 transmitters; Vemco, Halifax, Nova Scotia, Canada) were attached to the sharks by a scuba diver equipped with a Hawaiian sling type spear. A metal dart retained the transmitter in the shark's superficial tissue. The tag was attached to a fastener by a crimped 10-cm stainless steel wire (tensile strength 90.9 kg).

Tags transmitted a unique code, so that each shark could be identified. The tags were also equipped with sensors to measure the shark's depth (m) and water temperature (°C) at the shark's location. Tags were programmed to transmit data at 69 kHz every 60 s during the sampling period from 19 June to 19 August 2005. Transmissions were detected by receivers up to 600 m away depending on environmental conditions and bathymetry. Signals received by hydroacoustic receivers were date- and time-stamped and archived to memory. Four passive ultrasonic receivers (VR2; Vemco) were installed 6 m off the bottom in the four bays. Data recorded by the receivers were downloaded at the end of the sampling period with a laptop computer (VR1 PC interface; Vemco).

Environmental Data

Online tidal data, obtained from Fisheries and Oceans Canada (station 2840, Baie-Comeau), comprised two variables: high tide included data from 3 h before and 3 h after high water, and low tide included data from 3 h before and 3 h after low water. This distinction was made to create a time-buffer period and, thus, make allowance for sharks adjusting to the water movement of flow and ebb tides.

Surface water temperatures were obtained from an Institut Maurice Lamontagne (IML, Fisheries and Oceans Canada) thermograph network buoy off Baie-Comeau (49.202°N, 68.057°W). These data were used to monitor temperature at 1 m depth throughout the study period.

Light levels for the Baie-Comeau area were classified as "night" or "day" based on hourly data from Mobile Geographics LLC (tides.mobilegeographics.com/locations/332.html). Lunar phases obtained from the National Aeronautics and Space Administration (http://eclipse.gsfc.nasa.gov/SKYCAL/SKYCAL.html) were classified as "full moon" (7 days before to 7 days after the full moon or start of first quarter to start of last quarter) or "new moon" (7 days before to 7 days after the new moon or start of last quarter to start of first quarter).

Results

Detections per Shark

The acoustic receivers detected 96 653 signals from the eight Greenland Sharks over 62 days, from 19 June to 19 August 2005 (Table 1). All of the sharks transmitted signals on the same schedule, but the distribution of recorded signals was irregular. Lapses in signals for all sharks confirm that they left the zones covered by the receivers every day over the course of the summer. Shark 3 was detected most often (30 195 detections), whereas shark 2 was detected the least (1376). Shark 2 was also the only shark that did not remain in the study area until the end of the sampling period; it was last detected on June 21. Few signals from all sharks were detected from 19 June to 12 July. However, an increase

TABLE 1. Period of deployment and data collection for acoustic receivers in four bays off Baie-Comeau, Quebec, in summer 2005. Detections of Greenland Sharks (*Somniosus microcephalus*) (n = 96 653) ceased when the receivers were removed on 8, 20, and 21 August 2005.

Station no.	Deployment and recovery dates (d/m/y) (d/m/y)	Location	Receiver depth (m)	Dates of first and last detected signals (d/m/y)	Total signals detected
1	19/6/2005	49.267596°N	20	20/6/2005	77 379
	08/8/2005	68.127496°W		08/8/2005	
2	19/6/2005	49.287314°N	30	19/6/2005	
	08/8/2005	68.045956°W		08/8/2005	3 171
3	19/6/2005	49.280448°N	15	23/6/2005	
	20/8/2005	68.009428°W		19/8/2005	15 653
4	19/6/2005	49.280868°N	25	15/7/2005	
	21/8/2005	68.051043°W		19/8/2005	450

in detected signals began on 13 July, at which time six of the eight sharks traveled to station 1 (Figure 2).

Detections per Station

Station 1 (Baie des Anglais; depth 20 m) recorded the largest number of signals (80%; *n* = 77 379) and station 4 (Baie du Loup Marin; depth 25 m) recorded the least (0.47%; *n* = 450). Only two sharks (1 and 6) visited all four stations, and only station 2 (Baie du Garde-Feu; depth 30 m; *n* = 3171) was visited by all eight sharks. All sharks displayed similar movement patterns, swimming in and out of the stations at various speeds from the head of the bays to open water. Shark 1 made a return trip between stations 1 and 4 over a period of 29 h allowing us to calculate a long-distance average speed. Because it did so while transiting through stations 2 and 3, its minimum average cruising speed if swimming forward in a linear and continuous movement would have been approximately 0.3 m/s over a total distance traveled of 26 km. With the exception of shark 2, which left the study area shortly after being tagged, all sharks remained in close proximity to each other, traveling individually or in loose groups as

