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ORIGINAL PAPER

# Distribution and feeding ecology of the Greenland shark (*Somniosus microcephalus*) in Greenland waters

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**Abstract** Greenland sharks are widely distributed and most likely a highly abundant predator in arctic waters. Greenland sharks have previously been considered scavengers, but recent studies suggest that Greenland sharks also predate on live prey. In this study, distribution and feeding ecology in Greenland waters were investigated. Based on data from 25 years of surveys, Greenland sharks were usually caught at 400–700 m but were found at all depths between 100 and 1,200 m. Based on examination of stomachs from 30 Greenland sharks (total length of 258–460 cm), the most important prey items were Atlantic cod (65.6 % IRI), harp seal (9.9 % IRI), skates (5.2 % IRI) and wolffish (4.4 % IRI), but large geographical variations were observed. Prey composition and qualitative observations support the hypothesis of active predation. Consistent with other studies, the results of this work support the notion that the Greenland shark is an apex predator with the potential to influence trophic dynamics in the Arctic.

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**Keywords** Greenland shark · Feeding ecology · Distribution · Arctic · Body metrics

## Introduction

Greenland sharks (*Somniosus microcephalus*) are widely distributed and inhabit large parts of the North Atlantic and the Arctic Ocean including Greenland in- and offshore waters (MacNeil et al. 2012). There are no estimates of current abundance, but records of trade with shark livers in Greenland during 1890–1938 estimate annual shark landings of 44,000 individuals (Anon 1942). Sharks were primarily caught to utilize the liver for producing lamp and high-grade machine oil. Catches were closely related to fishing effort, and shark abundance showed no signs of decline during this period (Anon 1942). The demand for shark oil diminished in the late 1940s due to the invention of synthetic oil, and no large-scale catches have been conducted in Greenland or elsewhere since. In northwestern Greenland, sharks are still caught in low numbers to serve as food for sledge dogs and they are caught as by-catch by trawlers and long-liners throughout Greenland waters. However, catches are marginal compared to the earlier targeted commercial fishery (Greenland Institute of Natural Resources, unpublished data), and the Greenland shark is most likely abundant in Greenland waters.

Knowledge on the ecological role of Greenland sharks is limited. The diet is known to be diverse and includes different species of fishes, mammals, crustaceans, gastropods and cephalopods (Yano et al. 2007; McMeans et al. 2010; Leclerc et al. 2012). Despite this opportunistic feeding behavior across trophic levels, long-term feeding studies using anthropogenic contaminants and stable isotopes place the Greenland shark at a trophic level above seals and predatory fish such as Greenland halibut (*Reinhardtius hippoglossiodes*) and Atlantic cod (*Gadus morhua*, Fisk et al. 2002; Hansen et al. 2012). Scavenging events on marine mammals and fish have been reported (Beck and Mansfield 1969; Leclerc et al. 2011), but whether the shark feeds mostly as a scavenger or an active predator is unknown. There are reports of active predation from Sable Island, Canada, where a population of harbor seals (*Phoca vitulina*) is regulated by Greenland sharks (Lucas and Stobo 2000; Lucas and Natanson 2010) although this can be questioned (Bexton et al. 2012). Another recent study from Svalbard, Norway, concludes that Greenland sharks actively prey on fast-swimming mammals and fish (Leclerc et al. 2012). Such findings suggest that the ecological role of Greenland shark should be considered that of an apex predator. The shelf ecosystems in the northern North Atlantic are generally described as top-down regulated and species-poor (Frank et al. 2007), and the understanding of the arctic marine ecosystem must be reevaluated as an important and previously unaccounted for predator is introduced.

Greenland sharks are reported to feed primarily on Atlantic cod in Svalbard waters, on redfish (*Sebastes* spp.) in Icelandic waters and on marine mammals in both areas (McMeans et al. 2010; Leclerc et al. 2012). The only study from Greenland waters was based on specimens mainly caught in deep waters (>800 m) on the west coast and showed a diet dominated by Greenland halibut (Yano et al. 2007). However, sharks are present all over the continental shelf including shallower depths and in fjords, potentially interacting with commercial species such as Atlantic cod, redfish, Greenland halibut, wolffish (spotted wolffish *Anarhichas minor* and Atlantic wolffish *A. lupus*), northern shrimp (*Pandalus borealis*) and snow crab (*Cionoecetes opilio*). The impact of these interactions may be substantial, and the main objectives of this study were to evaluate the distribution of Greenland sharks in Greenland waters and describe the feeding ecology from areas not previously investigated.

## Materials and methods

### Sampling

From April to September 2012, 49 Greenland sharks were caught at different locations around Greenland. Only 30 sharks were used to evaluate feeding ecology as 19 sharks were carcasses without intestinal guts, inflicted by cannibalistic conspecifics (Fig. 1). Sampling was conducted during the Greenland Institute of Natural Resources (GINR) annual bottom trawl (RV Pâmiut) and gill net surveys (RV Sanna). Furthermore, longline samples were obtained from RV Dana in Ammassalik Fjord (eastern Greenland) and from local hunters in Disko Bay (western Greenland) and Qaqortoq Bay (southwestern Greenland). For all sharks caught in 2012, standard length (SL), fork length (FL), total length (TL), girth behind pectoral fins (GP), girth in front of dorsal fin (GD) and minimum girth around caudal peduncle (GCP) were measured (all in cm). Sexual maturity was only evaluated for females by the presence of oocytes.

