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Movements of Arctic and northwest Atlantic Greenland sharks (*Somniosus microcephalus*) monitored with archival satellite pop-up tags suggest long-range migrations

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ABSTRACT

Greenland sharks (*Somniosus microcephalus*) are large carnivorous sharks that appear to be widely distributed in Arctic seas and in deep, cold temperate waters. In order to examine their movement patterns, diving behaviour and temperature preferences, pop-up archival transmitting tags (PATs) were deployed on 15 Greenland sharks up to 5.1 m in length, both in the Canadian Arctic and in the northwest Atlantic off the eastern coast of Canada. Tags remained on the sharks up to 11 months (mean of 149 days, including four tags which came off prematurely) before popping off. All sharks travelled a minimum of 315 km, and some as much as 1615 km, at depths of up to 1816 m. All tagged Greenland sharks in the Arctic exited the relatively shallow, coastal waters of Cumberland Sound before sexual maturation, presumably moving to spend their adult lives in the deeper waters of the Davis Strait to the north. All the presumably mature Greenland sharks tagged in the NW Atlantic moved up to 1000 km off the continental shelf over abyssal waters to the south. There was extensive evidence of pelagic swimming in both regions, but diel vertical excursions into the water column were not observed. The mean temperature of 2.7 °C recorded in the Arctic sharks was much less than the 7.9 °C mean temperature observed in the Atlantic sharks, where a maximum temperature of 17.2 °C was recorded. Our results indicate that Greenland sharks can inhabit very deep waters, and they can inhabit very cold waters, but they do not necessarily have to inhabit deep, cold waters. It is possible that Greenland sharks migrate offshore over very deep waters to mate and/or give birth.

1. Introduction

Little is known about most deep-sea elasmobranchs: small size, inaccessible habitat, infrequent catches and negligible commercial value all constrain the ability to collect specimens, let alone understand their biology. However, the Greenland shark (*Somniosus microcephalus*) is not a rare small species; it is the largest fish in the polar oceans, very abundant in some areas, a frequent bycatch in some fisheries, and one of the largest carnivorous sharks in the world (Templeman, 1963; Yano et al., 2007; Castro, 2011). A list of the unknown features of Greenland shark biology appears to dwarf that which is known, and includes a lack of knowledge of its longevity and growth rate, any aspects of its reproduction, fecundity, size of female maturity, mating or pupping grounds, population structure, migrations or even confirmation that it predates versus scavenges its prey (MacNeil et al., 2012). Given its potential role as an apex predator in Arctic and deep-sea environments (Cortés, 1999), a basic understanding of Greenland shark life history and population dynamics would advance the understanding of Arctic and deep-sea ecosystems.

Greenland sharks are widely distributed in Arctic waters, with growing evidence of their presence in deep-sea waters further south (MacNeil et al., 2012). Movement between the two environments is limited. Tagging studies using conventional tags (Hansen, 1963) off Greenland, pop-up archival transmission tags (PATs) in the Gulf of St Lawrence and northeast Atlantic (Stokesbury et al., 2005; Fisk et al., 2012) and acoustic tags in the Canadian Arctic (Skomal and Benz, 2004), all reported limited movements, with almost all tagged sharks remaining within a 250-km radius of the tagging site for periods of up to several years. Most swimming was assumed to be benthic, although vertical excursions into the water column were suggested by the studies using electronic tags (Skomal and Benz, 2004; Stokesbury et al., 2005; Fisk et al., 2012). Therefore, the existing studies support the view that Greenland

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sharks are largely resident, slow-moving sharks inhabiting cold, deep waters.

The objective of this study was to examine movement patterns, diving behaviour and temperature preferences of Greenland sharks tagged with pop-up archival transmission tags, both in the northwest Atlantic off the east coast of Canada and in the Canadian Arctic. In doing so, we challenge the conventional wisdom that Greenland sharks are primarily benthic, cold-dwelling sharks with localised movements.

2. Methods

Greenland sharks in the Canadian Arctic were measured and tagged between 2007 and 2009 by scientific staff fishing groundfish longlines from either small boats or through the ice in Cumberland Sound on Baffin Island. Greenland sharks caught as incidental bycatch by commercial halibut longline fishermen in the northwest (NW) Atlantic (off Nova Scotia or Newfoundland) were tagged by fishermen trained in PAT tag deployment procedures. All boat-caught sharks were tagged while in the water, while sharks caught through the ice were pulled up onto the ice (using a combination of the gangion/hook in the mouth and a rope around the tail pulled with a snowmobile) for measurement and tagging. Tagged sharks showed no obvious injury above and beyond that of capture. Also recorded was the overall condition of the shark, as well as its sex, fork length (FL) and maturity. Males were considered sexually mature if their claspers were heavily calcified and could be rotated freely, and if their rhipidion could be opened and the terminal hook extruded. Female maturity could not be assessed without dissection, and therefore was inferred based on a presumed FL_{50} of 400 cm (MacNeil et al. 2012).