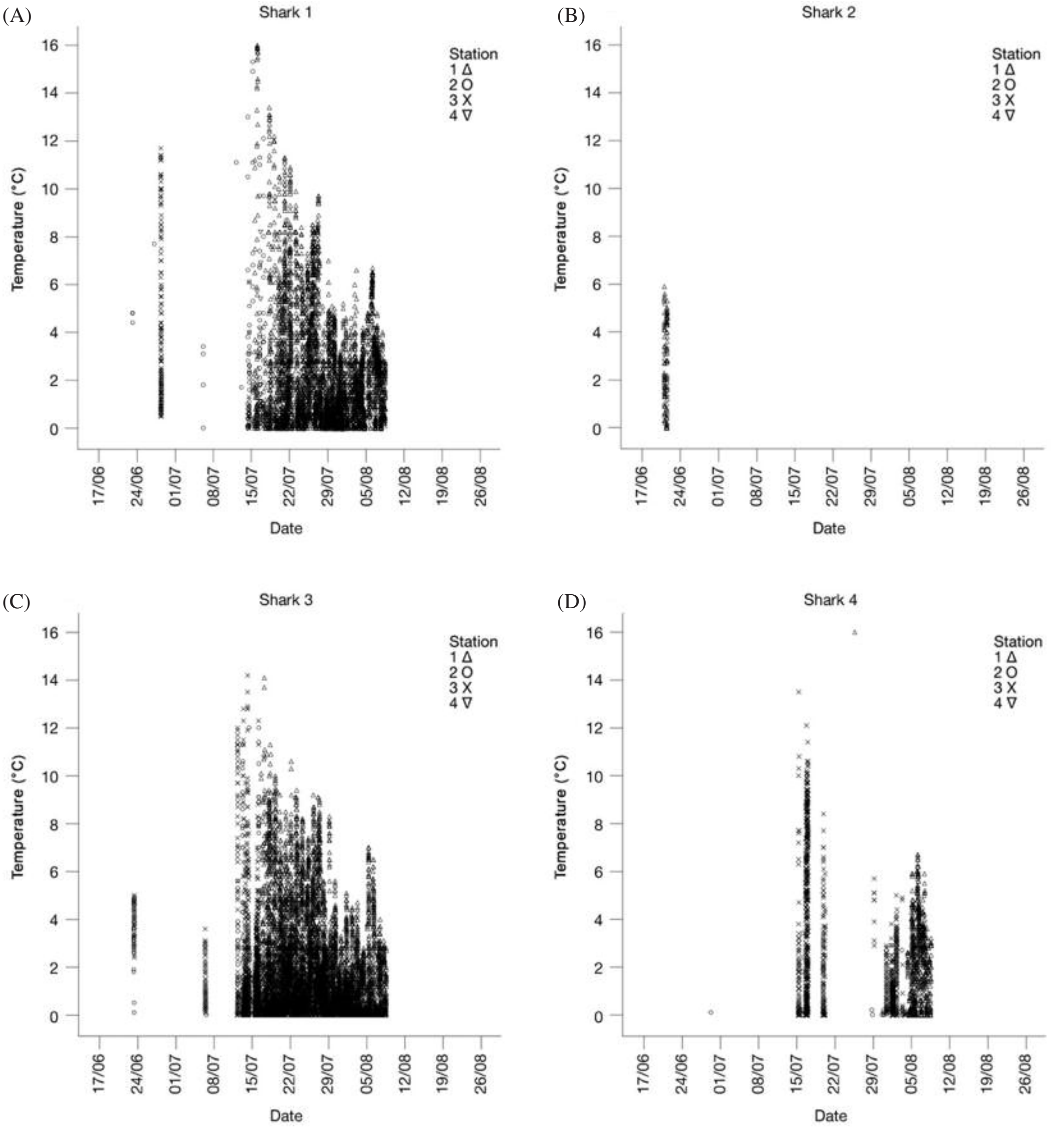

FIGURE 2. Temperature signals (°C) detected (*n* = 47 892) for all Greenland Sharks (*Somniosus microcephalus*) at all stations off Baie-Comeau, Quebec, from 19 June to 19 August 2005. *(Continued on next page.)*