Since 1988, GINR has conducted yearly bottom trawl surveys in Greenland waters and registered all catches of fish from 9,744 trawl stations between 59 and 76°N off the west coast and between 59 and 72°N off the east coast. Fishing depths ranged from 26 to 1,497 m (mean ± SD, 430 ± 311 m). Greenland sharks caught during these surveys were used to supplement catch records from 2012 when evaluating distribution and body metrics, giving a total of 106 Greenland sharks. Total length (TL) has been recorded for 68 individuals (TL range 106–510 cm), and body mass (BM, kg) of 41 individuals has been measured on digital scales (BM range 8.9–1,100 kg). None of these were sexed. It should be noted that different trawling gears have been used, but it has not been possible to correct for differences in catchability.

### Distribution and body metrics

Based on the distribution of catches of Greenland sharks from GINR trawl surveys, three geographical areas were defined: 'East' (east of 44°W, between 59°N and 69°N, 1,990 hauls), 'Southwest' (west of 44°W, between 59°N and 66°N, 3,154 hauls) and 'Northwest' (west of 44°W, between 66°N and 76°N, 4,600 hauls, Fig. 1). Frequency of occurrence within these areas was expressed as number of sharks caught in 1,000 hauls standardized to a duration of 15 min. The relationship between latitude and length (TL, $N = 113$) and between depth of capture and latitude was analyzed for sharks caught along the west ($N = 78$) and east coast ($N = 28$). Furthermore, frequency of occurrence ($N = 106$) and shark size ($N = 68$) were evaluated at 100-m depth intervals. Two models relating BM to morphometrics were fitted: a classical length–weight relationship ($BM = a \times TL^b$, where $a$ and $b$ are constants, $N = 40$) and a multivariate model obtained from stepwise regression ($N = 18$) using SL, FL, TL, GP, GD and GCP and all interactions as explanatory variables.

### Stomach content

Stomachs from 30 sharks were stored at −20 °C and shipped to GINR where the content was examined. Large items were separated followed by sorting of smaller items through a setup of four sieves with grid sizes of 22.4, 6.3,

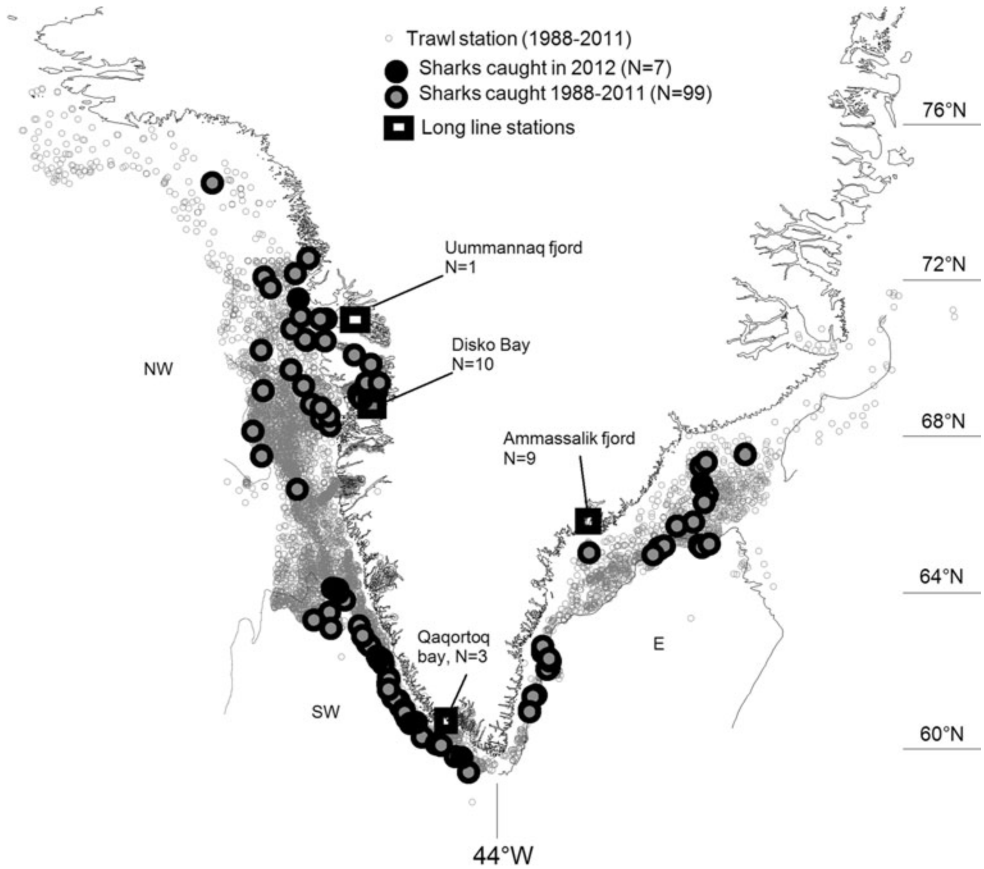


**Fig. 1** Each *circle* represents a trawling haul from 1988 to 2011 ($N = 9{,}744$). *Gray-filled circles* represent locations where Greenland sharks have been caught in bottom trawl prior to 2012 ($N = 99$), and *black-filled circles* represent sharks caught in bottom trawl in 2012 ($N = 7$). *Squares* represent inshore regions where the number of sharks caught in 2012 is specific for each region. Sharks from these areas were caught on longline ($N = 23$)

