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ORIGINAL PAPER

A missing piece in the Arctic food web puzzle? Stomach contents of Greenland sharks sampled in Svalbard, Norway

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Abstract Harbour seals in Svalbard have short longevity, despite being protected from human hunting and having limited terrestrial predation at their haulout sites, low contaminant burdens and no fishery by-catch issues. This led us to explore the diet of Greenland sharks (*Somniosus microcephalus*) in this region as a potential seal predator. We examined gastrointestinal tracts (GITs) from 45 Greenland sharks in this study. These sharks ranged from 229 to 381 cm in fork length and 136–700 kg in body mass; all were sexually immature. Seal and whale tissues were found in 36.4 and 18.2%, respectively, of the GITs that had contents ($n = 33$). Based on genetic analyses, the dominant seal prey species was the ringed seal (*Pusa hispida*); bearded seal (*Erignathus barbatus*) and hooded seal (*Cystophora cristata*) tissues were each found in a single shark. The sharks had eaten ringed seal pups and adults based on the presence of lanugo-covered prey (pups) and age determinations based on growth rings on claws ($\leq$1 year and adults). All of the whale tissue was from minke whale (*Balenoptera acutorostrata*) offal, from animals that had been harvested in the whale fishery near Svalbard. Fish dominated the sharks' diet, with Atlantic cod (*Gadus morhua*), Atlantic wolffish (*Anarhichas lupus*) and haddock (*Melanogrammus aeglefinus*) being the most important fish species. Circumstantial evidence suggests that these sharks actively prey on seals and fishes, in addition to eating carrion such as the whale tissue. Our study suggests that Greenland sharks may play a significant predatory role in Arctic food webs.

Keywords Arctic · Diet · Pinnipeds · Predator · Seals · *Somniosus microcephalus*

Introduction

Greenland sharks (*Somniosus microcephalus*) are cold-water adapted fishes that mainly inhabit the North Atlantic and Arctic region (Compagno 1984). This species is generally described as an opportunistic scavenger (Beck and Mansfield 1969; Fisk et al. 2002). Many different prey species have been found in the stomach of these sharks, including crustaceans, cephalopods, various fish species and marine mammals (Ridoux et al. 1998; Fisk et al. 2002; Yano et al. 2007; McMeans et al. 2010). Stomach content analyses, conducted in West Greenland and Icelandic waters, have shown that Greenland sharks in these areas mainly consume various fish, such as Greenland halibut (*Reinhardtius hyppoglossoides*), Arctic cod (*Boreogadus saida*), Atlantic cod, redfish (*Sebastes* spp.), Atlantic wolffish and the starry ray (*Raja radiata*) (Yano et al. 2007;

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McMeans et al. 2010). But in addition, the Greenland shark's diet is also known to include a variety of seal species, such as hooded seals, harbour seals (*Phoca vitulina*), bearded seals and ringed seals (Fisk et al. 2002; Yano et al. 2007). Stable isotope analyses and contaminant metabolite levels place Greenland sharks at a high position in Arctic food webs, suggesting that Greenland sharks feed on prey that is similar to other Arctic top predators (Cortés 1999; Fisk et al. 2002). However, this is somewhat at odds with the general description of this slow-moving, benthic shark that has been thought to feed largely on carrion.

Our interest in this shark species arose in connection with its possible impacts on the worlds' northernmost population of harbour seals, which reside on the west coast of Svalbard (Prestrud and Gjertz 1990). This small, genetically distinct population consists of about 2,000 individuals (Andersen et al. 2011; Lydersen and Kovacs 2011). A comprehensive study of this population revealed that the longevity of harbour seals in Svalbard was short compared with other harbour seal populations (Thompson et al. 2001; Lydersen and Kovacs 2005). This was surprising since this small population is protected from hunting, exposed to insignificant levels of surface predation, and has no known fishery-related mortality and low contaminant burdens compared with harbour seals from lower latitudes (Wolkers et al. 2004). However, potential marine predators, such as the Greenland shark, have not previously been considered with respect to this High Arctic harbour seal population (Lydersen and Kovacs 2005).

Little is known about the biology of Greenland sharks in the Svalbard area, despite the fact that there was an extensive fishery for this species that started at the beginning of the 1900s and went until the end of the 1940s. The oil from Greenland shark livers was valuable during this time, and Greenlandic and Norwegian fisheries caught over 100,000 sharks annually (Hoel 1949). Since the shark fishery ended, there has been no fishing for this shark in the Svalbard area, though some animals were caught as by-catch in shrimp trawls until the early 1980s when the use of grids in front of trawl openings reduced this source of shark mortality (Hop et al. 2002). Nothing is known about the number of Greenland sharks in the Svalbard area; however, it is reasonable to assume based on the sustained high numbers caught in the past, followed by many decades with very limited fishery-related mortality, that this shark species is likely very abundant in this area. Thus, in this study, we sought to find out whether Greenland sharks might have an impact on the harbour seal population in Svalbard, via exploring the diet of these sharks with special attention to their potential role as marine mammal predators.