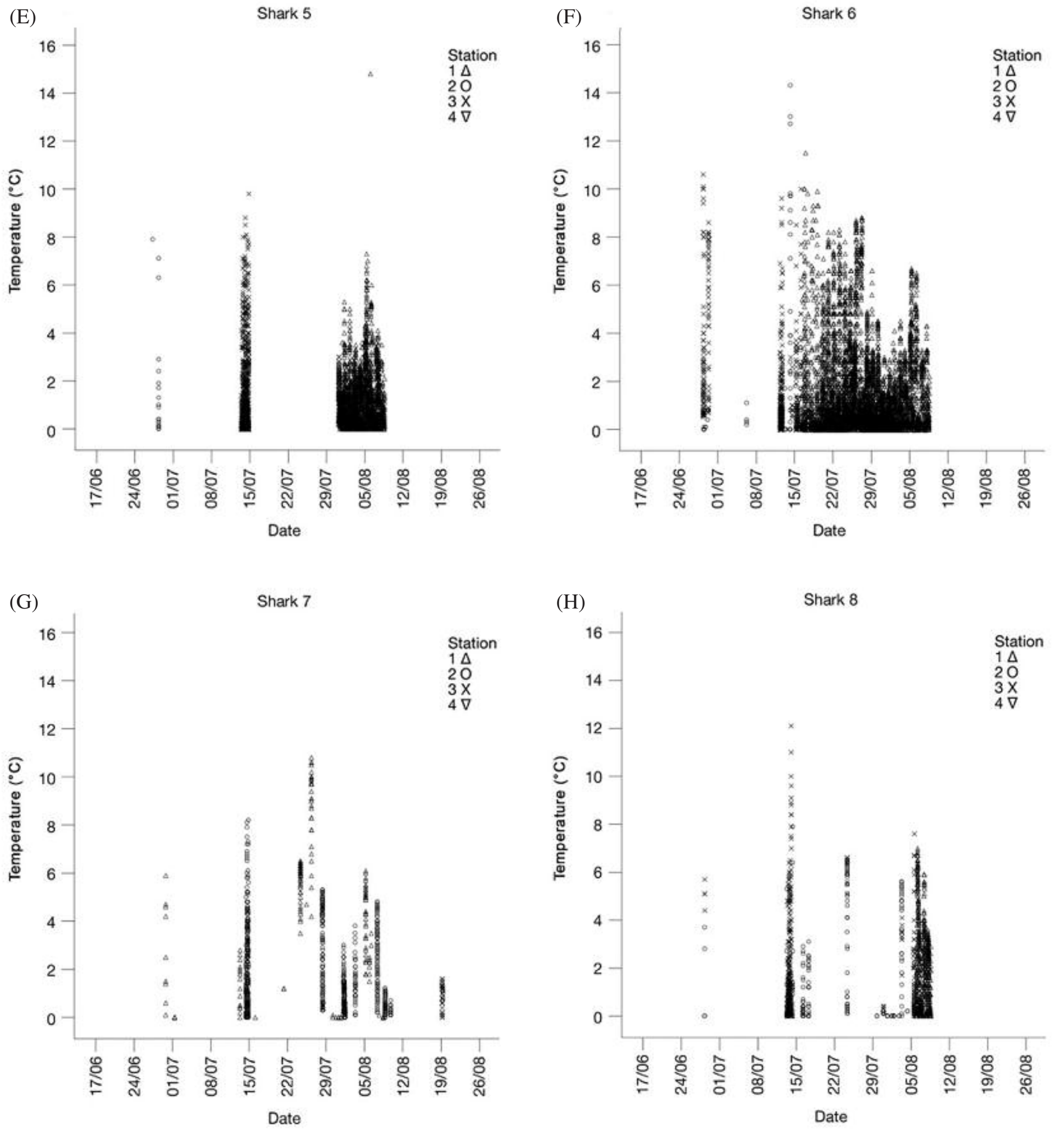

FIGURE 2 *(continued)*. Temperature signals (°C) detected (n = 47 892) for all Greenland Sharks (*Somniosus microcephalus*) at all stations off Baie-Comeau, Quebec, from 19 June to 19 August 2005.

they repeatedly transited in and out of the same stations from mid-July to the end of the study period.

Temperature

All sharks experienced the coldest ambient water temperatures during daylight hours (Figure 3). For sharks 1, 3, 4, 5, and 6, the number of detections progressively increased as average water temperatures began to decrease in mid-July (Figure 2). The maximum temperature of 16.1°C was recorded for shark 1 at station 1 (Baie des Anglais) on 15 July at 0712 (Figure 2). This is near to the maximum (17.7°C) recorded by the IML buoy at a depth of 1 m later that same day. However, the IML buoy was located nearly 9 km from our receiver at the head of Baie des Anglais. Data from the stationary IML buoy also show that water temperatures at the surface decreased by as much as 6°C overnight. The minimum temperature of −1.6°C was recorded for shark 1 at station 1 on 1 August at 2258.

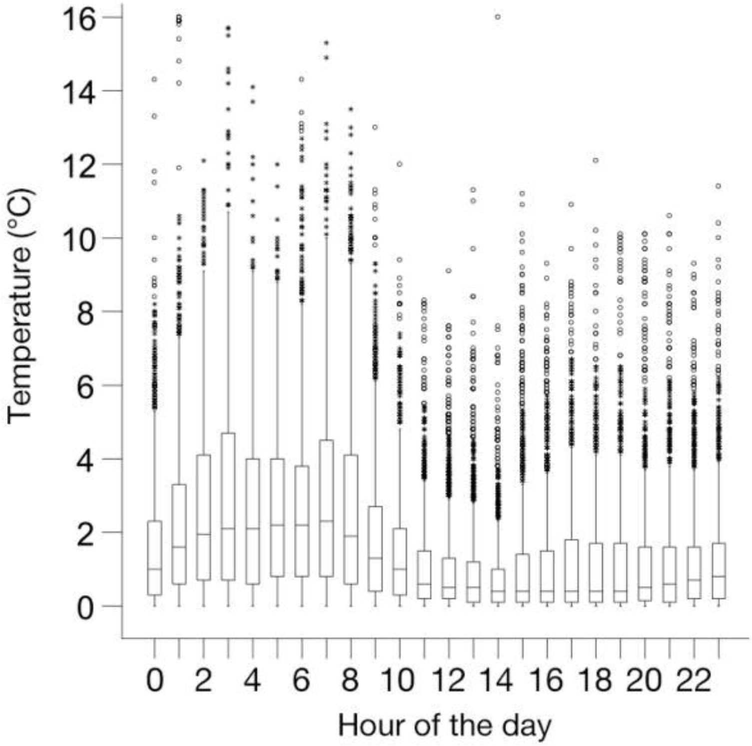

FIGURE 3. Hourly temperatures (n = 47,892) recorded for all Greenland Sharks (*Somniosus microcephalus*) at all stations off Baie-Comeau, Quebec, from 19 June to 19 August 2005. Box plots show median values (solid horizontal line), 50th percentile values (box outline), minimum and maximum values (whiskers), and outlier values (circles).

All sharks were rarely exposed to temperatures higher than 12°C (Figure 2), and remained only a few minutes in warmer water near the surface before heading back to deeper water offshore.

With the exception of shark 2, which left the study area shortly after being tagged, all sharks exhibited movement profiles that reflected diel temperature and depth differences. The sharks' incursions into shallow, warmer water at stations 1, 2, and 3 occurred throughout the day, although they were deeper during daylight hours, and typically lasted less than 30 minutes (Figure 4). The sharks returned to deeper, colder, and darker water after reaching the surface or the head of the bays. Their movements into shallow water at station 4, the only station located by a deep wall, were of even shorter duration, as there was no gradual slope to slow the sharks' movements in and out of shallow depths. The warmest temperature averages were reached between 0000 and 0800, when light levels at the surface were lowest (Figure 3).

Average temperatures transmitted by the tags at the first three stations were similar, ranging from 1.3°C to 1.8°C. Station 4, which had a steeper incline and greater depth than the other stations, had average tag readings of 0.4°C.

Light

The shallowest mean depths were recorded at night (Table 2). The back-and-forth movement pattern from deep to shallow water remained constant but mean depths progressively decreased as darkness set in (Figure 5). Signal detections were sporadic and showed no stable pattern while sharks transited between stations until mid-July. However, a steady diel vertical movement pattern associated with the daytime period became apparent from 20 to 27 July for sharks 1, 3, 4, 6, 7, and 8, and for shark 4 from 4 to 7 August, when their movements were mostly restricted to station 1. These six sharks exhibited the same diel vertical movement pattern; most of their signals detected at shallow depths coincided with high tide at night (Figures 6 and 7). There was no such pattern for signals detected at shallow depths during daylight hours. Although the nocturnal pattern observed from 20 to 27 July coincided with a full moon, the minimum average depths recorded for new moon (31.3 m) and full moon (30.9 m) phases over the course of the study were very similar; hence, nocturnal light levels did not appear to affect diel ver-

