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A review of Greenland shark (*Somniosus microcephalus*) studies in the Kongsfjorden area, Svalbard Norway

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Abstract Herein, we review and synthesize results from a series of research projects that were conducted to evaluate the role of Greenland sharks (*Somniosus microcephalus*) in the marine ecosystem in Kongsfjorden, Svalbard, Norway. A total of 76 sharks were caught on baited lines during the summers of 2008 and 2009 for these investigations. All of these animals, including the largest shark, a female weighing 700 kg, were sexually immature. Approximately half of the gastrointestinal tracts (GITs, $N = 33$) examined contained seal tissue (42.3 %), and some also contained minke whale (*Balaenoptera acutorostrata*) tissue (18.2 %). Atlantic cod (*Gadus morhua*), Atlantic wolffish (*Anarhichas lupus*) and haddock (*Melanogrammus aeglefinus*) were the dominant fish species consumed by the sharks. These fish species were found in 39.4, 18.2 and 18.2 % of the GITs, respectively. Many of the fishes were swallowed whole, including an Atlantic wolffish weighing 8.6 kg. Satellite pop-up tags deployed on 20 of the sharks showed that they travelled in the water column from the surface to depths greater than 1500 m, encountering temperatures from -1.5° to 7.4° . Accelerometers deployed on six of the sharks showed that they swim extremely slowly, with average speeds of 0.34 m/s and burst speeds of only twice this value. Various types of circumstantial evidence, including the condition of

the seals and fishes found in the sharks' stomachs, indicate that they are not only scavengers, but also active predators of both fish and mammalian prey. Given the swim speed of these sharks, we suggest that the only way they could successfully capture a healthy seal is via cryptically approaching seals that are asleep in the water. Greenland sharks clearly play a significant role as large predators in the Kongsfjorden marine ecosystem, a fact that has been largely overlooked until recently.

Keywords Arctic · Diet · Food web · Marine mammal predator · Pollution · Satellite tracking · Stable isotopes · Swimming performance

Introduction

Greenland sharks (*Somniosus microcephalus*) have been fished in Norwegian waters since before the 17th century (Carlson 1958). Historically, they were caught coastally along the whole Norwegian mainland, but the largest catches were taken in Arctic waters; often in connection with sealing in areas east of Greenland and in Svalbard's coastal waters as well as further to the east in the Barents Sea (Carlson 1958). During several years between 1934 and 1948, more than 1000 tonnes of shark liver oil were delivered from the Arctic catches by Norwegian fishermen, with maximum recordings of 1720 tonnes in 1934 and 1731 tonnes in 1948 (Carlson 1958). Records of annual catches from north and south Greenland in the period from 1900 to 1938 varied between 30,000 and 50,000+ sharks landed (Anon 1942). The Norwegian catches did not report the actual number of animals landed, only the amount of liver (or liver oil) delivered to the marketplace. Using data from Greenlandic catches regarding average liver mass,

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and the fact that on average the oil extracted from the livers accounted for about half of the liver mass (Anon 1942), to estimate the number of sharks caught in Norwegian waters, suggests a catch of approximately 150,000 sharks per year. Using data from Carlson (1958) that suggest that the liver contains about 60 % oil, and the average liver mass from the current study (35 kg, $N = 45$), produces an estimate of 50,000 sharks landed annually in the historical Norwegian catches. Regardless of which estimator is used, it is clear that the catches were extremely high for such a large, slow growing and presumably long-lived fish (Yano et al. 2007; MacNeil et al. 2012). The impacts of these catches on the shark population are not known, but there was no apparent decline in the catches during this period. In 1949, the price paid for Greenland shark oil dropped dramatically and the fisheries on the Norwegian side gradually ceased. There is no commercial fishery for this species in Norway today. Based on the vast, and apparently sustainable, fisheries 60+ years ago and the fact that these sharks have not been targeted for commercial purposes in the Norwegian waters since, it seems reasonable to assume that this species is likely plentiful in the Svalbard area now. However, no attempt has been made to assess the size of the Greenland shark population in the Norwegian Arctic, or elsewhere. The purpose of the research program reviewed herein was to explore whether Greenland Sharks occurred in the Kongsfjorden area, and if so to assess their function in the Kongsfjorden marine ecosystem, with particular emphasis on their potential role as consumers of marine mammals. Two field excursions were dedicated to this research program, the first using a 15-m-long fishing boat, the “Viking Explorer” (June 7–12, 2008) as the research vessel and the second year using the 60-m-long RV “Lance” (June 16–25, 2009). Fishing was conducted in both seasons using longlines (6 mm nylon) with 2 m long stainless steel (3 mm) lead lines and 25 cm long steel hooks (made by Mustad, www.mustad.no), baited with bearded seal (*Erignathus barbatus*) blubber and skin. The distance between each hook was about 50 m, and each line had 25–30 hooks. The lines were set across bathymetric gradients starting at depths of about 60–80 m and ending at depths of about 300 m. The locations of lines that caught sharks during the two seasons are depicted in Fig. 1. A total of 76 sharks were caught during these two field trips; 45 were taken on board, killed and sampled, while 21 were measured (length and girth) and released after being instrumented with various electronic devices. The remaining 10 animals were killed and partially eaten by conspecifics, while they were attached to the lines and could therefore not be included in the studies. The major findings from the various projects within this program are summarized below in this review.