Materials and methods

Field work

We conducted field work in Kongsfjorden, Krossfjorden and on the west coast of Prins Karls Forland (Fig. 1) from 5–12 June 2008 to 15–25 June 2009. We fished for Greenland sharks using long-lines (6 mm nylon) with 2.0-m-long stainless steel lead lines (3 mm) and large (25 cm long) steel hooks baited with bearded seal blubber and skin. The distance between hooks was approximately 50 m and each line consisted of 20–35 hooks. We set the lines across bathymetric gradients starting at depths of about 60–80 m and ending at depth of about 260–300 m. Weather permitting, the long-lines were generally pulled after 2 days in 2008 and after 1 day in 2009. In 2008, we used a 15-m-long fishing boat, the "Viking Explorer". Hooked sharks were taken off the long-line by hand; a strap was placed around the pectoral fins and the shark was lifted onboard with a winch. In 2009, we conducted the research from a 60-m-long research vessel, RV "Lance", and the sharks were brought on deck with a winch using a custom made sling-bed to avoid potential regurgitation of stomach contents and handling discomfort to the sharks.

On board the boat(s), we weighed the sharks using a digital weighing cell (±1 kg), bled them (for other studies) and then killed them via cutting through the spinal cord immediately behind the head and bleeding the gills. When eye reflexes had ceased, we measured total length and fork length to the nearest cm. The sex was determined and

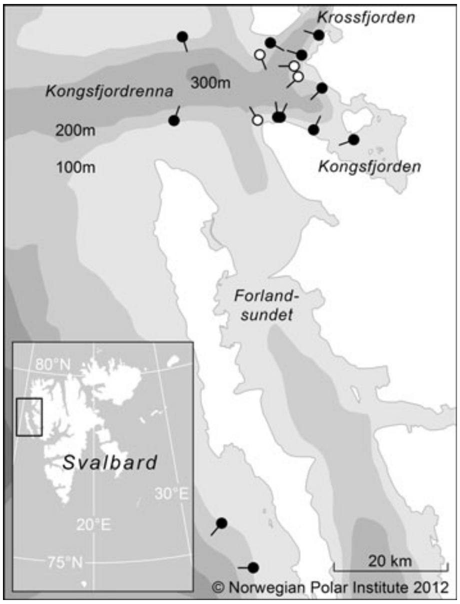

Fig. 1 Distribution of successful line-set locations for Greenland sharks ($n = 45$) caught during June 2008–2009 (*open symbols* 2008, *closed symbols* 2009) in Svalbard, Norway

sexual maturity status was assessed. For males, this was based on three criteria: the degree of rigidity of the claspers proximal to the head, the ease with which the basal part of the claspers rotated, and the degree of development of the rhipidion; assessment of maturity of females was based on the presence or absence of large ova in the oviduct (Clark and von Schmidt 1965).

Following external morphological measurements, we opened the abdominal cavity and removed the entire gastrointestinal tract (GIT). Then, we tied off gastrointestinal segments (tightly) with cotton string to keep their contents separate. We kept the GIT contents frozen (−20°C) until they were analysed.

Laboratory analyses

In the laboratory, we weighed the contents of each GIT to the nearest g and subsequently sorted the material into major taxonomic groups. We identified large prey items and stored them in a freezer; the rest of the stomach contents were filtered through two sieves with mesh sizes of 2 mm (top) and 1 mm (bottom). We found some otoliths loose in the GITs, but extracted others using the methods described in Secor et al. (1992) based on the species and size of the fish. Otoliths were preserved in a mixture of 1:1:1 glycerine, ethanol and distilled water to preserve their length. We preserved small animals and mammalian tissues in 96% ethanol until further processing.

We identified all prey items to the lowest possible taxonomic level. Incomplete bony fishes were identified using otoliths according to Härkönen (1986) in combination with a reference collection of otoliths kept at the Institute of Marine Research, Tromsø, Norway. Fish otoliths were matched accordingly to side, length and species. Unmatched otoliths were considered to be one individual prey item. Highly digested or damaged otoliths were categorised as "unidentified". Elasmobranch fish species were identified based on their dermal denticles according to Watt et al. (1997). Features used in identification of the cephalopod beaks were those described by Clarke (1986). Upper and lower parts of the cephalopod beaks were matched, and when only one part of a beak was found, it was counted as one individual prey item. Other marine invertebrates were identified using Klekowski and Weslawski (1991, 1992). Invertebrates in the stomachs were often not found as complete specimens, and we thus estimated their numbers based on counts of large fractions that were retrieved.

We performed measurements of the right otoliths (the most numerous side found) from fishes and the length of the lower beak of cephalopods using calipers (±0.1 mm). The mass and length of ingested fish and cephalopods were back-calculated from measured otoliths and beaks using the allometric, species-specific, equations described in Härkönen (1986) and Clarke (1986), respectively. We only measured otoliths with minimal or no erosion. In addition, we measured fish mass and length to the nearest g and cm, respectively, directly for whole specimens. We estimated the biomass of prey items other than fish and cephalopods based on weighting the items to the nearest g (i.e. no attempts were made to back-calculate their total original masses).