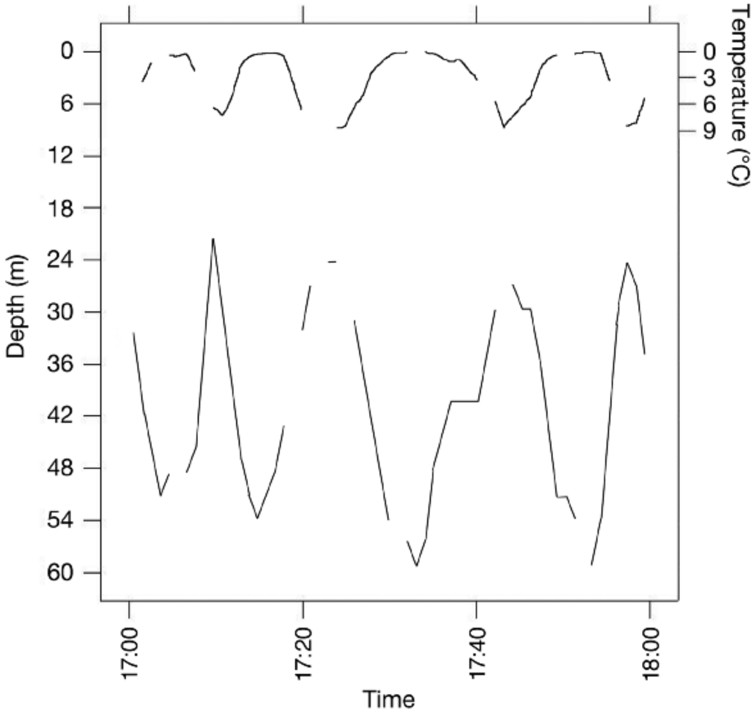

FIGURE 4. Depth (lower lines) and water temperature (upper lines) recorded for Greenland Shark (*Somniosus microcephalus*) 4 at station 1 (Baie des Anglais) on 16 July 2005, from 1700 to 1800.

tical movements. The difference between the number of signals detected for both lunar phases varied by 0.5% based on an equal number of nights for each variable. Regardless of the lunar phase, the shallowest depths and warmest temperatures were recorded between 0000 and 0800 when ambient light levels were lowest (Figures 3 and 5).

Tide

The warmest temperatures and shallowest depths recorded for sharks 1, 3, 4, 6, 7, and 8 coincided with high tide at night or early in the morning when ambient light levels underwater were still low (Figures 6 and 7).

Depth

Temperature and depth were inversely related for all sharks (Figures 3 and 5). Sharks 1, 2, 3, and 6 swam all the way to the surface (0 m) during the day and at night (Tables 2 and 3). The deepest recorded depth was 119.9 m, which was the deepest point within the range of station 4.

TABLE 2. Mean night-time depth and temperature range experienced by eight Greenland Sharks (*Somniosus microcephalus*) tagged off Baie-Comeau, Quebec, in summer 2005.

Tide	Number of detections	Depth (m)			Temperature (°C)		
		Minimum	Maximum	Mean	Minimum	Maximum	Mean
High	15 333	0.0	119.9	28.7	−1.6	14.8	1.9
Low	15 121	1.8	118.1	33.5	−0.3	16.1	1.3

TABLE 3. Mean daytime depth and temperature range experienced by eight Greenland Sharks (*Somniosus microcephalus*) tagged off Baie-Comeau, Quebec, in summer 2005.

Tide	Number of detections	Depth (m)			Temperature (°C)		
		Minimum	Maximum	Mean	Minimum	Maximum	Mean
High	31 381	0.0	86.4	35.9	−0.5	15.3	1.2
Low	34 818	0.0	114.6	36.4	−0.4	16.0	1.3

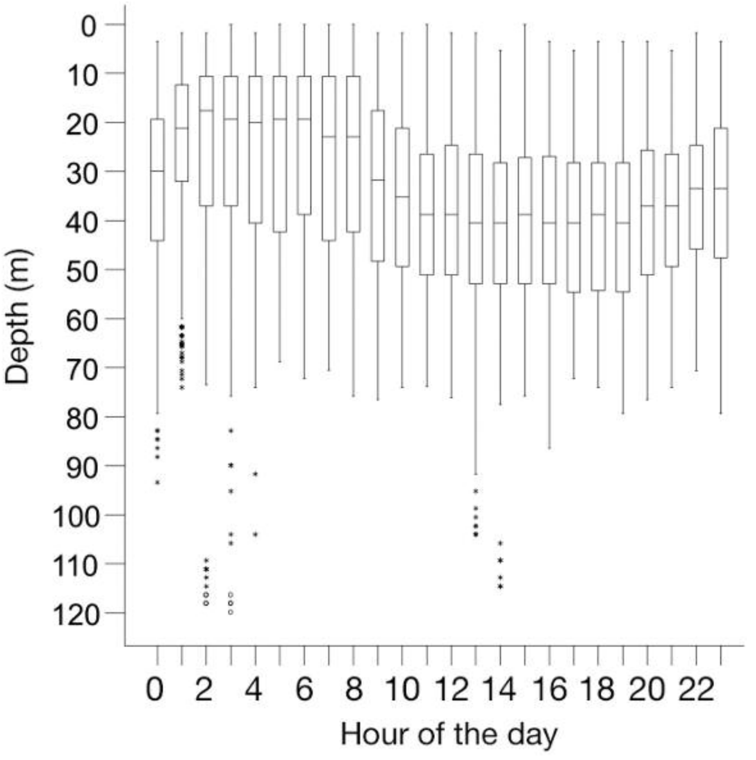

FIGURE 5. Hourly depths (n = 48 761) recorded for all Greenland Sharks (*Somniosus microcephalus*) at all stations off Baie-Comeau, Quebec, from 19 June to 19 August 2005. Box plots show median values (solid horizontal line), 50th percentile values (box outline), minimum and maximum values (whiskers), and outlier values (circles).