2.0 and 1.0 mm. Each prey item was determined to the lowest possible taxonomic level. Species identification of digested wolffish was based on teeth as described by Nielsen and Bertelsen (1992). Parts of seal were determined according to skin, by comparison of bones from the GINR Reference Collection and from Ridgway and Harrison (1981). Macroalgae were identified according to Pedersen (2011), and cephalopod beaks were identified using Clarke (1986). All items were weighed to the nearest gram. TL of all fishes was measured if possible or estimated to the nearest centimeter. For one specimen of spotted wolffish, TL was estimated from otolith size according to Campana (2004). For two specimens of eelpouts (*Lycodes* sp.) and five specimens of skates (Rajidae), TLs were estimated through interspecific comparison of bone sizes from the Reference Collection at the Natural History Museum of Denmark, University of Copenhagen. This reference collection was also used to identify five specimens of Atlantic cod, where TLs were estimated through intraspecific bone comparison. Eelpouts and Atlantic cod were identified from premaxilare and maxilare. Skates were identified from parts of the cartilaginous skeleton.

For all prey fish, original biomass was reconstructed from length–weight relationships acquired from FishBase (Froese and Pauly 2012) and used in all further analyses. Coefficients of greater eelpout (*L. esmarkii*) were considered to be representative for specimens of the genus eelpout, and coefficients of thorny ray (*Amblyraja radiata*) were considered representative for specimens of the family Rajidae. Coefficients for redfish were calculated from the GINR database ($a = 0.01$, $b = 3.0976$, $r^2 = 0.99$, $N = 3{,}231$ of beaked redfish *S. mentella*). Biomass of fish that could not be determined to species or genus level was calculated from estimated coefficients ($a = 0.01$, $b = 3$). For cephalopods, BM (g) and pen length (PL, mm) were calculated from the formulas: $\mathrm{BM} = 0.164 \times \mathrm{LRL}^{4.242}$ and $\mathrm{PL} = 27.254 + 8.257 \times \mathrm{LRL}^{1.807}$ (Zumholz and Frandsen 2006), where LRL is lower rostral length in mm (Clarke 1986). For specimens of Bivalvia, Gastropoda, Echinodermata and Malacostraca, original biomass was estimated to correspond to measured biomass as specimens were relatively intact. For mammals, the original biomass was not reconstructed as we found no evidence of entire adult specimens being ingested. Therefore, it was assumed that the original weight of a piece of mammal most accurately reflected the amount consumed.

To evaluate the importance of different prey items, four parameters were calculated:

Frequency of occurrence of prey item i: $\% F_i = F_i/F_t \times 100$, where $F_i$ is the number of individuals containing

**Table 1** Overview of the 30 sharks used in the stomach content analysis

| No. | Region | Depth (m) | Month | TL (cm) | Body mass (kg) | Sex | Stomach content (kg) |
|---|---|---|---|---|---|---|---|
| 1 | NW | 175 | Jul | 258 | 144 | F | 2.034 |
| 2 | NW | 170 | Jul | 276 | | F | 0.110 |
| 3 | NW | 175 | Jul | 315 | | F | 0.894 |
| 4 | NW | 180 | Jul | 345 | | F | 2.070 |
| 5 | NW | 190 | Jul | 290 | | M | Empty |
| 6 | NW | 175 | Jul | 357 | | F | 13.280 |
| 7 | NW | 200 | Jul | 325 | | M | 5.877 |
| 8 | NW | 200 | Jul | 287 | | F | Empty |
| 9 | NW | 185 | Jul | 274 | | M | 0.050 |
| 10 | NW | 190 | Jul | 298 | | F | Empty |
| 11 | NW | 390 | Jul | 312 | | F | 0.101 |
| 12 | NW | 360 | Jul | 322 | | M | 5.826 |
| 13 | SW | 310 | Apr | 326 | 278 | M | Empty |
| 14 | SW | 310 | Apr | 447 | 1,078 | F | Empty |
| 15 | SW | 178 | Jul | 420 | 740 | F | 1.511 |
| 16 | SW | 132 | Jul | 442 | 850 | F | 18.363 |
| 17 | SW | 354 | Sep | 354 | 430 | F | 0.135 |
| 18 | SW | 159 | Sep | 460 | 1,060 | F | 30.845 |
| 19 | SW | 150 | Sep | 447 | 1,100 | F | 20.477 |
| 20 | SW | 240 | Sep | 360 | | F | 4.104 |
| 21 | E | 555 | Aug | 370 | 540 | F | 3.744 |
| 22 | E | 350 | Sep | 312 | 337 | F | 8.974 |
| 23 | E | 460 | Sep | 346 | 416 | F | 0.092 |
| 24 | E | 454 | Sep | 355 | 464 | F | 0.090 |
| 25 | E | 394 | Sep | 306 | 246 | F | 0.113 |
| 26 | E | 380 | Sep | 264 | 168 | F | 0.062 |
| 27 | E | 567 | Sep | 386 | 560 | F | 0.188 |
| 28 | E | 596 | Sep | 365 | 430 | F | 2.654 |
| 29 | E | 596 | Sep | 336 | 338 | F | Empty |
| 30 | E | 600 | Sep | 351 | 452 | F | 1.591 |