We used claws from the fore-flippers of seals to estimate minimum age by counting growth rings as described by McLaren (1958). We extracted total genomic DNA from the seal tissue samples using the commercially available DNA EZNA (Omega Bio-tek) tissue DNA kit, following the kit's protocol for DNA Isolation. Minor modifications to the protocol included an extended incubation period in the proteinase K solution (overnight) at 55°C. Precautions were taken to avoid cross-contamination of samples in the laboratory. Cytochrome oxidase subunit 1 (cox1) sequences of target seal species and related species were retrieved from GenBank and manually aligned in BioEdit (Hall 1999). Conserved regions were targeted for designing primer pairs. The degenerate primers were obtained from DNA Technology AS, Risskov, Danmark. Three target regions were selected: (1) a 205 bp fragment using the primer pair *seal2f* 5′-ACTACTGGCCTCCTCYATAGTAG-3′ and *seal3r* 5′-GRTATTGAGAYATTGCAGGRGGTT-3′; (2) a 143 bp fragment using the primer pair *seal4f* 5′-TTCTGATTCTTYGGACAYCCGA-3′ and *seal5r* 5′-AAGCCRATRGAYATTATTGCT-3′; and (3) a 217 bp fragment using the primer pair *seal6f* 5′-CCCAACAYTTYCTAGGTCTAT-3′ and *seal7r* 5′-GGACATCCRTGYAGTCATTCG-3′. The fragments covered only short target regions in order to take significant DNA degradation into account, as initial PCR amplification attempts targeting longer regions using standard barcoding primers failed entirely. PCR amplification of the target regions was performed using AmpliTaq Gold® Fast PCR Master Mix (Applied Biosystems) following the vendor's standard instructions. A protocol starting with a denaturing step at 94°C for three min, followed by 40 cycles at 94°C for 30 s, 40°C for 15 s, 72°C for 20 s and a final extension at 72°C for 2 min was used. The very low temperature annealing step was necessary in order to get PCR products; at higher annealing temperatures, PCR amplification generally failed. This was because of the high level of degradation of the DNA in some samples. Even with the very low PCR stringency, several samples yielded no PCR products. PCR products that were obtained were purified using 10× diluted Exo-SAP-IT (USB Corporation) and subsequently sequenced according to the instructions of the BigDye 1.1 sequencing kit (Applied Bioscience). The obtained nucleotide sequences were aligned and edited with the software sequencher 4.1 (GeneCodes). The targeted region 6/7 was most informative for species identification of the samples.

Blubber pieces (ranging from 210 to 750 g) and skin fragments (0.5–1 cm in length) from whales were found in several of the Greenland shark GITs. Samples of these whale tissues were preserved in 96% ethanol for genetic identification. See Leclerc et al. (2011) for analytical details.

Statistical analyses

We determined the fork length to body mass relationship for the sharks using a non-linear regression model fitted by least squares (see Le Cren 1951). The form of the equation is $\mathrm{BM} = a \times \mathrm{FL}^{b}$ (expressed logarithmically by $\log \mathrm{BM} = \log a + b \log \mathrm{FL}$), where BM is the body mass (kg), FL = fork length (cm), and a and b are constants. To test for differences between sexes, an analysis of covariance (ANCOVA) was used to test for homogeneity of intercepts (a) and slopes (b) (Snedecor and Cochran 1967) using the software R (Version 2.12.0).

For analyses of the Greenland sharks' diet, we used common indices for stomach contents analyses as described in Hyslop (1980). They included: (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 non-empty 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 items in term 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). In addition, the composition of the diet was expressed using an index of relative importance (IRI) defined by Cortés (1997) and Pinkas et al. (1971) as: $\mathrm{IRI} = ((\%N + \%B) \times \%\ F)$. The IRI was expressed as a percentage, where % IRI for n prey types at the given identified taxonomic levels is defined as $\%\mathrm{IRI}_i = 100\,\mathrm{IRI}_i / \sum_{i=l}^{n} \mathrm{IRI}_i$ (Cortés 1997; Liao et al. 2001). The influence of shark body size on the tendency to consume seals was explored via a T test (2-tailed, unequal sample sizes) comparing total length of sharks that had seals in their GITs vs those that did not.

In order to investigate whether our sample size of Greenland shark GITs was large enough to give a representative picture of the sharks' summer diet in this region, we plotted a cumulative prey curve (Ferry and Cailliet 1996). Only the main prey species ($S = 14$; see below) were included in this analysis; small invertebrates (polychaetes, gastropods, bivalves, echinoderms), algae, rocks, etc. were assumed to be secondary prey or accidentally ingested items. The mathematical equation of this relationship is expressed as: $S_n f(n)$, where S is the number of prey organisms found in a given number of stomachs (n). The curve was plotted using data (a matrix of all main prey species for each individual shark) that had been randomized 100 times using the software R (Version 2.12.0).

Results

We caught a total of 76 Greenland sharks during the two field seasons. Ten were partly cannibalized by other sharks and are not used here, 21 were released after being instrumented with various tracking devices that will be reported elsewhere, while 45 (17 males and 28 females) were used in this study (Table 1). Most of the sharks were caught in Kongsfjorden, while two were caught off the west coast of Prins Karls Forland (Fig. 1).