Discussion

In this study, we tracked eight Greenland Sharks fitted with acoustic transmitters for 60 days off the port city of Baie-Comeau, Quebec. Most signals (n = 89 608; 92.7%) were detected from 13 July to 8 August when six of the eight sharks (sharks 1, 3, 4, 5, 6, and 7) progressively transited upriver to station 1 from stations 2, 3, and 4. Most of these signals were produced by sharks 1, 3, 5, and 6 (n = 78 369). This group movement to the bay with the quickest access to deep, cold water coincided with the onset of the warmest surface water temperatures of the summer (up to 21.5°C). However, several days without any signals detected before and after this movement show that the sharks spent most of the sampling period beyond the range of the receivers (Figure 2). Nonetheless, the data obtained suggest that, in addition to water temperature, at least two other environmental factors, light and tide, may influence the short incursions of Greenland Sharks into shallow water at night.

Temperature

Previous research on Greenland Shark distribution has been conducted mainly in the Arctic Ocean and adjacent seas where water temperatures remain cold year round and vary little with depth (−1.8°C to −0.5°C; Skomal and Benz 2004). However, wider temperature variations off boreal Baie-Comeau during our study (−1.6°C to 21.5°C) appear to affect the movements of Greenland Sharks at shallow depths. Campana *et al.* (2013) also recorded wide temperature fluctuations surrounding tagged Greenland Sharks in the northwest Atlantic (2.6–17.2°C) but did not observe diel vertical migrations.

Sharks tagged in Baie-Comeau reached the shallowest average depths at night when surface waters were colder and darker than during daylight hours (Figures 3 and 5). This suggests that Greenland Sharks are sensitive to warmer surface temperatures and choose to move into shallow water when temperatures there are coolest (although they are much warmer than those at depth). The duration and number of movements into shallow water could, thus, be partly determined by water temperature. Data analysis over 60 minutes (16 July, 1700–1800) (Figure 4) shows that one of the sharks swam through temperature gradients of 10°C three times. The movements of six of the eight sharks were similar except for speed and the number of incursions inside the bays.

Hulbert *et al.* (2006) found that the movements of the Pacific Sleeper Shark consisted of systematic vertical

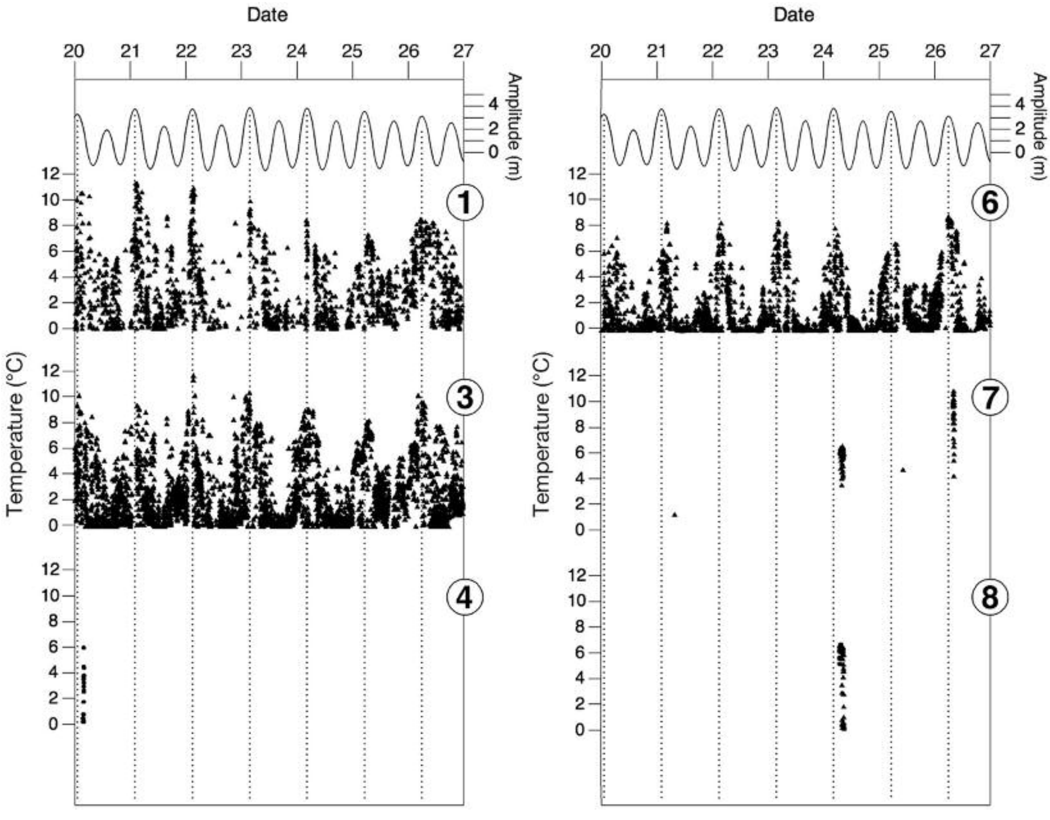

FIGURE 6. Tidal cycle (amplitude; lines) and temperature signals (points) from Greenland Sharks (*Somniosus microcephalus*) 1, 3, 4, 6, 7, and 8 at all stations from 20 to 27 July 2005. Dotted vertical lines indicate high tide at night.

oscillations with short transitions. Similarly, the sharks in our study as well as those studied by Stokesbury *et al.* (2005) spent little time in warmer water before moving to colder water offshore, demonstrating a preference for water in the 1–2°C range (Figure 3). Swimming in cold water could also allow the Greenland Shark to regulate its body temperature. The Small-Spotted Catshark hunts in warmer water at night and then returns to deep water during the day, where colder temperatures help with digestion (Sims *et al.* 2006). If the Greenland Shark is more scavenger than active predator, cold water may slow the digestive process thus compensating for a slower metabolic rate and sporadic feeding.