All sharks were tagged with Wildlife Computers Mk-10 pop-up archival transmitting tags (PATs) just prior to release. Based on published length-at-maturity data (females) and evaluation of clasper condition (males), all Arctic sharks were considered immature. Based solely on lengths, three of the four NW Atlantic sharks were considered mature. PATs were attached by darting a nylon umbrella tip about 8 cm into the dorsal musculature just lateral to the posterior end of the first dorsal fin. The angle of dart insertion was such that the umbrella tip engaged the cartilaginous radials immediately underneath the dorsal fin, thus reducing the possibility of premature release. The umbrella tip was attached to the PAT with a monofilament leader of 400-pound test, sheathed in plastic tubing to reduce trauma to the shark due to continual rubbing near the point of insertion. Each PAT was also fitted with an emergency cutoff device provided by the manufacturer, which physically released the tag if it went below 1800 m (which is the maximum nominal safe depth for tag operation).

PATs were programmed to record depth ($\pm$0.5 m), temperature ($\pm$0.1 °C) and relative light intensity at 10 s intervals for a period of 2–11 months after release. The tag data were internally binned at 6 h intervals and the summarised data transmitted to an Argos satellite after release of the PAT from the shark. All but one of the tags transmitted successfully after release. Most (but not all) of the PATs were programmed to release from the shark if a constant depth was maintained for a period of 4 d, in the event that tag-induced mortality was high. However, this did not occur.

Shark location at the time of pop-up was determined with an accuracy of <1 km through Doppler-shift calculations provided by the Argos Data Collection and Location Service. The reconstruction of migration pathways between the time of tagging and pop-up could not be determined because swimming depths exceeded light measurement capabilities of the tag. The estimated distance between pop-up and tagging was measured as a straight-line distance, but not over land.

3. Results

A total of 15 Greenland sharks were tagged. Sharks tagged in the Arctic ($n=11$) ranged between 243 and 325 cm FL, with all nine of the males being immature or maturing and the two females likely to be immature based on size. In contrast, the four sharks tagged in the NW Atlantic were much larger, ranging between 376 and 516 cm FL. Although the fishermen who caught the Atlantic sharks did not assess maturity, at least some were likely to have been mature based on size. Water depth at all tagging locations ranged between 300 and 900 m.

Transmissions were received from 14 of the 15 PATs that were applied to Greenland sharks in the NW Atlantic and in the Arctic, although one of the Arctic tags reported few data other than a pop-up location. All but four of the tags popped off on the programmed date; none of the premature releases were triggered by emergency cut-off depths or extended periods at a constant depth. The time at liberty for the analysed tags ranged between 48 and 350 days, with a mean of 149 days (Table 1).

All of the Greenland sharks tagged in the Arctic travelled a minimum of 300 km from the tagging site by the time of tag pop-up, exiting Cumberland Sound where they were tagged (Fig. 1). Tags 44403, 78371 and 78372 all popped off outside of Cumberland Sound after only 5–7 weeks, so the sharks must have

Table 1
Tag and release data for Greenland sharks captured in Cumberland Sound (Arctic) and off the eastern coast of Canada (NS).

Argos PTT	Location	FL (cm)	Sex	Deployed	Lat release ddmm N	Long release ddmm W	Pop-off date	Lat popoff ddmm N	Long popoff ddmm W	Days at liberty	Minimum km travelled
70244	CS	243	Male	6-Sep-07	6549	6600	5-Nov-07	6820	5910	60	665
34524	CS	287	Male	22-Apr-08	6606	6626	12-Nov-08	7151	5817	204	1100
44403	CS	265	Male	17-Apr-08	6606	6626	9-Jun-08	6432	6028	53	380
44404	CS	289	Male	17-Apr-08	6606	6626	20-Aug-08	7603	6619	125	1530
44405	CS	265	Male	18-Apr-08	6607	6627	29-Aug-08	7325	6027	133	1240
44415	CS	280	Female	18-Apr-08	6607	6627	22-Oct-08	7453	5954	187	1405
78371	CS	281	Male	16-Apr-08	6607	6627	3-Jun-08	6414	6152	48	315
78372	CS	275	Male	16-Apr-08	6607	6627	18-Jun-08	6445	6146	63	320
34517	CS	316	Male	15-Aug-08	6604	6556	31-Jul-09	7056	6314	350	955
66397	CS	272	Male	13-Apr-09	6555	6627	01-Oct-09	7632	7143	170	1615
67740	CS	325	Female	19-Aug-09	6608	6601	Did not report				
67737	NS	376	Unknown	21-Jun-07	4249	5029	31-Dec-07	3711	5507	193	735
67738	NS	432	Unknown	5-Aug-07	4250	5031	31-Dec-07	3823	6146	148	1075
80344	NS	404	Unknown	6-Jan-08	4418	5736	27-Jun-08	3507	7031	173	1505
80345	NS	516	Female	27-Feb-08	4317	6034	29-Aug-08	3540	7255	184	1365