Morphometrics and maturity status

The average total length, fork length and body mass of the female Greenland sharks were 314 ± 37 SD cm (range 245–404 cm), 296 ± 34 cm (range 229–381 cm) and 329 ± 141 kg (range 159–700 kg), respectively. Corresponding values for male sharks were 292 ± 24 cm (range 246–332 cm), 273 ± 20 cm (range 231–305 cm) and 250 ± 75 kg (range 136–375 kg) (Table 1). The females were significantly longer (two-sample t test, $t = 2.586$ $P = 0.013$ based on fork length and heavier (two-sample t test, $t = 2.224$ $P = 0.032$) than the males; 9 of the 10 longest sharks were females. However, we found no significant differences with regard to intercept (a) or slope (b) between males and females for the length–body mass relationship (ANOVA, intercept $P = 0.4816$, slope $P = 0.3614$). The resulting length–body mass equation with sexes combined was: $\mathrm{BM} = 1.109 \times 10^{-6} \times \mathrm{FL}^{3.41990}$ ($R^2 = 0.9187$) (Fig. 2). The slope of 3.42 ($b > 3.0$) indicates that shape is not uniform throughout development. All sharks were classified as sexually immature based on inspection of males' clasper and rhipidon characteristics and absence of large ova in females.

Diet

Twelve of the 45 GITs investigated (26.7% F) were empty (Table 1) and were excluded from further analysis. The average mass of the stomach contents in the remaining 33 GITs was 3.3 ± 3.5 kg (range <0.01–12.3 kg). The following taxonomic groups were identified in the GITs: mollusks; echinoderms; crustaceans; polychaetes; fishes and mammals (Table 2). Most prey items were found in the

Table 1 Sex, fork length, total length, body mass and GIT contents mass of Greenland sharks caught during June 2008–2009 in Svalbard, Norway

Shark number	Date of harvest (mm/dd/yy)	Sex	Fork length (cm)	Total length (cm)	Body mass (kg)	GIT content mass (kg)
SM-01	06/07/08	M	231	246	136	Empty
SM-02	06/07/08	M	299	324	375	<0.1
SM-03	06/07/08	F	312	334	327	3.1
SM-04	06/07/08	F	274	294	272	Empty
SM-05	06/07/08	M	305	332	372	1.2
SM-06	06/07/08	F	275	284	214	Empty
SM-07	06/07/08	F	273	287	252	1.7
SM-08	06/07/08	F	289	304	298	<0.1
SM-09	06/07/08	M	253	270	158	0.2
SM-10	06/10/08	M	274	295	242	<0.1
SM-11	06/10/08	F	278	291	260	1.8
SM-12	06/10/08	F	282	296	258	0.6
SM-13	06/10/08	F	296	308	347	3.2
SM-14	06/10/08	M	265	276	214	10.7
SM-15	06/10/08	F	338	360	494	0.2
SM-16	06/10/08	M	273	288	281	Empty
SM-17	06/09/08	F	318	340	327	Empty
SM-18	06/09/08	M	291	312	313	Empty
SM-19	06/09/08	F	287	307	295	Empty
SM-20	06/09/08	F	250	264	181	Empty
SM-21	06/09/08	F	294	309	273	6.1
SM-22	06/09/08	F	286	297	262	3.4
SM-23	06/09/08	F	229	245	159	0.2
SM-24	06/09/08	F	360	389	660	2.3
SM-25	06/08/08	F	317	339	377	<0.1
SM-26	06/08/08	M	267	281	257	Empty
SM-27	06/08/08	M	282	300	319	Empty
SM-28	06/08/08	F	263	281	215	<0.1
SM-29	06/08/08	M	296	308	262	1.3
SM-30	06/08/08	F	260	283	223	4.2
SM-31	06/12/08	M	261	283	179	9.8
SM-32	06/12/08	M	274	291	220	Empty
SM-33	06/16/09	F	260	278	208	4.0
SM-34	06/16/09	F	290	313	279	2.0
SM-35	06/20/09	M	298	324	305	0.6
SM-36	06/20/09	F	282	296	209	<0.1
SM-37	06/22/09	F	325	348	397	<0.1
SM-38	06/22/09	F	303	325	334	6.8
SM-39	06/22/09	F	381	404	700	6.8
SM-40	06/22/09	F	342	365	631	Empty
SM-41	06/23/09	F	289	308	236	6.9
SM-42	06/23/09	M	288	308	311	3.5
SM-43	06/25/09	M	263	274	197	12.3
SM-44	06/25/09	F	314	337	392	<0.1
SM-45	06/25/09	M	245	259	163	<0.1