Morphometrics

The average fork length and body mass of the Greenland sharks collected in Svalbard were 296 ± 34 SD cm (range 229–381 cm) and 329 ± 141 kg (range 159–700 kg) for females ($N = 28$), and 273 ± 20 cm (range 231–305 cm) and 250 ± 75 kg (range 136–375 kg) for males ($N = 17$) (see Leclerc et al. 2012 for full details). These sharks are smaller than the largest Greenland sharks reported in the literature (640 cm and 1023 kg), but within the size range most commonly reported (288–504 cm) for the Canadian, Greenland and European Arctic (MacNeil et al. 2012). The females had a significantly longer (two-sample t test, $t = 2.586$ $P = 0.013$) fork length and were heavier (two-sample t test, $t = 2.224$ $P = 0.032$) than the males. Nine of the 10 largest sharks were females (Leclerc et al. 2012). No significant differences were found between the sexes with regard to the intercept (a) or slope (b) of length–body mass relationships for males and females (ANCOVA, intercept $P = 0.4816$, slope $P = 0.36$). The resulting length–body mass equation with the sexes combined was: $BM = 1.109 \times 10^{-6} \times FL^{3.41990}$ ($R^2 = 0.92$) (Fig. 2). The slope of 3.42 ($b > 3.0$) indicates that shape is not uniform throughout development; the relationship is not linear, and the sharks become more rotund for a given length as they become bigger (Leclerc et al. 2012). All of the sharks examined were classified as being sexually immature based on inspection of the rigidity of the males’ claspers and the size of the male’s spurs and in the case of the females the rhipidon characteristics (and the absence of large ova). Yano et al. (2007) suggested that female and male Greenland sharks become sexually mature at >400 and 260 cm, respectively, though he acknowledged that there is significant uncertainty with these values. None of the sharks measured in this study had reached these lengths.

Stomach content analyses

Analyses of the Greenland sharks’ diet were conducted using the following common indices for stomach contents analyses: (1) frequency of occurrence ($\% F = (F_i / F_t) \times 100$, where F_i is the number of sharks with a particular prey item i , and F_t is the total number of nonempty GITs); (2) the numerical proportion of each countable prey type in the diet ($N_i \% = (N_i / N_t) \times 100$, where N_i is the total number of a particular prey type i and N_t is the total number of prey items); and (3) the percentage of each prey item in terms of biomass ($B \% = (B_i / B_t) \times 100$, defined as total reconstructed biomass B_i of an estimated prey type i divided by the total of biomass for all prey types B_t (= reconstructed biomass for fish and cephalopods and the biomass as found for the other prey items—see Leclerc

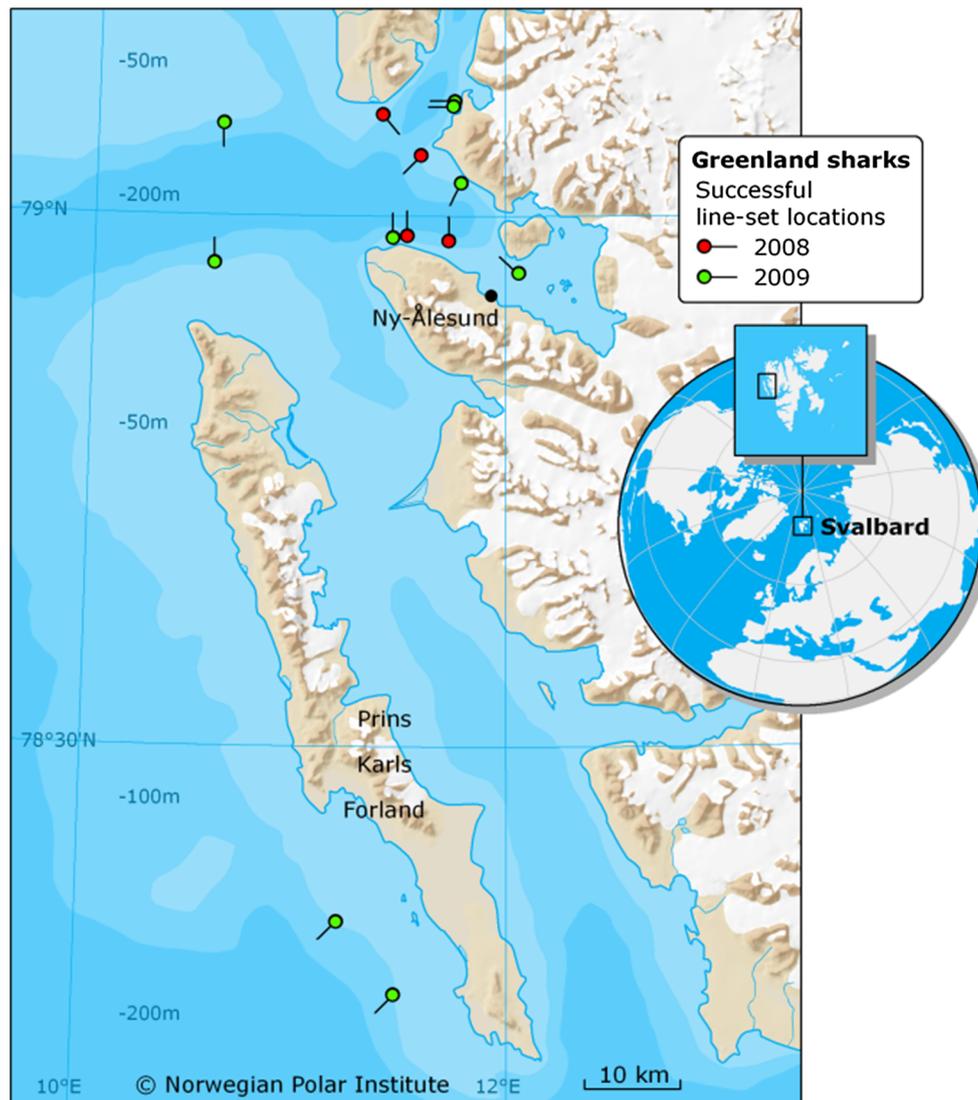


Fig. 1 Distribution of successful line-set locations for Greenland sharks caught during 2008 (red circles) and 2009 (green circles) in Svalbard, Norway. The circle represents the start point of the fishing