Light

Hulbert *et al.* (2006) reported uninterrupted sequences of diel vertical movements of the Pacific Sleeper Shark lasting up to 330 h (about 14 days), although most lasted 25 h or less. The longest sequence of signal detections in our study, which was interrupted by the removal of three acoustic receivers, lasted 27 days and may have been triggered by environmental conditions (Figure 2).

In the Arctic Ocean, the Greenland Shark experiences extended periods of darkness because of the depths it frequents (1200 m or more) (Yano *et al*. 2007), ice cover, and the high latitude. This suggests that vision often plays only a minor role during the shark's search for prey. This view is supported by anatomical studies indicating that most arctic Greenland Sharks have severely limited vision as a result of parasitism (Borucinska *et al.* 1998). Hulbert *et al.* (2006) contend that foraging of the Pacific Sleeper Shark is primarily guided by olfactory cues.

It is not known whether the Greenland Shark hunts at night or during the day nor whether it feeds opportunistically over a daily period. Inuit hunters have long attracted sharks to the surface by projecting light into ice holes (Idrobo 2008), presumably to simulate sunlight passing through a seal's breathing hole. Overwintering Belugas, restricted to ice holes, may also be preyed upon by Greenland Sharks (MacNeil *et al.* 2012).

Intense light levels could reduce the shark's stealth advantage as it swims toward potential prey at the surface, as well as hinder its vision, since it spends most of

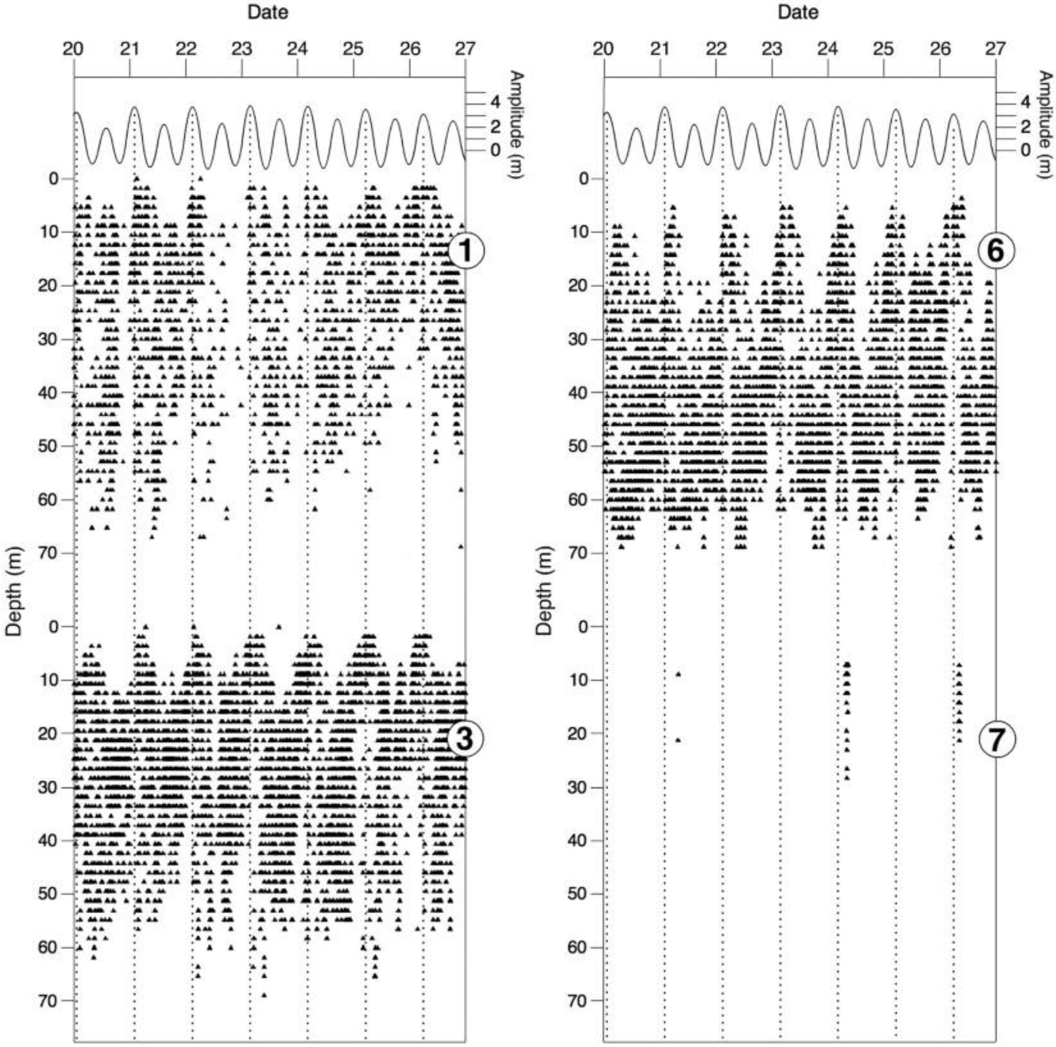

FIGURE 7. Tidal cycle (amplitude; lines) and depth signals (points) from Greenland Sharks (*Somniosus microcephalus*) 1, 3, 6, and 7 at all stations from 20 to 27 July 2005. Dotted vertical lines indicate high tide at night.

its existence in low-light conditions or in total darkness below the photic zone (< 200 m). Winter conditions in the St. Lawrence Estuary are similar to those of the Arctic, but for the rest of the year, the Greenland Shark may travel from total darkness to a highly luminous environment on a daily basis. However, the intensity of ambient light appears to have an effect on the movements of Greenland Sharks as shown by the negative relation between shark depths and light (Figure 5). This may be caused by a number of factors. The shark could be attracted by the seasonal abundance of prey, such as Snow Crabs (*Chionoecetes opilio*), at shallow depth. However, as the Greenland Shark is a generalist feeder as well as a scavenger, it may be sampling the water column rather than following a particular prey species. Unlike the prey of the Pacific Sleeper Shark, which feeds throughout the water column (Hulbert *et al.* 2006), fish and invertebrate prey of Greenland Sharks, including Greenland Halibut (*Reinhardtius hippoglossoides*), Atlantic Wolffish (*Anarhichas lupus*), redfish (*Sebastes* spp.), cephalopods, and various crabs are mostly benthic or demersal species that do not have diel vertical movements from bottom to surface. Fish remains found in the stomachs of Greenland Sharks are often whole (Castro 2011), which would indicate that prey was sucked off the bottom through the shark's downward-facing mouth.