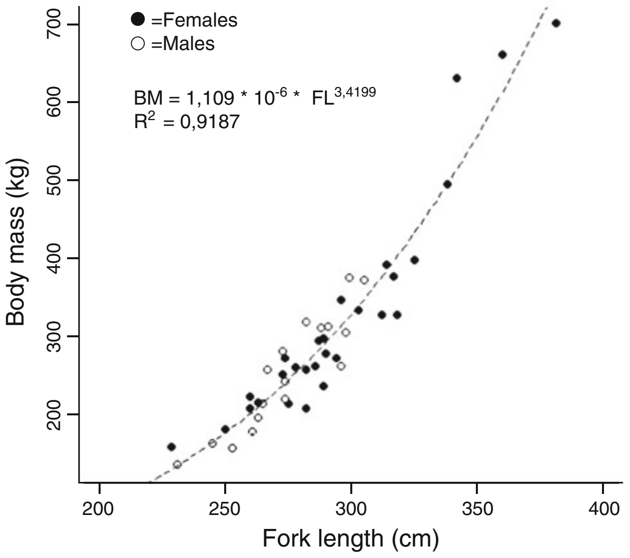

Fig. 2 Relationship between fork length and body mass according to sex (female *filled circle*, male *open circle*) for Greenland sharks ($n = 45$) caught during June 2008–2009 in Svalbard, Norway

cardiac and pyloric parts of the stomach. We found only small fish bones, crustaceans, seal hairs and whale skin in the pyloric caecum, or in the proximal, or spiral intestine.

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. All whale tissue pieces that were in a condition sufficient for genetic identification were confirmed to be minke whales taken in the Norwegian harvest (see Leclerc et al. 2011 for details). The seal remains found in the Greenland sharks stomachs included seal claws, a lower jaw, a scapula and flipper, chunks of muscle and blubber, and even a whole pup in lanugo (Tables 2, 3). Four of the sharks (SM-05, SM-24, SM-35, SM-43) had consumed at least two different seals. This latter finding was determined in one case by two different mitochondrial haplotypes from the same seal species being identified, in two cases where two different seal species were present, and finally in a case where adult claws were found in the same stomach that contained a whole neonate in lanugo. Based on growth zones in the claws of the fore-flippers ($n = 6$), the sharks had consumed four ringed seals that were 1 year old or younger and two adult seals that were at least 8 and 9 years old, respectively (Table 3). The most important mammalian species in the shark diet was ringed seals (16.0% IRI), followed by minke whale (2.4% IRI), bearded seal and hooded seal (both <0.1% IRI) (Table 2). Shark body size did not have an influence on whether or not their GITs contained seal tissues ($P = 0.78$). Only, one seal sample was associated with scavenging invertebrates (i.e. brittle stars).

Most of the Greenland sharks had consumed fish of several species (Table 2). These were present as whole specimens as well as material in various stages of digestion. Fish from two families were identified from the 74 otoliths extracted from the GITs, including six identifiable species of bony fishes; 7% of the otoliths were too decalcified to permit identification. The most important fish prey was Atlantic cod (55.8% IRI) followed by Atlantic wolffish (10.2% IRI) and haddock (*Melanogrammus aeglefinus*, 5.4% IRI) (Table 2). Other bony fish included spotted wolffish (*A. minor*), redfish (Sebastes spp.) and American plaice (*Hippoglossoides platessoides*). Additionally two species of elasmobranchs were identified (starry rays and Greenland sharks). The average length of the six bony fish species was 50.1 ± 12.3 SD cm (range 24.9–85.1 cm) (Fig. 3). Relatively undigested specimens of Atlantic cod and Atlantic wolfish retrieved as more or less intact specimens with the skin still attached had been swallowed whole. The largest whole fishes we found in shark stomachs were an Atlantic wolfish that was 85 cm with 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 important invertebrates we found in the shark stomachs were the boreoatlantic armhook squid (*Gonatus fabricii,* 4.2% IRI) and the great spider crab (*Hyas araneus,* 0.4% IRI) (Table 2). We considered the remaining invertebrates found in the GITs, such as polychaetes, gastropods, small bivalves and echinoderms (Table 2), to be secondary prey items released from the stomachs of consumed fish or animals accidentally ingested while feeding on benthic fish. Similarly, some algae (9.1% *F*, 3.6 g), rocks (21.2% *F*, 76.6 g), a small piece of metal and some fishing line (3.0% *F*, 13.9 g) were found in the GITs, but not considered to be part of the diet.

The cumulative prey curve, based on 14 main prey species, reached an asymptote at $n = 28$ (Table 4, Fig. 4).

Discussion

The Greenland sharks collected in this study ranged between 159–700 kg in body mass and 245–404 cm in total length. All individuals, including the largest male (332 cm, 375 kg) and the largest female (404 cm, 700 kg), were sexually immature. Maturity in Greenland sharks has been reported to be reached at total lengths of about 450 cm for females and about 300 cm for males (Yano et al. 2007). Using the length–body mass relationships from the present study (including an extrapolation beyond the mass range documented), this would correspond to body masses of about 1,300 kg for females and 330 kg for males. According to these length data and these mass calculations, the largest males in our study should have

Table 2 Composition of the diet of the Greenland shark collected in Svalbard, Norway, June 2008 and 2009