line, and the line attached to the circle the direction it was set. Modified from Leclerc et al. (2012)

et al. 2012 for more details). The overall composition of the diet was expressed using an index of relative importance (IRI) defined by Cortés (1997) and Pinkas et al. (1971) as: $IRI = ((\% N + \% B) \times \% F)$. The IRI was expressed as a percentage, where % IRI for n prey types at the given identified taxonomic levels is defined as $\% IRI_i = 100 IRI_i / \sum_{i=1}^n IRI_i$ (Cortés 1997; Liao et al. 2001).

Twelve (26.7 %) of the 45 gastrointestinal tracts (GITs) collected were empty and excluded from further analysis. Most of the Greenland sharks had consumed various species of fish (Table 1), some of which were whole specimens in various stages of digestion. The incomplete bony fishes were identified based on otoliths, while elasmobranch fish species were identified based on their dermal

denticles (see Leclerc et al. 2012 for more details on this methodology and also for details regarding the identification of invertebrates). Fish are a common food type found in Greenland sharks stomachs from other locations in the Arctic and North Atlantic (see MacNeil et al. 2012 for a summary).

The most important fish species found in the Greenland shark diet in Svalbard was Atlantic cod (*Gadus morhua*, 55.8 % IRI) followed by Atlantic wolffish (*Anarhichas lupus*, 10.2 % IRI) and then haddock (*Melanogrammus aeglefinus*, 5.4 % IRI) (Table 1). Other bony fish species found in the shark GITs included spotted wolffish (*Anarhichas minor*), redfish (*Sebastes* spp.) and American plaice (*Hippoglossoides platessoides*). Additionally, two species

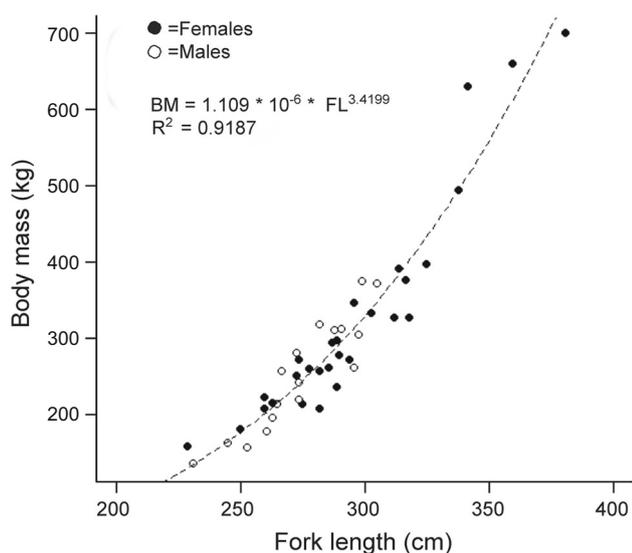


Fig. 2 Relationship between fork length and body mass for Greenland sharks ($N = 45$) caught in June 2008 and June 2009 in Svalbard, Norway. Filled circles females, open circles males. From Leclerc et al. (2012)

of elasmobranchs were identified (starry rays *Raja radiata* and Greenland sharks). Several specimens of Atlantic cod and Atlantic wolffish were found as almost intact specimens, with the skin still attached; these had been swallowed whole. The largest whole fishes found in the Greenland shark stomachs were an Atlantic wolffish that was 85 cm long and had a body mass of 8.6 kg, and an Atlantic cod that was 77 cm long, with a body mass of 4.2 kg.

The most numerous invertebrates found in the shark GITs were the boreoatlantic armhook squid (*Gonatus fabricii*, 4.2 % IRI) and the great spider crab (*Hyas araneus*, 0.4 % IRI) (Table 1). The other invertebrates found in the GITs, such as polychaetes, gastropods, small bivalves and echinoderms, were thought to be secondary prey items released from the stomachs of consumed fish or seals, or animals accidentally ingested while feeding on benthic fish. A similar array of invertebrates has been reported in the stomachs of Greenland sharks from other parts of their range (see MacNeil et al. 2012 for details).

Tissue samples from various marine mammals found in the Greenland sharks stomachs were determined to species level using genetic analysis when enough tissue was present (see Leclerc et al. 2012 for details). Whale tissues were found in 18.2 % of the GITs that contained food, while seal tissues were found in 36.4 % of the GITs with contents (Table 1). All of the whale pieces that were in good enough condition for genetic identification were confirmed to be from minke whales (*Balaenoptera acutorostrata*). The most important mammalian species in the sharks' diet was ringed seals (*Phoca hispida*—16.0 % IRI),

Table 1 Composition of the diet of the Greenland shark collected in Svalbard, Norway, June 2008 and 2009 ($n = 33$, frequency of occurrence (% F), total prey by number (% N), total reconstructed biomass (% B) and index of relative importance (% IRI). From Leclerc et al. (2012)