BM could not be measured for sharks caught by local fishermen nor by RV Sanna

prey item i and $F_t$ is the total number of non-empty stomachs. Numerical proportion of prey item i: $\% N_i = N_i / N_t \times 100$, where $N_i$ is the total number of prey item i and $N_t$ is the total number of prey items in all stomachs. Biomass proportion of prey item i: $\% B_i = B_i/B_t \times 100$, where $B_i$ is the reconstructed biomass of prey item i consumed and $B_t$ is the reconstructed biomass of all prey items consumed (Hyslop 1980). Index of relative importance of prey item i: $IRI_i = (\% N_i + \% B_i) \times \% F_i$. IRI for each prey group is expressed as $\% IRI = IRI_i/IRI_t \times 100$, where $IRI_t$ is the sum of $IRI_i$ for all prey items (Pinkas et al. 1971; Cortés 1997). For non-prey items, e.g., rocks, human garbage and scavenging amphipods (Lysianassidae), only

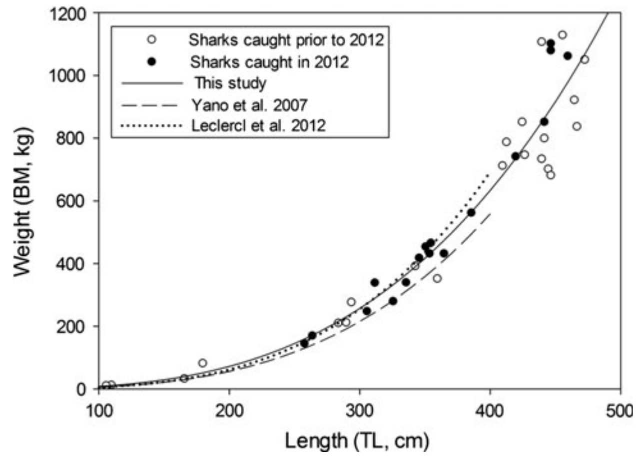


**Fig. 2** Relationship between length and body mass (BM, kg). *Open circles* represent sharks caught prior to 2012 ($N = 23$), and *black-filled circles* represent sharks caught in 2012 ($N = 17$). The model of Leclerc et al. (2012) was based on fork length (FL, cm) and has been converted to total length (TL, cm) using the relationship described in this study

frequency of occurrence was calculated. Male and female Greenland sharks were grouped for all purposes.

To evaluate the importance of different prey among the three geographical areas, prey biomass was grouped into four categories: 'Fish,' 'Mammals,' 'Cephalopods' and 'Other.' 'Other' includes Gastropoda, Echinodermata and Decapoda. According to studies of Yano et al. (2007), McMeans et al. (2010) and Leclerc et al. (2012), the most essential prey fishes in Greenland shark diet are Atlantic cod, wolffish, Greenland halibut and redfish. In this study, the importance of these was analyzed by comparing reconstructed biomass between the geographical areas, where the remaining prey fishes (including unidentified fish) were grouped into the category 'Other.' Finally, size distributions (mean ± SD) of the seven most important prey fishes were calculated. All statistical tests were made in RStudio (2012).

## Results

### Body metrics

Body metrics were available from 49 Greenland sharks (39 females and 10 males). Two sharks had partly eaten tails, and TL was estimated using the FL-TL relationship: ($TL = 1.0593 \times FL + 4.9387$, $r^2 = 0.9713$, $N = 47$). Mean female TL ± SD was 344.4 ± 50.7 cm (range 258–460 cm, $N = 39$), and BM ranged from 143.5 to 1,100.0 kg. Mean male TL ± SD was 309.2 ± 19.7 cm (range 274–335 cm, $N = 10$). BM was only measured for a single male (TL = 326 cm, BM = 278 kg), as the remaining nine were caught as carcasses or by local hunters without access to

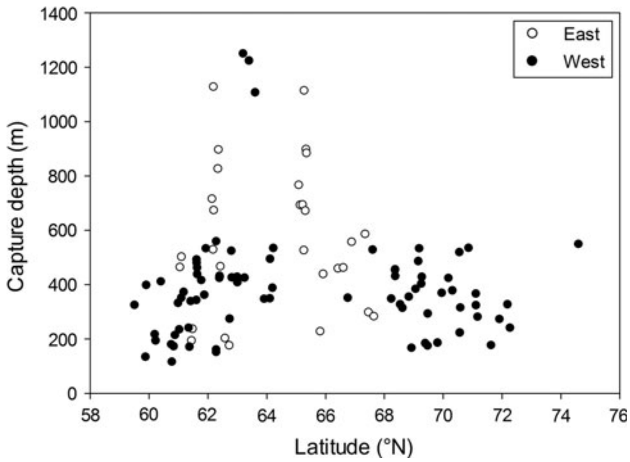


**Fig. 3** Depth of capture at given latitude on the west coast (59–75°N, depth range 100–1,300 m, $N = 78$) and east coast (61–67.5°N, depth range 180–1,150 m, $N = 28$). Notice that five sharks have been caught deeper than 1,000 m, but length could only be evaluated for four of them