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

$n = 33$, Frequency of occurrence (% *F*), total prey by number (% *N*), total reconstructed biomass (% *B*) AND index of relative importance (% IRI)

been mature, but this was not the case. Sexual size dimorphism, with females being larger than males, has been reported previously for Greenland sharks (Bigelow and Schroeder 1948; Yano et al. 2007) and is consistent with this study. But ontogeny of this size dimorphism cannot be tracked because there is no functional means to

Table 3 Tissue type, mass, genetic identification, number and age estimate of the seals found in the Greenland shark GITs collected in 2008–2009 on the west coast of Spitsbergen, Svalbard (Norway)

Shark number	Type of tissue	Mass (gm)	Identification	Number of seals	Age estimate
SM-02	Claw	1	*Pusa hipida*	1	Undetermined
SM-03	Flipper	710	Unidentified	1	1 year
	Hair	<1	Unidentified		Undetermined
	Hair	<1	Unidentified		Undetermined
SM-05	Claw	2	*Pusa hipida*	2	7 years
	Flipper	880	*Pusa hipida*		White coat
	Hair	<1	*Pusa hipida*		Undetermined
SM-08	Hair	<1	–	1	Undetermined
	Hair	<1	–		Undetermined
	Hair	<1	*Pusa hipida*		Undetermined
SM-11	Scapula	320	–	1	Undetermined
	Hair	<1	–		Undetermined
	Hair	<1	–		Undetermined
	Hair	<1	*Pusa hipida*		Undetermined
SM-23	Flipper	210	*Pusa hipida*	1	White coat
	Hair	<1	–		Undetermined
SM-24	Meat	64	*Pusa hipida*	2	Undetermined
	Bone	103	*Pusa hipida*		Undetermined
	Hair	<1	–		Undetermined
	Jaw	18	*Cystophora cristata*		Undetermined
SM-25	Hair	<1	Unidentified	1	Undetermined
SM-33	Whisker	<1	*Pusa hipida*	1	Undetermined
SM-35	Claw	7.78	*Pusa hipida*	2	9 years
	Scapula	510	*Erignathus barbatus*		Undetermined
	Whisker	<1	*Erignathus barbatus*		Undetermined
	Skin + hair	<1	*Erignathus barbatus*		Undetermined
	Hair	<1	–		Undetermined
SM-41	Whole pup	2,580	*Pusa hipida*	1	White coat
	Hair	<1	*Pusa hipida*		Undetermined
	Hair	<1	*Pusa hipida*		Undetermined
	Skin + hair	<1	*Pusa hipida*		Undetermined
SM-43	Blubber + Skin + hair	6,349	*Pusa hipida*	2	Undetermined
	Blubber + Skin + hair	1,444	*Pusa hipida*		Undetermined
	Blubber + Skin + hair	47	*Pusa hipida*		Undetermined
	Blubber + Skin + hair	198	*Pusa hipida*		Undetermined
	Blubber + skin + hair	438	*Pusa hipida*		Undetermined
	Blubber + skin + hair	1,346	*Pusa hipida*		Undetermined
	Blubber + skin + hair	288	*Pusa hipida*		Undetermined
	Blubber + skin + hair	2,170	*Pusa hipida*		Undetermined
	Hair	<1	*Pusa hipida*		Undetermined

determine age in this species. Maximum Greenland shark total lengths of at least 640 cm (and possibly more than 7 m) have been reported (Bigelow and Schroeder 1948; Compagno 1984). According to a greater extrapolation of our length–body mass relationships (well beyond the mass range documented), such an individual would weigh more than 6,000 kg making Greenland sharks even larger than white sharks (*Carcharodon carcharias*) (Compagno 2001) and thus possibly the largest predatory shark.

We recovered some food items in the GITs of the Greenland sharks as whole specimens with the skin still intact. The largest whole fishes were an Atlantic cod which

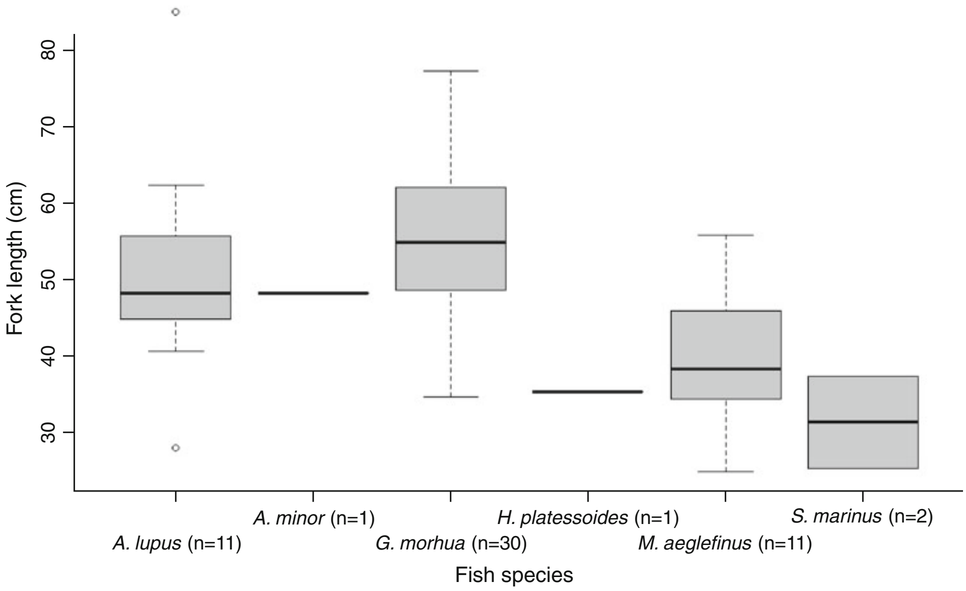

Fig. 3 Length distributions of six bony fish species found in the gastrointestinal tracts of Greenland sharks ($n = 45$) caught during June 2008–2009 in Svalbard, Norway