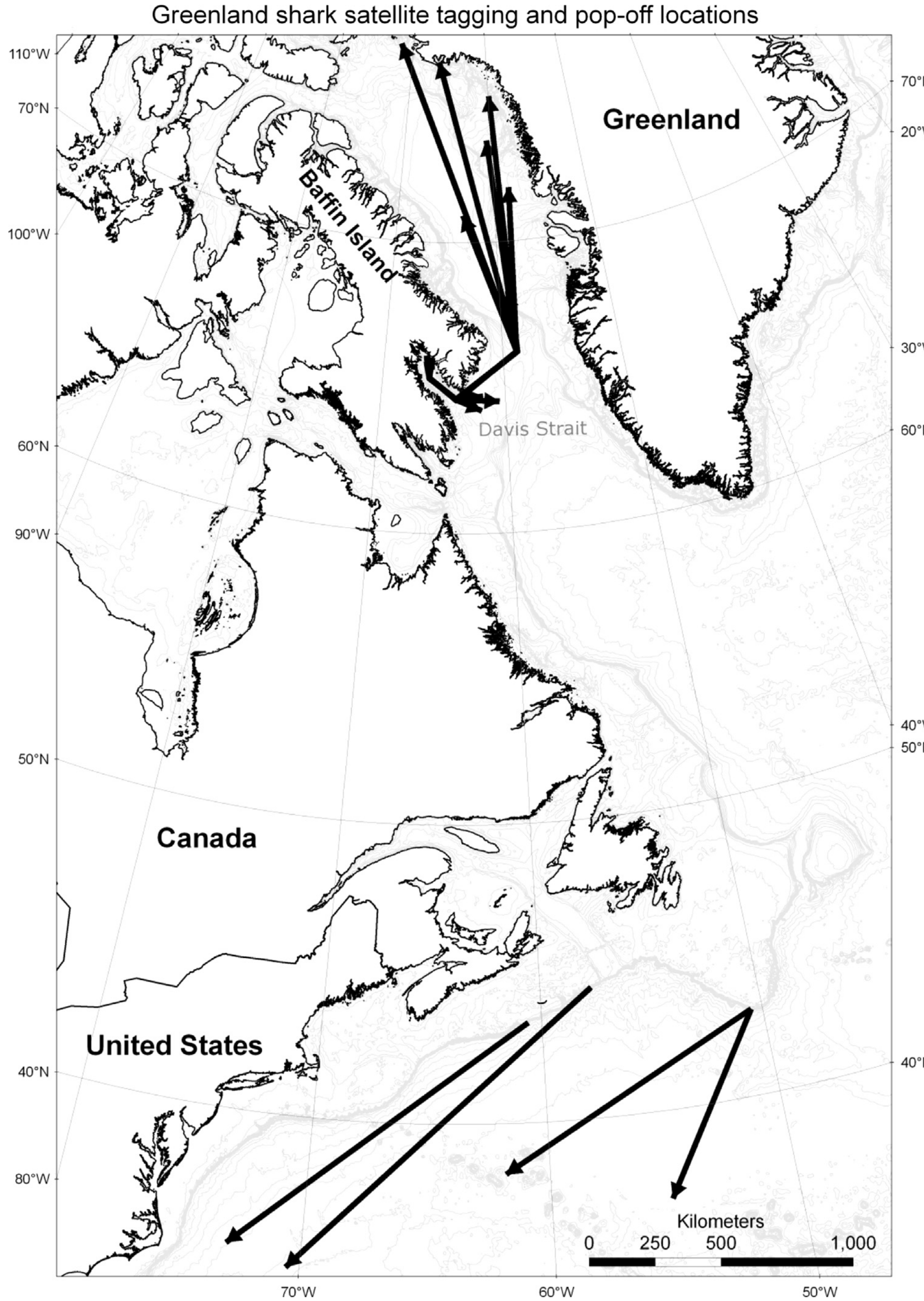

Fig. 1. Map showing net movement of 14 Greenland sharks tagged in the Arctic and off the eastern coast of Canada. Arrowheads indicate popup locations.

exited the Sound in the spring relatively quickly. Tag 70244 also exited the Sound quickly in the fall, since it popped off on the east side of the Davis Strait after only 2 months. More than half of the remaining sharks subsequently swam north to, or across, the Davis Strait towards Greenland. The minimum distance travelled by all of the Arctic sharks ranged between 315 and 1615 km (mean of 953 km) (Table 1), with distance travelled significantly correlated with time at large for periods of less than 205 days ($p < 0.01$, $r^2 = 0.69$). There was no significant correlation between time at large and distance travelled when the single long-term tag deployment (350 days) was included in the regression. Mean net displacement rate from the tagging site was 7.7 ± 2.1 km day^{-1}. There was no significant relationship between direction, magnitude or rate of movement with the length of the sharks ($p > 0.2$), nor was there a significant difference between males and females (chi-squared test, $p > 0.4$).