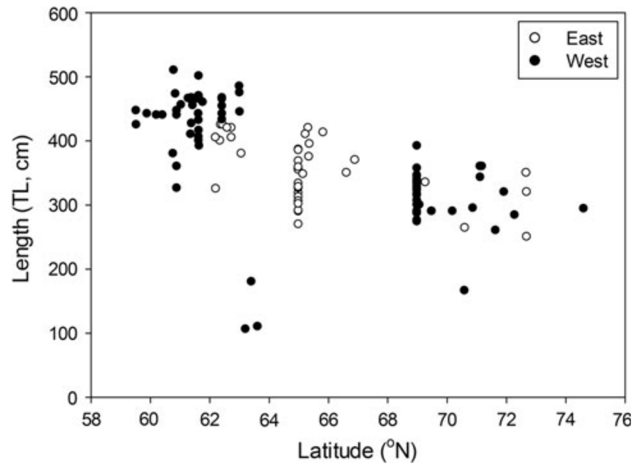


**Fig. 4** Greenland shark length (TL, cm) at different latitudes ($N = 113$). The largest sharks were caught at lower latitudes

digital scales. Males were significantly smaller (TL) than females (Student's *t* test, $t = 3.443$, $df = 38.9$, $P < 0.01$). One female (TL = 447 cm, no. 19 in Table 1) was found to be sexually mature, having 455 oocytes in the ovarian duct weighing 49.0 kg in total (mean egg diameter ± SD = 5.1 ± 0.6 cm).

The length–weight relationship was $BM = 4.416 \times 10^{-6} \times TL^{3.1346}$ ($P < 0.0001$, $R^2 = 0.92$, TL: 106–460 cm, BM: 8.9–1,100.0 kg, Fig. 2). The stepwise regression resulted in the following model: $BM = 424.896 - 1.534 \times TL - 4.188 \times GP + 0.0202 \times TL \times GP$ ($P < 0.0001$, $R^2 = 0.99$, TL: 258–447 cm, BM: 143.5–1,100.0 kg). One outlier was excluded (no. 18 in Table 1).

## Distribution and frequency

From 1988 to 2012, 106 Greenland sharks were caught in 9,744 trawl hauls in Greenland waters between 59.5°N and 74.6°N off the west coast and between 59.5 and 67.6°N off the east coast (Fig. 1). Depth of capture ranged from 114 to 1,248 m. Greenland sharks were most frequent in 'Southwest' followed by 'East' and 'Northwest' (13.8, 11.6 and 7.4 sharks per 1,000 hauls, respectively). Greenland sharks from 'Southwest' were caught near the continental shelf break, whereas sharks in 'Northwest' were more widely distributed with the highest density in the Disko Bay area. There was no overall trend between capture depth and latitude for neither the east coast nor the west coast as sharks at low latitudes (<66°N) were caught at all depths between approximately 100 and 1,200 m (Fig. 3). The reason for the apparent high prevalence of sharks in deeper waters between 62 and 66°N is a sampling artifact as most stations in deep waters are located in this latitudinal range. Very few or no sharks were caught in large areas between 64.2 and 69.3°N on the west coast or on the east coast between 62.7 and 65.1°N despite a high trawling effort (Fig. 1). The areas where no sharks have been caught encompass 'Disko Banke,' 'Store Hellefiskebanke' and 'Lille Hellefiskebanke' on the west coast, and 'Skjoldungen Banke' on the east coast.

Greenland sharks were most frequently caught between 400 and 700 m, and within this interval, occurrence decreased with depth. Generally, sharks caught at depths shallower than 1,000 m were between 300 and 400 cm (TL, range 166–510 cm). In this depth interval, only one shark was <200 cm (TL). In total, five sharks were caught deeper than 1,000 m (Fig. 3), but for one of these, length was not measured. Of the remaining four, three were <200 cm. In total, four sharks <200 cm (TL) have been caught since 1988 and sizes (TL/BM) of these were as follows: 106 cm/8.9 kg, 110 cm/10.6 kg, 166 cm/31 kg and 180 cm/80 kg. These sharks were caught on the west coast at 63.2°N 54.2°W, 63.6°N 54.3°W, 70.6°N 55.8°W and 63.4°N 55.3°W. The largest sharks have been caught at low latitudes, and sexually mature females (specimens approximately 450 cm in TL or larger) have only been caught in southwestern Greenland (south of 63°N, Fig. 4).