was 77 cm long and weighed 4.2 kg and an Atlantic wolffish that was 85 cm and weighed 8.6 kg. An entire white-coated ringed seal pup was also found in one shark stomach. However, many of the larger seal pieces and all the whale blubber found in the GITs of the sharks were chunks that were obviously bitten off. The condition of these various prey items suggests that the Greenland sharks used at least two prey capture mechanisms, suction was suspected where there was no sign of contact between the teeth and prey and biting when large prey had clearly been cleaved into pieces. Squaliform sharks, including the Greenland shark, do show morphological specializations for suction feeding: small teeth and mouth; a laterally enclosed mouth; hypertrophied abductor muscles; and

Table 4 Composition of the Greenland shark diet expressed in per cent of total reconstructed biomass (% *B*) and index of relative importance (% IRI), for main prey. F = females ($n = 21$) and M = males ($n = 10$)

Prey item	% *B*		% IRI	
	F	M	F	M
Mollusca				
Gonatus fabricii	<0.1	<0.1	3.9	8.4
Crustacea				
Hyas araneus	0.1	<0.1	0.45	0.6
Pisces				
Anarhichas lupus	18.0	22.1	8.4	10.8
Gadus morhua	58.2	36.1	63.7	31.7
Melanogrammus aeglefinus	12.5	4.9	9.7	1.4
Other Pisces				
Raja radiata	3.8	1.4	5.6	4.9
Somniosus microcephalus				
Anarhichas minor				
Hippoglossoides platessoides				
Sebastes marinus				
Mammalia				
Phocidae				
Erignathus barbatus	6.3	32.8	6.2	37.9
Pusa hispida				
Cystophora cristata				
Balaenidae				
Balaenoptera acutorostrata	1.0	2.6	2.0	4.3

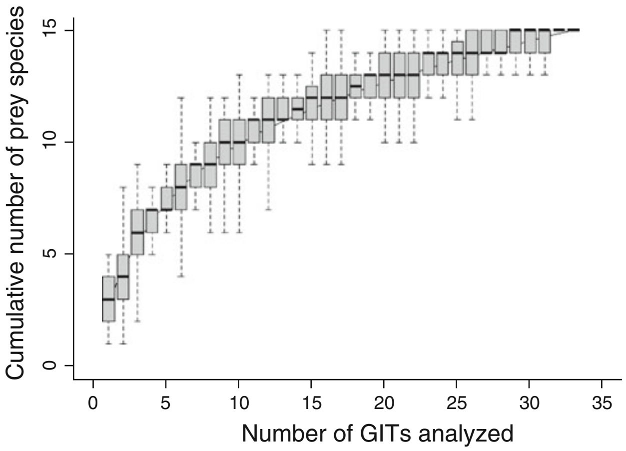

Fig. 4 Randomized cumulative prey curve (for major prey items) in the stomach contents of Greenland sharks caught during June 2008–2009 in Svalbard, Norway

rapid buccal expansion, which allow them to swallow prey quickly (see Motta and Wilga 2001). However, when scavenging or preying on larger prey items, Greenland sharks clearly do some biting as indicated by the bowl-shaped wounds that we saw on some of the cannibalized sharks in our study; similar bite marks have also been reported previously in other studies of the feeding behaviour of this species (e.g. Jensen 1914; Beck and Mansfield 1969).

The Greenland sharks' diet in Svalbard was mainly composed of fish (81.2% IRI) with Atlantic cod being the most important species, followed by Atlantic wolfish and haddock (Table 2). This is consistent with studies of Greenland shark diet from other areas, where fish comprise most of the diet, although the fish species vary geographically. Greenland halibut was found to be the dominant prey in west Greenland (Yano et al. 2007) while redfish dominate in Icelandic waters (McMeans et al. 2010). This is likely based in part on relative availability of the different fish species in different areas.

Similar to other large predatory sharks (i.e. white sharks and tiger sharks (*Galeocerdo cuvier*); LeBoeuf et al. 1982; Lowe et al. 1996), the Greenland sharks in this study also fed on seals. Ringed seals were the dominate seal prey (16.0% IRI) which reflects their relatively high abundance in the study area; they are numerically the dominant seal species in Svalbard fjords (Hop et al. 2002). In addition, bearded seal and hooded seal tissues were each found in a single shark stomach. Bearded seal was used as bait for sharks in the present study, but tissue found in the Greenland shark GIT was incompatible with the size and shape of the baits used. Bearded seals are common in the study area on a year-round basis (Hop et al. 2002), and the low occurrence of this seal in the shark GITs compared with ringed seals might be related to the bearded seal's large body size, which might make them more difficult for the Greenland shark to prey upon. Hooded seals are also large seals and they are uncommon in the study site. There was no difference in the size of sharks that had eaten seals compared with those that had not in our study; seal eating was spread across the size range with both the smallest shark and the second largest having eaten seals. Our sample size was too small to explore potential combined effects of sex and body size.