Diel movements may also be due to physiological constraints, including light aversion and temperature tolerance. Because many of its prey species are found in both deep and shallow water, the Greenland Shark may selectively spend most of the day in deep water under dark conditions to avoid higher light levels in shallow water.

Unlike arctic populations of Greenland Sharks and Pacific Sleeper Sharks, in which most individuals are affected by the copepod *Ommatokoita elongata*, an ocular parasite (Borucinska *et al.* 1998; Benz *et al.* 2002), fewer than 10% of the more than 100 sharks we observed in the St. Lawrence between 2003 and 2012 and none of the tagged sharks in this study hosted this parasite. Although vision is not believed to play a significant role in the foraging behaviour of arctic populations of sleeper sharks, we have repeatedly observed and filmed Greenland Sharks visually avoiding divers and objects, such as boulders, in the St. Lawrence (Harvey-Clark *et al.* 2005). If their undamaged eyes are not used as mere light sensors, as has been suggested for arctic populations (Borucinska *et al.* 1998), vision may in fact play a more predominant role in the St. Lawrence. Because the eyes of the Greenland Shark are mostly accustomed to darkness even in the St. Lawrence, they could in turn be more sensitive to the higher levels of ambient light near or at the surface (Stokesbury *et al.* 2005).

Light aversion affecting vertical movements has also been proposed for the Sixgill Shark (Bigelow and Schroeder 1948; Compagno 1984). This may explain why the sharks in this study appeared to need a transition period, as their shallowest average depths occurred between 0000 and 0800, at least 3 h after night had set in and 3 h after sunrise (Figure 5). The sharks progressively left the deeper, darker areas offshore to reach shallow water during the night, with some occasionally swimming all the way to the surface. The reverse phenomenon occurred after sunrise when the number of signals detected at shallow depths gradually decreased as light levels increased.

Daytime turbidity may also affect sharks' depth distribution. Our observations while deploying acoustic transmitters mostly took place under dark conditions at depths greater than 10 m or when visibility was reduced because of plankton blooms, pollen accumulations at the surface, or increased freshwater runoff from local tributaries. Therefore, the shark may also be present, albeit in lower numbers, at shallow depths during daylight hours when the sky is overcast or during conditions of increased turbidity. Varying levels of ambient light could, thus, be partly responsible for daytime detections of Greenland Sharks in shallow water in the Baie-Comeau area.

Tide

Tides appeared to influence movements of the sharks. Diel vertical movement profiles show that the shallowest depths and the warmest temperatures were mostly recorded during high tide at night and early in the morning (Figures 6 and 7). Conversely, the average depths and temperatures recorded during high tide in daylight hours were deeper and colder (Figure 8). This could indicate that the sharks remained on the outer edge of receiver range and that they were not letting themselves be carried into shallow areas by the rising tide. There is, thus, the appearance of habitat selection, as the sharks' shallow water movements associated with high tide were mostly nocturnal. At night, the influx of colder offshore water, as well as the absence of sunlight, produced a cooling effect on surface waters, as recorded by the IML buoy, thus rendering shallow depths more hospitable to the Greenland Shark. The Sixgill Shark is also known to move closer to the surface during high tide at night (Andrews *et al.* 2009).

Depth

The effect of tide cycles at the study site (tidal range ≤ 3.5 m) is small considering that the range of depths sharks reached daily often surpassed 70 m. For all sharks, the shallowest depths were recorded between 0000 and 0800 (Figure 5). In every case, sharks that reached the surface or shallows at the head of the bays immediately headed back into deeper water.

The acoustic system we used did not measure the distance between the transmitter and the receiver, which makes it difficult to evaluate the actual position of the shark in relation to the sea floor. However, more than 95% of the sharks sighted while scuba diving (> 100 encounters since 2003) swam no more than 2 m off the bottom, at depths ranging from 6 m to 40 m. Also, the location of Greenland Sharks in the water column is likely to be directly associated with that of their mostly benthic prey (Ridoux *et al.* 1998; Fisk *et al.* 2002; Yano *et al.* 2007; Leclerc *et al.* 2012). Stomach contents from St. Lawrence Greenland Sharks as well as their highly abraded rostrum suggest that they feed on prey and animal remains found on the sea floor (Harvey-Clark *et al.* 2005). This evidence suggests that recorded depths were near the bottom and that the sharks rarely swam vertically up the water column. Our observations differ from those of Skomal and Benz (2004) in that their specimens tagged in the Arctic swam vertically from deep water offshore. They also differ from Hulbert *et al.* (2006), who suggest that the Pacific Sleeper Shark does not follow bottom contours exclusively while foraging.

Biological Factors

Greenland Sharks may enter shallow bays for many reasons, including to pursue prey, to reproduce, or to rid themselves of parasites that are sensitive to reductions in salinity caused by the many freshwater tributaries in the Baie-Comeau area.