## Stomach content

Stomach content analysis was based on 30 sharks caught from April to September 2012 (Table 1). Six sharks had empty stomachs including no. 13 and 14 (Table 1), and thus, analyses were based on 24 sharks caught from July to September. Stomach content wet mass ranged between 0.05 and 30.8 kg, totaling 123.5 kg. 1.4 kg was non-prey

**Table 2** Composition of the diet of 24 Greenland sharks from Greenland waters caught from July to September 2012 presented as frequency of occurrence (% *F*), numerical proportion (% *N*), reconstructed biomass (% *B*) and index of relative importance (% IRI)

| | % *F* | % *N* | % *B* | % IRI |
|---|---|---|---|---|
| *Prey items* | | | | |
| Mollusca | | | | |
| Bivalvia | 12.5 | 1.4 | <0.1 | 0.3 |
| Cephalopoda | | | | |
| Teuthida | | | | |
| *Gonatus fabricii* | 16.7 | 16.7 | 2.6 | 6.1 |
| Gastropoda | 12.5 | 1.4 | <0.1 | 0.3 |
| Arthropoda | | | | |
| Malacostraca | | | | |
| Decapoda | | | | |
| *Lithodes maja* | 4.2 | 0.5 | <0.1 | <0.1 |
| *Hyas araneus* | 8.3 | 0.9 | <0.1 | 0.2 |
| Amphipoda[a] | 25.0 | | | |
| Echinodermata | | | | |
| Asteroidea (starfish) | 4.2 | 0.5 | <0.1 | <0.1 |
| Ophiuroidea (brittlestars) | 8.3 | 0.9 | <0.1 | 0.1 |
| Echinoidea (Sea urchins) | 4.2 | 0.4 | <0.1 | <0.1 |
| Chordata | | | | |
| Myxini | | | | |
| Myxiniformes | | | | |
| *Myxine glutinosa* | 4.2 | 0.9 | <0.1 | <0.1 |
| Chondrichthyes | | | | |
| Rajiformes | | | | |
| Rajidae | 33.3 | 4.2 | 3.8 | 5.0 |
| Egg capsule | 8.3 | 0.9 | <0.1 | 0.1 |
| *Amblyraja radiata* | 8.3 | 0.9 | 0.6 | 0.2 |
| Actinopterygii | | | | |
| Gadiformes | | | | |
| *Boreogadus saida* | 4.2 | 0.5 | <0.1 | <0.1 |
| *Gadus morhua* | 37.5 | 47.7 | 44.9 | 65.6 |
| *Macrourus berglax* | 4.2 | 0.5 | 0.7 | <0.1 |
| Pleuronectiformes | | | | |
| *Hippoglossoides platessoides* | 8.3 | 2.3 | 0.4 | 0.4 |
| *Reinhardtius hippoglossoides* | 4.2 | 0.5 | 1.1 | 0.1 |
| Scorpaeniformes | | | | |
| *Cyclopterus lumpus* | 12.5 | 1.4 | 0.8 | 0.5 |
| *Myoxocephalus scorpius* | 4.2 | 0.5 | 0.3 | <0.1 |
| *Sebastes* sp. | 8.3 | 1.9 | 0.7 | 0.4 |
| Perciformes | | | | |
| *Anarhichas lupus* | 8.3 | 0.9 | 2.9 | 0.6 |
| *Anarhichas minor* | 16.7 | 2.3 | 9.8 | 3.8 |
| *Lycodes* sp. | 12.5 | 1.9 | 0.8 | 0.6 |
| Unknown fish | 25.0 | 3.2 | 0.6 | 1.8 |
| Mammalia | | | | |
| Carnivora | | | | |
| *Cystophora cristata* | 4.2 | 0.5 | <0.1 | <0.1 |
| *Erignathus barbatus* | 8.3 | 0.9 | 6.5 | 1.2 |
| *Pagophilus groenlandicus* | 25.0 | 2.8 | 18.1 | 9.9 |
| Phocidae | 16.7 | 2.3 | 4.8 | 2.3 |
| *Ursus maritimus* | 4.2 | 0.5 | 0.4 | <0.1 |
| Undetermined digested material | 70.8 | | | |
| *Non-prey items* | | | | |
| Porifera | 4.2 | | | |
| Heterokontophyta | | | | |
| Phaeophyceae | | | | |
| Laminariales | 8.3 | | | |
| *Agarum clathratum* | 4.2 | | | |
| *Laminaria nigripes* | 8.3 | | | |
| Rocks | 25.0 | | | |
| Fishing equipment | 8.3 | | | |
| Garbage | 8.3 | | | |

For non-prey items and undetermined digested material, only % *F* was calculated

[a] Not considered a prey item as we expect these to be swallowed while either ingesting baited hooks on longlines and/or if eating on carcasses from the sea floor

items such as rocks, macroalgae, fishing gear, lysianassid amphipods, human garbage (including small metal pieces and an entire Pepsi can) and Porifera. The remaining 122.1 kg were prey items of which 97.0 % could be categorized to one of the following taxonomical groups: fish (Chondrichthyes, Cyclostomata and Osteichthyes), Mammalia, Cephalopoda, Decapoda, Bivalvia, Gastropoda and Echinodermata. 3.0 % was highly digested biological material and could not be categorized. Frequency of occurrence (% *F*), numerical proportion (% *N*), reconstructed biomass (% *B*) and index of relative importance (% IRI) of all prey items are presented in Table 2.