Prey item	% F	% N	% B	% IRI
Mollusca				
Bivalvia sp.	6.1	1.4	<0.1	0.2
Gastropoda sp.	12.1	7.0	<0.1	1.7
Cephalopoda				
<i>Gonatus fabricii</i>	27.3	7.6	<0.1	4.2
Echinodermata				
Ophiuroidea				
<i>Ophiopholis aculeata</i>	6.1	1.4	<0.1	0.2
Ophiuroidea spp.	12.1	4.9	<0.1	1.2
Echinoidea				
<i>Strongylocentrotus droebachiensis</i>	6.1	1.4	<0.1	0.2
Gorgonocephalidae sp.	3.0	0.7	<0.1	<0.1
Crustacea				
Malacostraca	30.3	–	<0.1	–
Amphipoda	6.1	2.1	<0.1	0.3
Decapoda				
<i>Hyas araneus</i>	9.1	2.1	0.1	0.4
Polychaeta sp.	6.1	2.1	<0.1	0.3
Pisces				
Chondrichthyes				
<i>Raja radiata</i>	18.2	1.4	0.5	0.7
<i>Somniosus microcephalus</i>	3.0	0.7	<0.1	<0.1
Osteichthyes				
Anarhichadidae				
<i>Anarhichas lupus</i>	18.2	7.6	20.1	10.2
<i>Anarhichas minor</i>	3.0	0.7	1.3	0.1
Anarhichas sp.	3.0	0.7	–	–
Gadidae				
<i>Gadus morhua</i>	39.4	21.0	49.1	55.8
<i>Melanogrammus aeglefinus</i>	18.2	7.6	7.1	5.4
Gadidea sp.	21.2	7.0	–	–
Pleuronectidae				
<i>Hippoglossoides platessoides</i>	3.0	0.7	0.4	0.1
Pleuronectidae sp.	3.0	0.7	–	–
Scorpaenidae				
<i>Sebastes marinus</i>	6.1	1.4	0.5	0.2
<i>Sebastes</i> spp.	3.0	0.7	–	–
Unidentified osteichthyes	12.1	3.5	–	–
Mammalia				
Phocidae				
<i>Erignathus barbatus</i>	3.0	0.7	0.5	<0.1
<i>Pusa hispida</i>	30.3	8.3	17.7	16.0
<i>Cystophora cristata</i>	3.0	0.7	<0.1	<0.1
Unidentified phocidae	6.0	1.4	0.8	0.3
Balaenidae				
<i>Balaenoptera acutorostrata</i>	18.2	4.9	1.7	2.4

followed by minke whales (2.4 % IRI), bearded seals (*Erignathus barbatus*) and hooded seals (*Cystophora cristata* –both <0.1 % IRI) (Table 1). Four of the sharks had consumed at least two different seals. This was determined in one case by two different mitochondrial haplotypes from the same seal species being identified, in two cases two different seal species were present, and in another case adult ringed seal claws were found in the same stomach that contained a whole white-coated pup. Based on growth zones in the claws of the fore-flippers of ringed seals (McLaren 1958) ($n = 6$), the sharks had consumed four ringed seals that were less than 1 year old and two adult ringed seals that were at least 8 and 9 years old, respectively. Body size of the sharks did not have an influence on whether or not their GITs contained seal tissues ($P = 0.78$, t test, 2-tailed for unequal sample sizes). Only, one seal sample appeared to be associated with scavenging; this body was accompanied by brittle stars in the sharks stomach. Reports of marine mammal tissues in the stomachs of Greenland sharks, with and without scavenging invertebrates, are common from throughout their range (Fisk et al. 2002; MacNeil et al. 2012).

The high occurrence of minke whale blubber in the GITs of the Greenland sharks in Svalbard warranted some special attention, given that some species of sharks do attack whales (such as the cookie-cutter shark, *Isistius brasiliensis*), though it seemed unlikely that such a slow shark could catch such fast prey. The Norwegian DNA register for all whales taken in the annual commercial minke whale harvest (since 1996, containing some 10,000 specimens) provided the answer (LeClerc et al. 2011). In all cases, the blubber found in the sharks' stomachs could be traced back to whales in the DNA register. During the whaling operations, the blubber is thrown overboard; it floats at the surface making it available for various scavengers, which clearly includes Greenland sharks given the results of the LeClerc et al. (2011) study. The whale tissue found in the various Greenland sharks stomachs could be traced back to five individual minke whales: two that were harvested in Kongsfjorden and three that were harvested further south on the west side of Svalbard. The largest distance between the collection points of the whale and those of the shark containing its tissues was about 100 km (LeClerc et al. 2011). The whales had all been harvested 2–3 weeks before the sharks were captured.

A recent review of Greenland shark diet concluded that this shark is a generalist feeder that targets both benthic and pelagic organisms (MacNeil et al. 2012). It is well established that Greenland sharks are scavengers; however, increasing amounts of circumstantial evidence suggests that it is also an active predator of both seals and fast-swimming fishes. Most of the seal and fish contents in the shark stomachs in Svalbard were intact specimens that