All but one of the tagged sharks (shark 2), as well as dozens of other Greenland Sharks of both sexes consisting of mature males and immature females that were observed and recorded by scuba divers, appeared to be aggregating (including nose to tail swimming) over a period of several weeks. In addition, philopatry of

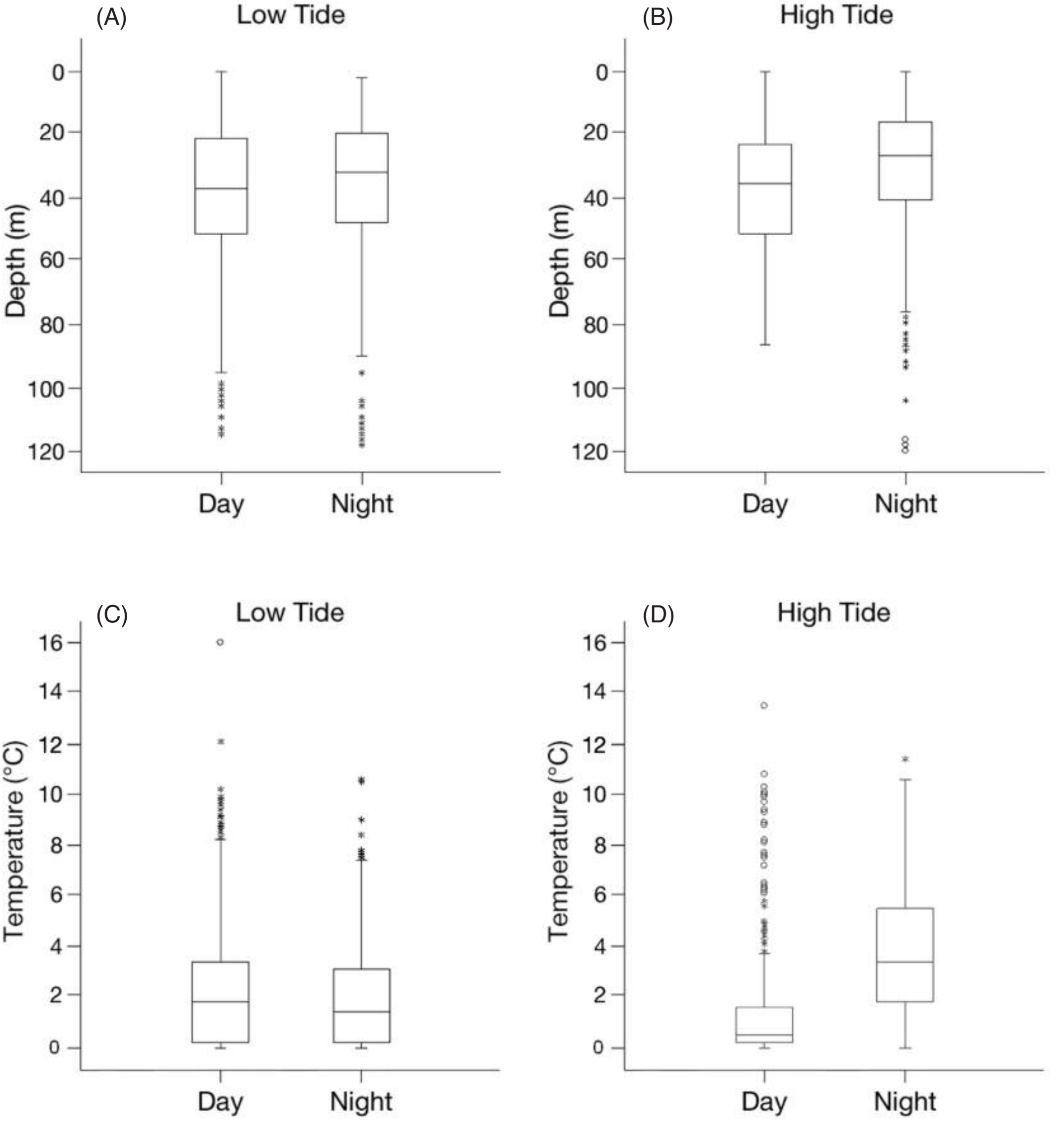

FIGURE 8. Daily depth (n = 48 761) at (A) low and (B) high tide, and temperature (n = 47 892) at (C) low and (D) high tide for all Greenland Sharks (*Somniosus microcephalus*) at all stations off Baie-Comeau, Quebec, from 19 June to 19 August 2005. Box plots show median values (solid horizontal line), 50th percentile values (box outline), minimum and maximum values (whiskers), and outlier values (circles).

Greenland Sharks observed over a period of 4 years in the Baie-Comeau area, including some of the sharks tagged in 2005 as well as sharks recorded during dives, could be partly a result of the permanent or seasonal presence of specific prey, such as the Snow Crab and Greenland Halibut; this phenomenon is known in other species, including the White Shark (*Carcharodon carcharias*) (Klimley *et al.* 1992, 2001) and the Sixgill Shark (Andrews *et al.* 2010).

However, the known local prey items of the Greenland Shark are found on the bottom, from surface waters to the deepest parts of the Laurentian Channel. Possible exceptions are pinnipeds, but very few were observed during the study period. Although remains of Grey Seals (*Halichoerus grypus*) and Harbour Seals (*Phoca vitulina*) have repeatedly been recovered from Greenland Shark specimens in the St. Lawrence, and considering that the Greenland Shark may actively prey on seals in the Greenland Sea (Leclerc *et al.* 2012), it has not been determined whether seals from the St. Lawrence are taken as carrion, in which case feeding would have taken place on the sea floor.

Although no juvenile sharks were seen at shallow depths in the Baie-Comeau area between 2003 and 2015, observed philopatry may be associated with pupping (Hueter *et al.* 2004; Feldheim *et al.* 2014; Hussey *et al.* 2014) taking place beyond the range of scuba divers. Despite the visual absence of juveniles, since 2003, we have observed at least three females that appeared gravid (Harvey-Clark *et al.* 2005; JG and CHC, unpublished data).

Conclusions

Three environmental factors, temperature, light, and tides, were found to influence the movements of the Greenland Shark. Movement patterns indicated a preference for deep, cold water during daylight hours and for shallow, warmer water at night. Ascending movements into shallow water mostly coincided with darkness and high tide. This improved understanding of the spatio-temporal distribution of the Greenland Shark should allow for improved assessment of risks to this species in the St. Lawrence Estuary, such as those arising from commercial fisheries, which have been occurring for over a century (JG, unpublished data). A better understanding of the influence of physical variables could also help predict the effects of climate change on the overall distribution and temperature-driven behavioural patterns of the Greenland Shark as the thermal structure of the water column shifts due to global warming.

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