In total, 11 species of fish and four species of marine mammals were identified in shark stomachs. Additionally, redfish, eelpouts and skates were identified. Atlantic cod were observed in 37.5 % of the stomachs and based on IRI (65.6 % IRI) found to be more than six times as important as harp seal (*Pagophilus groenlandicus*, 9.9 % IRI), the second most important prey item. Skates (5.2 % IRI) and wolffish (spotted and Atlantic combined, 4.4 % IRI) were also found to be important. Of minor importance were eelpouts, lumpsucker (*Cyclopterus lumpus*), American plaice (*Hippoglossoides platessoides*) and redfish ($0.1 < \%$ IRI $< 1.0$). Furthermore, Greenland halibut, hagfish (*Myxine glutinosa*), roughhead grenadier (*Macrourus berglax*), shorthorn sculpin (*Myoxocephalus scorpius*), polar cod (*Boreogadus saida*) and egg capsules from skates were found as prey items but were of little importance

**Table 3** Size (TL ± SD) of the most important prey fishes sorted after importance (IRI)

| Species | *N* | Mean TL ± SD |
|---|---|---|
| *Gadus morhua* | 103 | 40.6 ± 7.6 |
| Rajidae | 11 | 36.5 ± 8.5 |
| *Anarhichas* spp. | 7 | 68.0 ± 20.6 |
| *Lycodes* sp. | 4 | 33.0 ± 8.3 |
| *Cyclopterus lumpus* | 3 | 21.3 ± 1.2 |
| *Hippoglossoides platessoides* | 5 | 26.4 ± 4.2 |
| *Sebastes* sp. | 4 | 24.0 ± 11.6 |

(% IRI ≤ 0.1). See Table 3 for size distribution of the most important prey fish. One invertebrate, boreoatlantic armhook squid (*Gonatus fabricii*), was of relatively high importance (6.1 % IRI) as 36 specimens were registered in four sharks (16.7 % *N*). However, as the majority (33 specimens) was found in a single stomach, the importance is most probably not reflected accurately by IRI. Mean PL ± SD of boreoatlantic armhook squid was 166.1 ± 32.5 mm (*N* = 36). Additionally, 15 otoliths from bony fish and 233 eye lenses from fish, cephalopods and mammals were identified.

Seal remains were found in 50 % of the stomachs weighing between 0.022 and 15.6 kg and consisted of pieces of skin, blubber, muscle tissue, bones, flippers, skulls, jaws, claws, intestines and lanugo fur (white fur from pups). Harp seal accounted for half of the seal observations and consisted of at least four adults and one sub-adult (a yearling). Lanugo fur was present in two sharks (no. 7 and 28 in Table 1), but it was not possible to determine whether these pups were harp seal or ringed seal (*Pusa hispida*). In one stomach (no. 16 in Table 1), remains of three seals were identified: one adult bearded seal (*Erignathus barbatus*, 1.2 % IRI) identified from skin and intestines, another adult seal identified from intestines and one fetus of unknown species. Furthermore, based on the growth rings in the front flipper claws, a 6-year-old bearded seal was identified (no. 21 in Table 1). The only observation of hooded seal (*Cystophera cristata*, <0.1 % IRI) was identified from a lower jaw, as it was identical in size and characteristics to the jaw of a fully grown 14-year female from the GINR Reference Collection. Newly ingested pieces of muscle tissue and skin from a polar bear (*Ursus maritimus*, wet mass = 0.688 kg, <0.1 % IRI) were identified (no. 1 in Table 1).

Faunae associated with carcasses such as lysianassid amphipods and gastropods (Britton and Morton 1994; MacNeil et al. 2012) were found in 25.0 and 12.5 % of the stomachs, respectively, whereas brittle stars were observed in 8.3 % and sea urchins and starfish in 4.2 % of the stomachs (=one observation). Macroalgae were found