We did not find any harbour seal tissue in the GITs in this study, though this species has been found in Greenland sharks elsewhere in the North Atlantic Arctic (Yano et al. 2007), and these sharks are thought to be the major factor responsible for the decline of the harbour seal population in Sable Island (Bowen et al. 2003; Lucas and Natanson 2010) and perhaps also involved in declines elsewhere (Thompson et al. 2001). Given our small sample size, and the small population size of harbour seals in Svalbard compared with the high abundance of local populations of traditional Arctic seal species, it may only be a matter of chance that we did not document harbour seal in the shark's diet. The location of our net sets in the coastal fjords might also have biased our seal species findings. Although harbour seals are occasionally sighted in Kongsfjorden during summer, they tend to concentrate their feeding at the shelf edge west of Spitsbergen (Gjertz et al. 2001). But our attempts to fish in this area resulted in broken lines because of high seas and a lack of manoeuvrability using RV Lance to pull lines, so our offshore effort was minimal. But the fact that 36.4% of the shark stomachs in our study contained seals suggests that it is likely that this shark is a significant source of mortality for all seals in the region.

Although the sample size in our study is relatively small, the cumulative prey curve suggests that it was sufficient to provide a representative picture of the sharks' diet during early summer in the Svalbard area. The fact that most of the sharks in the study fed mainly on the same prey types gives further support to the small sample size being adequate to explore diet in this High Arctic area with rather low species diversity.

Greenland sharks have been described as opportunistic benthic scavengers, due in part to their lethargic nature. They clearly do scavenge offal if it is available, such as their consumption of floating minke whale blubber strips in this study, which were a by-product of the fishery in the Svalbard area (see Leclerc et al. 2011 for details). However, there is increasing circumstantial evidence that Greenland sharks also prey actively on seals and various fast-swimming fishes (e.g. Sigler et al. 2006). For example, bleeding, beached corpses (newly attacked) of young harbour seals on Sable Island, with wounds typical of Greenland sharks, suggest strongly that the seals are taken alive (Lucas and Stobo 2000; Lucas and Natanson 2010), and the condition of marine mammal remains found in other sleeper shark species also suggest active hunting by close relatives (Crovetto et al. 1992; Sigler et al. 2006; van den Hoff and Morrice 2008). In Svalbard's fjords, carcasses of seals rapidly end up in the shallows if they are sufficiently fat to float, or on the sea floor at times of year when seals are thin and sink. In either case, they are rapidly attacked by carnivorous invertebrates such as brittle stars and various species of amphipods that one would expect to be present in the shark GITs if dead seals were routinely scavenged by the sharks. However, only one GIT contained a few of these invertebrates suggesting that most of the seals were killed by the sharks. The high frequency of seals in Greenland shark diets (Bigelow and Schroeder 1948; Fisk et al. 2002; present study), as well as whole fish specimens, suggests strongly that the Greenland shark is an active predator.

If the Greenland shark is a predator of fast-swimming seals and fishes, the question arises as to how they catch them? There has never been a direct observation of such a predation event, but we surmise that a combination of a slow stealthy approach and the shark's cryptic colouration might allow them to get close enough to take resting/sleeping prey. Nansen (1924) also suggested that these sharks took prey that was sleeping.

Although there is no current abundance estimates for Greenland sharks in the North Atlantic, it seems likely that they are quite abundant. Historical catch data show that the annual take of this shark species was enormous during the years there was a market for their liver oil. Catch reports from Greenland show that over 50,000 Greenland sharks were taken annually for many decades in the first half of the 19th century (Anon 1942). Norwegian catch statistics generally reported liver weight or liver oil weight/volume and not the number of sharks taken, but based on these records for the period 1933–1948, about 100,000–200,000 sharks were taken annually in the Norwegian harvest (Anon 1942; Hoel 1949), without apparent declines in catches. The fishery stopped suddenly when synthetic oils became available and has remained inactive during the past 60 years. There is no doubt that this shark was extremely numerous in North Atlantic Arctic waters, and with the termination of the Greenland shark fisheries in this region, abundance is likely to have increased though no estimates are available to support this conjecture.

In conclusion, our study shows that the summer diet of Greenland sharks is dominated by fish in the Svalbard area, but that they are also active, significant predators of seals, possibly including harbour seals. Additionally, they do feed on carrion on the surface and appear to be able to feed throughout the water column given the diverse types of prey in their diet. This High Arctic predator warrants further study and inclusion in Arctic food web studies, as well as being taken into consideration in mortality estimates conducted for Arctic seals, including harbour seals in Svalbard.

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