were not associated with carnivorous invertebrates that normally attack any dead animal as soon as it reaches the seafloor (LeClerc et al. 2012; Nielsen et al. 2014). Additionally, there are records of bleeding, newly dead seal corpses on beaches at Sable Island off eastern Canada that had corkscrew wounds that have been attributed to Greenland shark attacks (Lucas and Natanson 2010). Some recent investigations are, however, challenging this suggestion, and instead attributing these wounds to anthropogenic sources (Bexton et al. 2012) or to attacks by gray seal (van Neer et al. 2015). There is similar circumstantial evidence suggesting that close relatives of Greenland sharks actively prey on both seals and fast-swimming fishes. The Pacific sleeper shark (*S. pacificus*) has been documented to consume live, fast-swimming Pacific salmon (*Oncorhynchus* spp) (Sigler et al. 2006). Additionally, the Antarctic sleeper shark (*S. antarcticus*), which is closely related to or possibly even the same species as *S. pacificus* (Murray et al. 2008), have left bite wounds on live southern elephant seals (*Mirounga leonina*), presumably during predation attempts (van den Hoff and Morrice 2008). Another line of evidence that suggests that these sharks attack sleeping mammalian prey comes from a study using life history transmitters on juvenile Steller sea lions (*Eumetopias jubatus*). In this otariid study, seals were eaten by a cold-blooded predator (Horning and Mellish 2014), and the only one in the region that is large enough to be suspect is the Pacific sleeper shark. All these observations suggest that sleeper sharks, including the Greenland shark, are active predators. Given the high rate of occurrence of seals and fast-swimming fishes, and the condition of the material in the stomachs of sharks from Kongsfjorden, it is unlikely that all of these prey items are the result of scavenging.

Dietary studies employing stable isotopes and fatty acid analysis

To further explore the ecological role of the Greenland sharks in Kongsfjorden, shark muscle and blood plasma samples were analyzed for stable isotopes (SI) of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) and fatty acid (FA) analyses (McMeans et al. 2013). For comparative reasons, samples obtained from sharks in Cumberland Sound were included because sharks at this Canadian site are known to eat a lot of Greenland halibut (*Reinhardtius hippoglossoides*). Based on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, it was shown that the Greenland sharks in Kongsfjorden fed at a higher trophic position (4.8) than the Cumberland Sound sharks and that most (70 %) of their carbon was derived from phytoplankton-based food chains (McMeans et al. 2013). These results are consistent with a heavy reliance on pelagic fishes and seals, and they support the findings from the

stomach content analyses (described in the section above). The Greenland sharks from Kongsfjorden had FA profiles in both muscle and plasma (e.g., low 20:1n-9, high 22:5n-3) that suggested a low proportion of Greenland halibut and high proportion of gadoids and seals in their diet compared to Greenland sharks sampled in Cumberland Sound. The high proportions of seal FAs in both slow (muscle) and fast (plasma) turnover tissues indicate that trophic interactions between Greenland sharks and seals are a common occurrence in Kongsfjorden, i.e., seals are a regular part of the shark diet. The results suggest that Greenland sharks likely play a significant role in Arctic marine food webs as a top predator of fishes and marine mammals.

Persistent Organic Pollutants (POPs)

Based on their suspected longevity alone, but also on their trophic position in the food web (described above), it was expected that the Greenland sharks in Kongsfjorden would have high levels of various persistent organic pollutants. One study within this Greenland shark research program explored the association between POPs and vitamins A and E (Molde et al. 2013), since POPs have been shown in other studies to interfere with vitamins A and E homeostasis in fish (Palace et al. 1997). POPs in the plasma of the Greenland sharks from Svalbard were found to be extremely high (Table 2); they were actually the highest values reported to date for any marine animal from the Svalbard region, including being higher than levels found in polar bears (*Ursus maritimus*) and white whales (*Delphinapterus leucas*) (see Molde et al. 2013 for more details). Significant inverse relationships were found between retinol (a Vitamin A) concentrations and concentrations of the dioxin-like compounds PCB-118 and PCB-156/171, and the nondioxin-like compounds PCB-99 and PCB-128. There were also significant inverse relationships between retinol palmitate (another Vitamin A) and several POP compounds, and significant positive associations including those between α -tocopherol (a Vitamin E) and several PCB congeners (Molde et al. 2013). The plasma levels of POPs in Greenland sharks from

Svalbard appear to have higher POP contaminant levels compared to Arctic Canada (Table 2; versus Fisk et al. 2002; Molde et al. 2013) and Iceland (Strid et al. 2007), but similar to those that have been found in sharks from northeast Greenland (Corsolini et al. 2014). Since Molde et al. (2013) was a correlative study, the potential interplay between POPs and vitamin dynamics, and the potential consequences of the high POP levels in the sharks, must be interpreted with caution, pending further research.

In another study, PCBs chiral signatures were measured in Greenland sharks and their potential prey in Arctic marine food webs in Kongsfjorden and from Cumberland Sound (Canada) to assess temporal and spatial variation in PCB contamination at the stereoisomer level (Lu et al. 2014). Marine mammals had species-specific enantiomer fractions (EFs), likely due to a combination of in vivo biotransformation and direct trophic transfer. Greenland sharks from Cumberland Sound collected in 2007–2008 had similar EFs to those from sharks collected a decade ago in the same location (PCBs 91, 136 and 149) and also similar to their conspecifics from Svalbard for some PCB congeners (PCBs 95, 136 and 149). However, other PCB EFs in the sharks varied temporally (PCB 91) or spatially (PCB 95), suggesting possible spatiotemporal variation in the diet of the sharks, since biotransformation capacity is unlikely to have varied within this species from region to region or over the time frame studied.