All of the Greenland sharks tagged in the NW Atlantic travelled a minimum of 735 km to the southwest of the tagging site (Fig. 1). All of the tags popped off at locations up to 1000 km offshore of the continental shelf, suggesting that much of their movement had taken place over abyssal waters. The minimum distance travelled ranged between 735 and 1505 km (mean of 1170 km) (Table 1), with distance travelled uncorrelated with time at large or shark length ($p > 0.5$). Mean net displacement rate from the tagging site was 6.8 ± 3.3 km day^{-1}. Since only one of the sharks was sexed, movement differences between the sexes could not be determined.

Depth-temperature profiles of individual Greenland sharks showed similar patterns between the Arctic and the NW Atlantic,

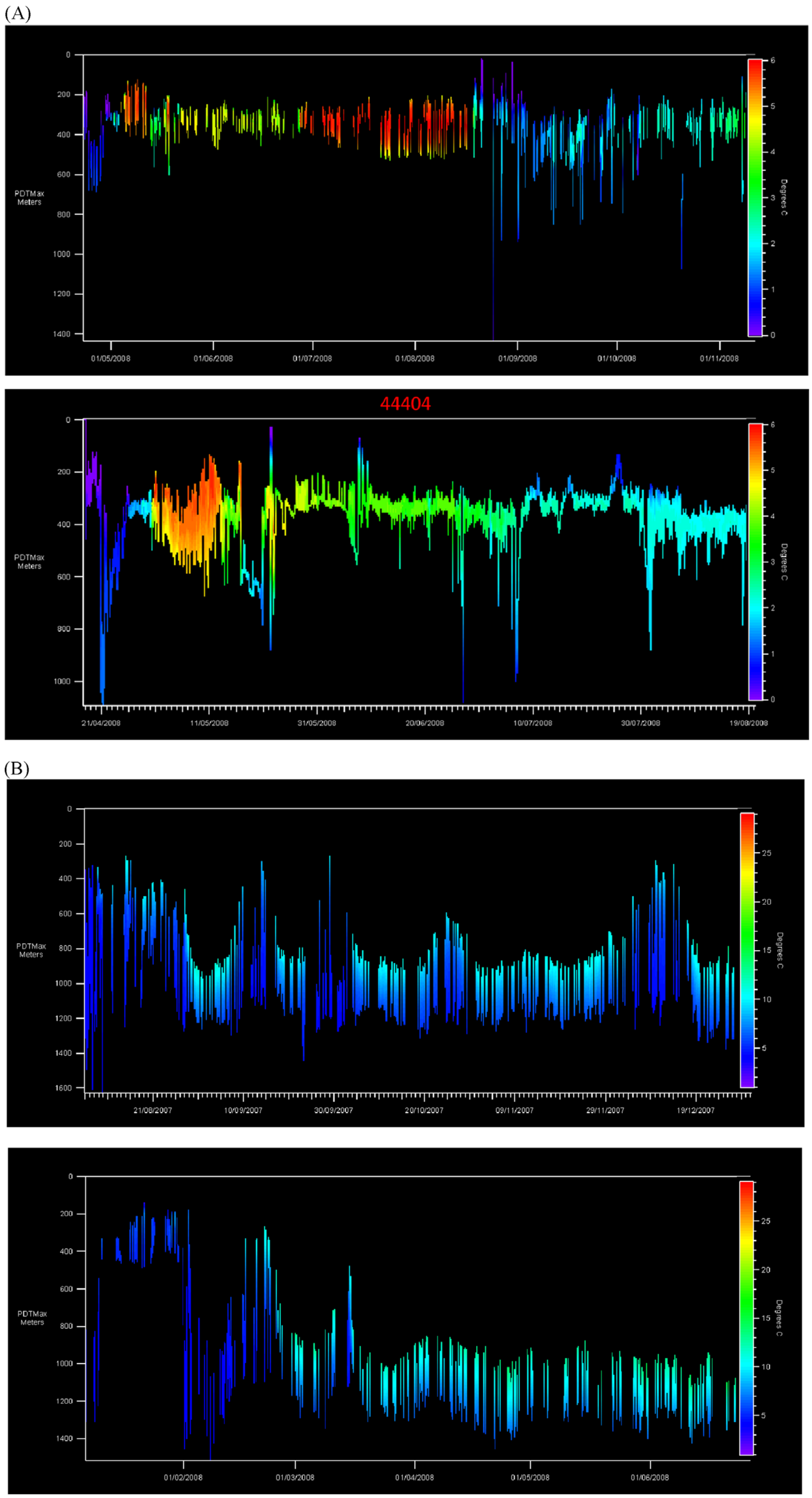

Fig. 2. (A) Depth-temperature profiles of individual Greenland sharks from the Arctic (tag ID 34524 and 44404; see Table 1 for details). (B) Depth-temperature profiles of individual Greenland sharks from the NW Atlantic (tag ID 67738 and 80345; see Table 1 for details).

but at different mean levels (Fig. 2). Sharks in both areas tended to spend extended periods (weeks or months) at a mean depth that changed only gradually. However, Greenland sharks in the Arctic typically showed 6-h vertical excursions on the order of 100–200 m, punctuated by abrupt vertical excursions of up to 1440 m (Fig. 2A). In contrast, the daily vertical excursions of sharks in the NW Atlantic was somewhat larger, often on the order of 200–400 m. In both areas, individual sharks were often exposed to temperature variations of about 6 °C over the course of several months. Depth-temperature profiles for all sharks are shown in Supplementary material.

Although the depth data collected by the PAT tags do not indicate if the shark was on the bottom or in the water column, there was strong evidence that most of the Greenland sharks swam pelagically at least some of the time. Pelagic swimming was most clearly demonstrated in the northwest Atlantic sharks, all of whose tags popped off many hundreds