Satellite tracking

In an effort to gather information on movements and habitat preferences of the Greenland sharks in the Svalbard area, 20 individuals were instrumented with Pop-off Archival Tags (Mk-10 pop-up archival transmitting tags (PATs), Wildlife Computers, Redmond, WA, USA) (Fisk et al. 2012). The PATs were secured to the sharks by inserting a nylon umbrella dart approximately 10 cm into the dorsal muscle just lateral to the first dorsal fin. The umbrella tip was attached to the PAT with a monofilament leader (400-lb test). For more details on animal handling procedures, see Fisk et al. (2012). The PATs were programmed to record depth (± 0.5 m), temperature (± 0.1 °C) and light intensity at 10-s intervals for a preset period ranging from 3 to 12 months. The data were internally binned within 6-h intervals, and the summarized data were transmitted to an Argos satellite when the tag floated up to the surface after release of the PAT from the shark. Binned data included minimum, maximum and mean depth, temperature and light level for each 6-h period. In 2008, PATs were programmed to release from the shark if a constant depth was maintained for a period of 96 h (which might indicate that a shark had died or if the instrument reached a

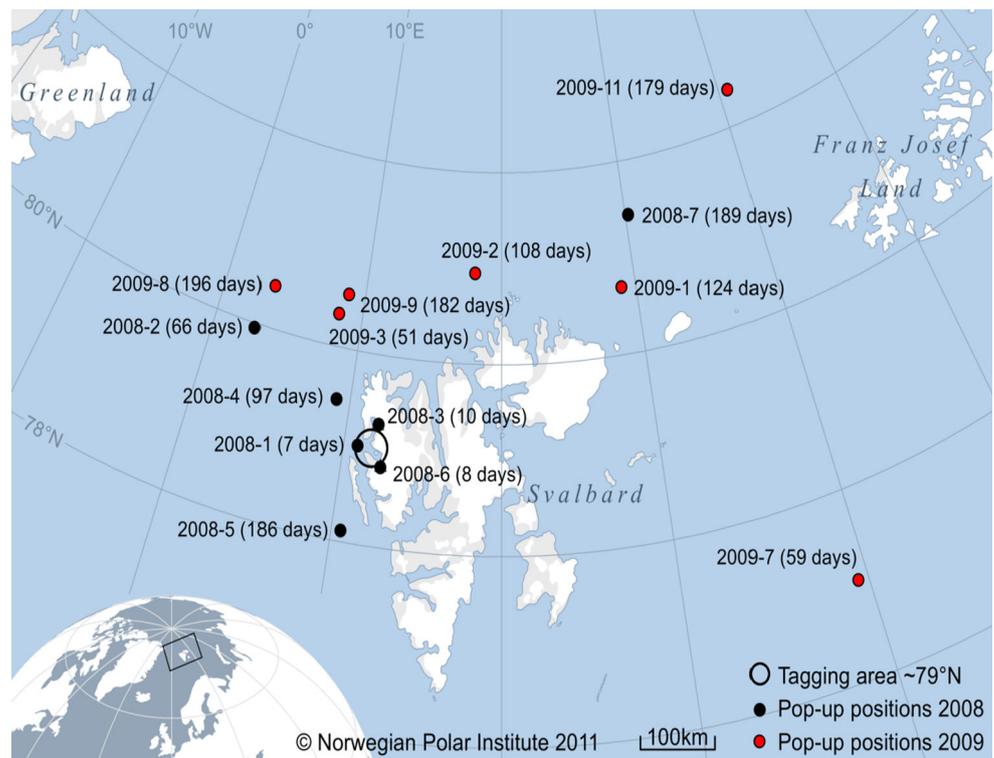
Table 2 Concentrations of various contaminants measured in plasma of Greenland sharks collected in the Kongsfjorden area, Svalbard. From Molde et al. (2013)

	Mean	SD	Range
Plasma \sum PCB	5766	3716	1344–16,106
Plasma \sum Chl	1551	1152	323–5756
Plasma \sum DDT	8069	8793	900–59,707

Values are in ng/g lipid

PCB polychlorinated biphenyls, DDT dichlorodiphenyltrichloroethanes, Chl chlordanes)

Fig. 3 Tagging location (open black circle), pop-off locations and number of tracking days for 14 Greenland sharks tagged with pop-off archival satellite tags in June 2008 and 2009 in Kongsfjorden, Svalbard, Norway. From Fisk et al. (2012)



depth of 1500 m (which is the maximum nominal safe depth for the tag). This function was not used in 2009.

Fourteen of the 20 tags reported data; the six that failed to do so likely popped off under sea ice. Most of the tagged sharks had moved north from the tagging area in Kongsfjorden. They had travelled a range of distances that was not directly correlated with the duration of the tracking record (Fig. 3). Most tags popped off less than 500 km from the tagging site; the average daily distance travelled ranged from 0.6 to 16.6 km/d. Total distances travelled, measured as the shortest line between the tagging site and the pop-off location (without crossing land), suggested that animal 2009-7, which travelled 980 km in 59 days (Fig. 3), performed the longest trip.

The tagged Greenland sharks swam within a wide range of water depths, but mainly occupied the top 150 m of the water column (Fig. 4). This is in contrast to Greenland sharks tagged in the Canadian Arctic or on the coast of Nova Scotia, Canada, which swam at mean depths of 367 ± 4 m (range 84–959 m) and 949 ± 10 m (144–1816 m), respectively (Campana et al. 2015). These different average depths are consistent with dietary differences in these areas. Svalbard sharks tend to eat more air-breathing marine mammals, and they also tend to occupy shallower waters, while deep swimming sharks in Canada eat more deep-dwelling benthic fishes. About one-third of the Svalbard Greenland sharks approached the surface at some point in their data record (0–8 m), and in the other extreme one shark reached a depth of at least

1560 m (which engaged the release mechanism on the tag). The average swimming depth increased from summer though autumn and winter in Svalbard waters (see Fisk et al. 2012 for more details).