of kilometres offshore of the continental shelf in water depths of at least 4 km. Mean daily maximum swimming depth for these sharks was 1104 m, with a maximum recorded depth of 1816 m, implying that these sharks were swimming 2–4 km above the ocean bottom for most or all of their time at liberty (e.g. Fig. 2B). The evidence was less marked for most of the Arctic sharks, but still clear. For example, shark tag 34517 popped off in the middle of the Davis Strait in 2100 m of water, with tag depth readings of around 600 m shortly before pop-off, indicating that it had been swimming pelagically before pop-off. Six of the remaining tags popped off either in the northern Davis Strait or on the eastern side of the Strait towards Greenland, indicating that they must have either swum pelagically across the deep Davis Strait or hugged the coastal waters.

There were large differences in depths and temperatures occupied by the sharks in both areas. The mean time-weighted depth (within a 6-h interval) of Greenland sharks in the Arctic was 367 ± 4 m, ranging from 84 to 959 m (Fig. 3). Minimum and maximum depths were 0 and 1562 m, respectively. In contrast, the mean time-weighted depth of sharks in the NW Atlantic was considerably deeper at 949 ± 10 m, ranging from 275 to 1556 m (Fig. 3). Minimum and maximum depths were 144 and 1816 m, respectively. Time-weighted temperature distributions tended to be much warmer for NW Atlantic sharks than Arctic sharks (Fig. 4), with means of 7.9 ± 0.1 °C in the Atlantic versus 2.7 ± 0.1 °C in the Arctic. Temperature ranges in the Atlantic (2.6–17.2 °C) were also considerably warmer than those in the Arctic (0–6 °C).

Diel vertical migrations were not apparent in any of the Greenland sharks, either on an individual level or when aggregated within locations. Neither maximum daily depth nor the difference between 6-h depth and maximum daily depth differed significantly across the within-day 6-h time intervals ($P > 0.1$). Similarly, the mean within-day, noon vs midnight difference in maximum depth did not differ significantly from zero ($P > 0.05$).