The temperatures of the water masses occupied by the Greenland sharks tagged in Svalbard ranged from -1.5 to 7.4 °C, but most temperature measurements were between 3 and 5 °C (Fig. 4), with an average of 3.8 ± 1.4 °C. These temperature data were similar to that recorded by sharks in the Canadian Arctic (Campana et al. 2015). Only one PAT (shark 2009-2) reported sub-zero temperatures (including the low of -1.5 °C). There were in fact very few temperatures reported below 0.5 °C; however, most individuals experienced a temperature of 0 °C at some point in their data records. The average temperatures of the water masses the sharks occupied decreased from summer though autumn and winter (see Fisk et al. 2012 for more details), which might be linked to the season depth patterns displayed by the sharks; perhaps they stay in favoured temperatures by increasing their depth in winter. The movements displayed by the tagged Greenland sharks suggest that this species likely ranges broadly in northern waters and likely hunts throughout the entire water column.

Swimming behavior

In order to examine the swimming behavior of this apparently lethargic shark species, seven individuals were instrumented with data-logging tags (W1000-PD2GT,

Fig. 4 Depth and temperature records (mean \pm SE) for Greenland sharks tagged with pop-off archival satellite tags in Kongsfjorden, Svalbard, Norway, in June 2008 and 2009. It should be noted that y-axes (temperature and depth) are different between the two graphs. From Fisk et al. (2012)

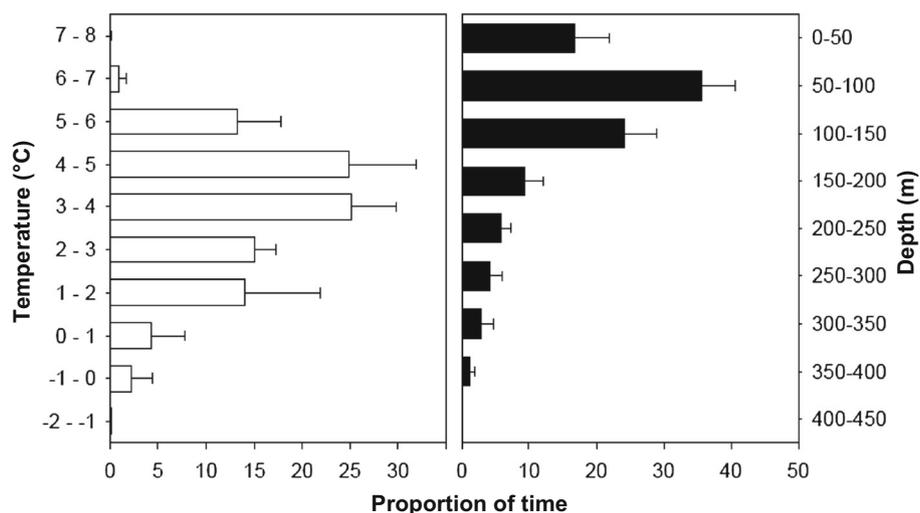


Fig. 5 A Greenland shark released in Kongsfjorden, Svalbard, Norway, after being equipped with an accelerometer (red box) and a pop-off archival satellite tags (gray tubular instrument further back on the shark). The shark is a female with fork length of 3.14 m and estimated body mass of 343 kg. Photograph: Armin Mück, NRK

Little Leonardo Co, Tokyo, Japan). These data loggers recorded swim speed, depth, temperature and lateral and longitudinal acceleration with very high resolution (see Watanabe et al. 2012 for more details). The loggers were attached to an instrument recovery package that included a timer for release, a float and a VHF transmitter (Fig. 5) to facilitate recovery when the package floated at the surface following release. A 24-h deployment period was chosen, and six of the seven loggers were retrieved. Sharks bearing accelerometers experienced water temperatures between 2.6 and -1.2 °C (see Watanabe et al. 2012 for more details). The instrumented sharks swam at a wide range of depth (<273 m), and all of the sharks displaying movements between various depths, going to depth and then returning to shallower water again. The mean overall depth of swimming was 86 m. Swim speed was not recorded for the first two sharks (Table 3, sharks A and B), because the sampling interval was set to an interval that was too short for actual swim speed of the sharks (i.e., the propeller did

not move enough between samples to make an accurate recording). The interval was adjusted in later deployments (to 1 or 2 s), and the other four sharks (C–F) did successfully record swimming speed. The total mean speed was 0.34 m/s (Table 3). However, many of the recorded values were below the stall speed of the propeller sensor (0.17 m/s); this occurred during 57, 60 and 55 % of the records for sharks C, D and E, respectively. Tail beats were continuous throughout the deployment time (see f. inst. Figure 6a), except for short periods of gliding behavior during descent in three of the sharks. The dominant tail-beat frequency over the whole record for each of the sharks was within the range 0.14–0.16 Hz (Table 3). This means that it takes about 6.5 s for the tail to move from one side over to the other side and back again. “Burst” swimming events were observed in sharks C and F, with speeds up to 0.54 and 0.73 m/s achieved, with tail-beat frequencies up to 0.27 and 0.26 Hz and positive (i.e., upward) pitch angles up to 28° and 18°, respectively, for these two animals (see Fig. 6b for these parameters for shark F). Mean accelerations during these “bursts,” calculated as peak speed minus start speed divided by the duration of acceleration, were 0.0067 and 0.0086 m/s² for sharks C and F, respectively. For comparison, these parameters were compiled for 16 species of wild fishes based on values in the literature for species with body masses ranging from 0.2–3900 kg (Watanabe et al. 2012). Greenland sharks were found to have the lowest mass-specific swim speed, and the lowest tail-beat frequency among the fishes compared, regardless of whether body size was accounted for or not (Watanabe et al. 2012). The stride length (0.8) measured for the Greenland sharks (Table 3) is within the “normal” range for pelagic fish species, so it is the tail-beat frequency that is abnormally low, and which causes this fish to be an extraordinarily slow swimmer (Watanabe et al. 2012).