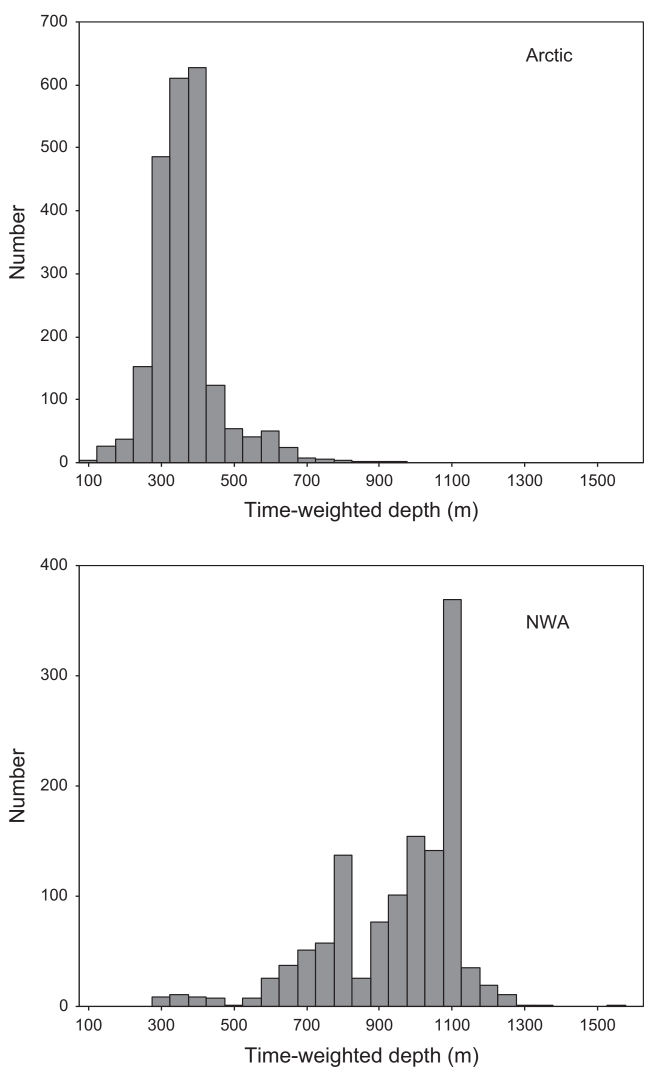

Fig. 3. Frequency histograms of time-weighted depths (6-h intervals) occupied by Greenland sharks in the Arctic and the northwest Atlantic Ocean (NWA).

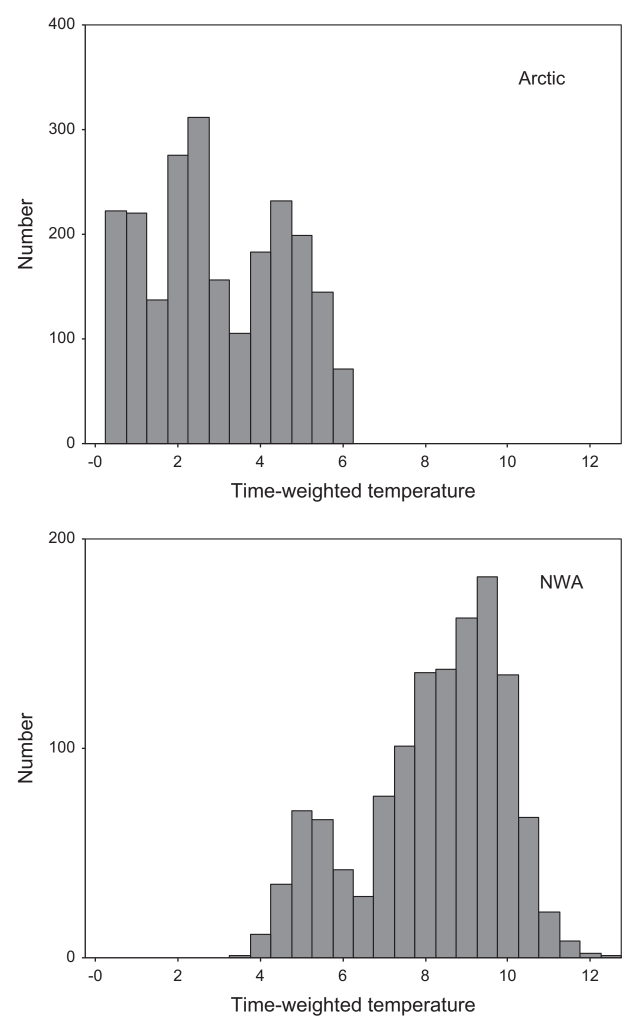

Fig. 4. Frequency histograms of time-weighted temperatures (6-h intervals) occupied by Greenland sharks in the Arctic and the northwest Atlantic Ocean (NWA).