Table 3 Descriptive information and swimming data from 6 Greenland sharks instrumented with data loggers in Kongsfjorden, June 2009. Modified from Watanabe et al. (2012)

Fish ID	Sex	Body mass (kg)	Swim speed (m/s)		Tail-beat frequency (Hz)	Stride length
			Mean	Max		
A	M	312	–	–	0.14	–
B	M	283	–	–	0.16	–
C	M	207	0.31	0.54	0.13	0.84
D	F	204	0.34	0.54	0.14	0.80
E	F	343	0.32	0.58	0.14	0.74
F	M	228	0.37	0.73	0.16	0.83
Mean		263	0.34	0.60	0.15	0.80

Body mass is estimated from length and girth measurements. Stride length is how far as proportion of body length the shark travels with a single tail-beat cycle

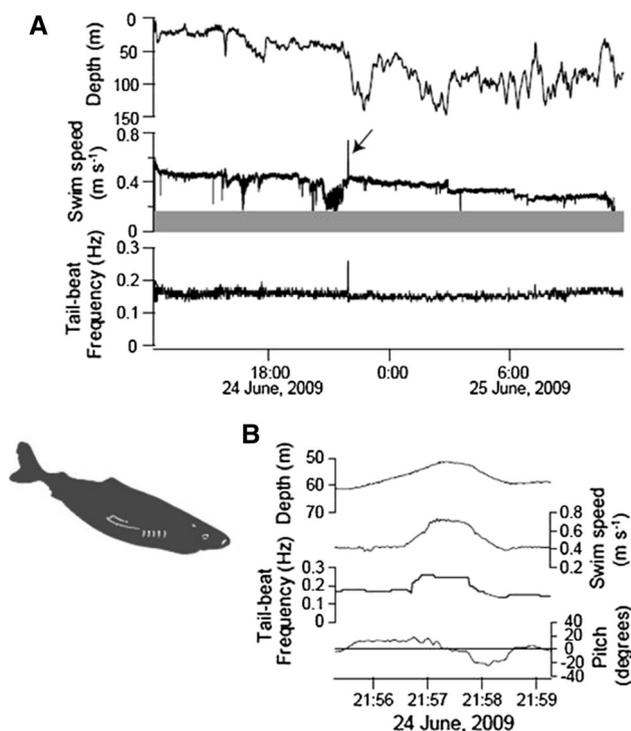


Fig. 6 Examples of various aspects of the swimming behavior of individual Greenland sharks. **a** A ~ 24-h record of depth, swim speed, and tail-beat frequency for shark F. The arrow indicates a burst swimming event, and the gray horizontal bar represents the stall speed of the speed sensor (0.17 m/s). **b** Depth, swim speed, tail-beat frequency and pitch (i.e., angle between long axis of shark's body and water surface, with positive values indicating ascent and negative descent) during the burst swimming event indicated by the arrow in (a). From Watanabe et al. (2012)

The mean and maximum swimming speed recorded for Svalbard Greenland sharks and also the accelerations during “bursts” of swimming are much lower than those recorded for various seal species that were recorded in the diet of the sharks in this region (for details, see Watanabe et al. 2012). The question then arises as to how these slow swimming sharks can catch live seals and fast-swimming fish species.

One thing in their favor in this regard is their cryptic coloration. It is likely that this helps the sharks approach live prey to close distances undetected. Then, at close distances their large buccal cavity creates suction power when the mouth opens that helps them to draw in prey. This likely also explains why so many prey items are found as whole specimens in the sharks' stomachs, even larger fish and smaller seals. However, it still seems unlikely that the sharks are able to get close enough to suck in an alert seal. It seems logical that predation events take place when the seals are sleeping. Phocid seals, including all the seal species found in the Greenland shark stomachs in the Kongsfjorden area, sleep in the water (Ridgway et al. 1975; Lyamin 1993) at the surface, in the water column and on the sea floor (exactly where in the water column they float is more or less determined by their body condition, i.e., buoyancy). Phocid seals exhibit bilaterally symmetrical sleep, similar to terrestrial mammals, and are thus immobile, and their eyes are closed (Ridgway et al. 1975; Lyamin 1993). In the Svalbard area sleeping in the water column gets seals out of reach from their primary predator, the polar bears (*Ursus maritimus*), which hunt them on the ice. But, it does make them vulnerable to predation by Greenland sharks. Given the very high mortality rates seals in Svalbard experience due to polar bears on the surface of the ice, and shark exposure in the water is almost certainly a lesser concern.

Conclusions

The main objective of this program was to explore the Greenland sharks' potential role in the marine ecosystem in Kongsfjorden, Svalbard. Based on historical catch statistics, the fact that no commercial harvesting has taken place for more than 50 years, and the ease with which a large number of sharks was caught in the area in this study, this shark species is likely an abundant species in the Kongsfjorden ecosystem. Diet studies revealed that Greenland sharks in this area mainly consumed large fish of a variety of species

as well as various seal species. The condition of the prey found in the sharks' stomachs, combined with other circumstantial evidence, strongly suggests that Greenland sharks are not only scavengers but also active predators. The novel findings from this small series of studies indicate that further study of this Arctic shark is clearly warranted.

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