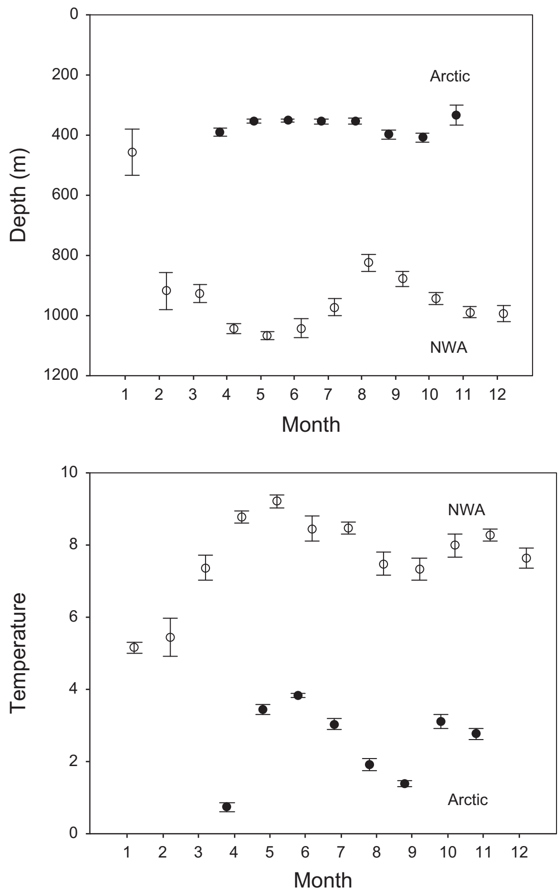

Fig. 5. Monthly patterns in depth (mean ± 95% CI) and temperature occupied by Greenland sharks in the Arctic and northwest Atlantic Ocean (NWA). Sharks in the Arctic tended to live in shallower but colder waters than those in the northwest Atlantic.

Therefore, if diel vertical migrations were taking place, either in the water column or along a sloped bottom, we could not detect it.

A seasonal pattern was evident for depths and temperatures occupied by sharks in both regions, but the cycles were parallel for temperature and unrelated for depth (Fig. 5). Mean time-weighted depths varied modestly (by no more than 75 m) across months in the Arctic, with minimum depths evident in the summer. In contrast, mean monthly time-weighted depths in the NW Atlantic varied by up to 240 m across the year, with depth minima in both late winter and late summer; Jan depths were considerably shallower, but reflected that of only a single shark. Mean monthly time-weighted temperatures ranged between 1–4 °C and 5–9 °C in the Arctic and Atlantic, respectively, with temperature maxima in late spring in both regions (Fig. 5).

4. Discussion

Our tagging results indicate that Greenland sharks are a more widely ranging species than was previously suspected (Hansen, 1963; Stokesbury et al., 2005; Fisk et al. 2012; MacNeil et al., 2012). None of the sharks travelled less than 300 km in a 1–2 month period, with the mean distance travelled being 1015 km in about 5 months. The scale of these movements is considerably greater than what has been previously reported. Of the 411 conventional tags applied off the west coast of Greenland by Hansen (1963), all 28 recaptures were made in the coastal waters of Greenland around the tagging site, all but one of which were on the west coast of Greenland. All but two of the tagged sharks moved less than 500 km from the tagging site over periods of up to 16 yr, although two tagged individuals travelled 1100 km before recapture. Since deep-water fisheries offshore of Greenland were less prevalent in the pre-1960 period than they are today, the recaptures reported by Hansen (1963) were likely skewed towards coastal recaptures. In the Gulf of St Lawrence estuary, one of the two sharks tagged with pop-up archival transmission tags (PATs) travelled 115 km upstream of the tagging site over a 2-month period, while the other shark did not leave the tagging site (Stokesbury et al., 2005). More recently, Fisk et al. (2012) reported that most of the 14 sharks tagged with PATs off of Norway remained within a $<$500-km radius of the tagging site for periods of up to 7 months, although one shark travelled 980 km. Working on a closely related species off Alaska, Hulbert et al. (2006) reported that most of the Pacific sleeper sharks (*Somniosus pacificus*) that they tagged with PATs moved less than 100 km from the tagging site, although some moved as much as 500 km.

Although the Greenland shark movements detected in this study were highly directional, their biological significance remains unclear. All of the Arctic sharks were tagged in Cumberland Sound, and all had exited the Sound by the time of tag pop-up. In some cases, this exit must have occurred fairly soon after tagging in the spring. About 500 km from the tagging site, a relatively shallow ridge about 600–650-m deep separates western Davis Strait from eastern Davis Strait (Greenland). Based on tag depth records, shark 44405 must have transited this ridge less than 5 weeks after tagging. Three other tags were also constrained by depth records to have made the ridge transit before August, with deep excursions to $>$1400 m by tags 34524 and 66397 indicating that they must have been in the Davis Strait by August and July, respectively. It is possible that these spring/summer movements out of the Sound were part of a seasonal migration. However, sharks moved out of the Sound both in the spring and in the fall, and the one shark tagged for more than 6 months did not return to the Sound the following year. Therefore, there was no clear evidence of a seasonal migration in the Arctic, leaving open the possibility that Greenland sharks in that region exit the relatively shallow, coastal waters of the Sound as they begin sexual maturation, and spend their adult lives in the deeper waters of the Davis Strait. Such an explanation is consistent with the absence of mature individuals among any of the ~100 Greenland sharks caught in Cumberland Sound since 2005 (A. Fisk, personal communication), and the absence of Greenland sharks of mature size in the coastal waters of Greenland (Hansen, 1963) and Norway (Fisk et al., 2012). Long distance seasonal or spawning migrations have frequently been reported in both pelagic (Campana et al., 2010) and benthic (Walker et al., 2008) sharks in shallower waters, but there are few or no migration studies on deep-water sharks.

The biological significance of the long distance movements made by Greenland sharks in the northwest Atlantic is also unclear, but appears to be different than that driving the long-distance movements of sharks in the Arctic. The Atlantic sharks may have been sexually mature at the time of tagging (based on size), and all moved substantial distances offshore over abyssal waters after tagging. There was no evidence of return, northward migrations either in the winter or the summer, and thus no evidence of a seasonal pattern in migration. A possible explanation is that Greenland sharks migrate offshore over very deep waters to mate and/or give birth. Such a hypothesis would be consistent with the movement patterns of both the Arctic and Atlantic Greenland sharks, as well as with the poor representation of mature individuals in the catches of coastal fisheries. Another possibility is that the larger sharks swim through the deep scattering layer (DSL) of the open ocean to feed, similar to that which has been inferred for other large deep-water shark species. Clearly, more research is required.

The pop-up location of some Greenland sharks over very deep waters in both the Atlantic and the Arctic provided strong evidence of pelagic swimming in both regions. However, the depth records of many of the other tagged sharks all suggested extensive periods in the pelagic zone. Based on tag depth records, shark 44405 must either have swum pelagically or made the transit across the shallow ridge separating western Davis Strait from the Greenland side (which is 500 km from the tagging site) less than 5 weeks after tagging. Three other tags were also constrained by depth records to have made the ridge transit before August, with deep excursions to >1400 m by tags 34524 and 66397 indicating that they must have been in the Davis Strait by August and July, respectively. Of the six sharks that transited the Davis Strait, all showed extensive vertical migrations (of up to 1440 m) in a single 6-h time interval, which is more consistent with swimming in the water column than along a sloped bottom. Although vertical movement alone cannot definitely distinguish between pelagic excursions and movement along sloped bottoms, our results suggest both extended periods of pelagic swimming and short-term vertical excursions into the water column by most or all of the sharks. These results are consistent with the observations of short-term vertical excursions in Greenland sharks recorded by acoustic tag monitoring (Skomal and Benz, 2004; Stokesbury et al., 2005) as well as those inferred by PAT tag recordings (Fisk et al., 2012). Vertical excursions have also been reported in the closely related Pacific sleeper shark (Hulbert et al., 2006).

Diel vertical excursions into the water column were not observed in this study, nor were they observed in the Greenland sharks monitored off of Norway (Fisk et al., 2012). In contrast, marked diel vertical movements were documented acoustically in the shallow waters of the Gulf of St Lawrence and the Arctic, respectively (Skomal and Benz, 2004; Stokesbury et al., 2005), as well as in Pacific sleeper sharks in the Pacific (Hulbert et al., 2006). Diel movements have also been documented in the large, deep-water sixgill shark (Andrews et al., 2009). The absence of diel movements in our study may reflect the generally deeper waters occupied by our tagged sharks.

Our study is consistent with previous observations that Greenland sharks and their congeners are the coldest-dwelling sharks in the world oceans (Bigelow and Schroeder, 1948). Nevertheless, the markedly warmer waters occupied by the Greenland sharks in the Atlantic relative to those in the Arctic was somewhat surprising, and unlike that observed in other studies on Greenland sharks. The mean temperature of 2.7 °C recorded in our tagged Arctic sharks was similar to the mean of 3.8 °C reported by Fisk et al. (2012) for Greenland sharks off Norway, and the range of 0.6–5.0 °C reported by Stokesbury et al. (2005) for sharks in the Gulf of St. Lawrence. However, the mean temperature of 7.9 °C observed in the Atlantic sharks is considerably warmer than that observed elsewhere, while the maximum observed temperature of 17.2 °C was very warm in comparison. Given the probability that at least some of the Atlantic sharks were sexually mature, it is possible that mature Greenland sharks prefer warmer waters than immature sharks. However, it is equally possible that Greenland sharks are not nearly as temperature limited in their distribution as was previously believed, and that Greenland sharks merely prefer to be in colder waters. Although there is no current evidence to suggest genetic isolation between Atlantic and Arctic Greenland sharks, it is conceivable that there are two populations with different temperature tolerances. Whatever the explanation, it is now apparent that Greenland sharks can inhabit very deep waters, and they can inhabit very cold waters, but they do not necessarily have to inhabit deep, cold waters.

In light of the very large distances travelled by all of the Greenland sharks monitored in this study, there would appear to be little potential impediment to mixing of individuals across, or even between entire ocean basins, including from the Arctic to the deep-water tropical zone, along the 5 °C isotherm. Such long-distance movements and mixing would suggest that overfishing or inappropriate management actions in one area could have serious implications for the status of the population throughout its range.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr2.2013.11.001.

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