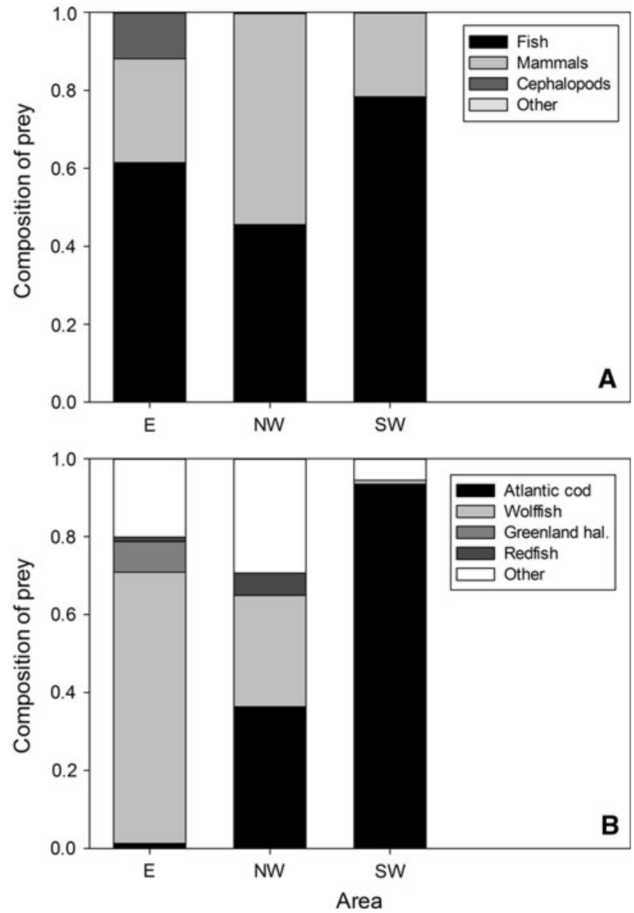


**Fig. 5** Composition of prey in three geographical areas (see text). **a** Reconstructed prey biomass sorted in four groups: 'Fish,' 'Mammals,' 'Cephalopods' and 'Other.' 'Other' is a summation of reconstructed biomass of Decapoda, Mollusca and Echinodermata. Total reconstructed biomasses in the areas were as follows: E = 37.2 kg, NW = 36.9 and E = 95.1 kg. **b** The relative importance of 'Greenland halibut,' 'Redfish,' 'Wolffish,' 'Atlantic cod' and 'Other.' 'Other' encompasses all remaining fishes (see Table 2). Reconstructed fish biomasses in the areas were as follows: E = 22.9 kg, NW = 17.3 kg and SW = 74.3 kg. *E* east (*N* = 9), *NW* northwest (*N* = 9) and *SW* southwest (*N* = 6)

in 20.8 % and rocks in 25.0 % of stomachs and were most likely swallowed accidently while feeding near the bottom. Two sharks from the west coast had been in contact with fishing gear as fishing hooks were found in one stomach and a gill net was found stuck between the teeth of another. This net most likely originated from Canadian waters, as the mesh size was 200 mm which is not used in Greenland but is a common mesh size in Canada.

Fish constituted between 45 and 75 % of the reconstructed biomass followed by mammals (25–55 %), but there were regional differences (Fig. 5a). Atlantic cod was of major importance in 'Southwest' (even when omitting specimens from shark no. 18 and 19 in Table 1 see discussion), whereas Atlantic cod was of no importance in

'East.' In 'East,' wolffish was the most important prey fish, and in 'Northwest,' wolffish and Atlantic cod were equally important. The group 'Other' only constituted up to a third of the reconstructed biomass of prey fish (Fig. 5b).

## Discussion

### Body metrics

The multivariate model performed slightly better in predicting weight than the single variable model. Previous studies have presented similar length weight relationships (e.g., Yano et al. 2007; Leclerc et al. 2012), but despite similar size ranges (see Fig. 2), they produce very different BM when extrapolating to large specimens. This study includes the heaviest shark ever reported (no. 19 in Table 1), but larger specimens of both sexes should be sampled to further validate the growth pattern.

### Distribution and frequency

In this study, all trawling stations shallower than 500 m have been hauled during day time (06 AM–06 PM), and since vertical migration patterns have been observed for Greenland sharks (Stokesbury et al. 2005; Fisk et al. 2012), the evaluation of distribution based strictly on bottom trawl should be carried out with caution. However, given the extensive trawl data used in this study, it should provide a good overview of the large-scale distribution pattern of Greenland sharks in Greenland waters. Tagging studies of Greenland sharks have revealed large-scale migrations (>900 km, Hansen 1963a; Fisk et al. 2012; Bushnell et al. unpublished data), and seasonal trends might not be reflected in the findings presented here as catches were concentrated in the summer and autumn.

Greenland sharks were caught with the highest frequency in 'Southwest' followed by 'East,' being less frequent in 'Northwest.' No sharks have been caught in large areas on the west and east coasts during summer and early autumn (Fig. 1), but whether this absence is linked to seasonal migration, foraging behavior and/or bathymetry is uncertain. Besides these areas, Greenland sharks appear to be present throughout Greenland waters at all depths. Previously, a positive correlation between capture depth and latitude has been reported (see Yano et al. 2007), but based on a much larger data set, we find that sharks are also caught in shallow waters at low latitudes (Fig. 3), suggesting that such a relationship does not exist in Greenland waters. Since 1988, only one of 64 specimens >200 cm (TL) was caught deeper than 1,000 m by bottom trawl, and we find sharks >200 cm (TL) to primarily occupy depths between 100 and 1,000 m with no distinct size-related trend. This also differs from a size- and depth-related trend reported by Yano et al. (2007), showing that the largest sharks are at the highest depths. It should be emphasized that sharks >200 cm in TL have been reported occasionally to perform rapid descends to depths deeper than 1,000 m; however, mean swimming depth of these sharks was above 1,000 m (Fisk et al. 2012). Yano et al. (2007) have not provided information on fishing effort; wherefore, it is not possible to evaluate whether these differences are caused by lack of sampling by Yano et al. (2007) in shallow waters at low latitudes or by seasonal differences in shark distribution.

According to GINR trawl data, small sharks (<200 cm, TL) were mainly caught at depths deeper than 1,000 m in west Greenland. This coincides with catches of sharks <150 cm (TL) reported by Yano et al. (2007) and suggests that there could be a nursing area in southwest Greenland beneath the continental shelf. The largest sharks were also caught at the lowest latitudes (Fig. 4). This trend is supported by commercial catch records from the northerly situated Disko Bay and Uummannaq areas (68–71°N) in 1936 where the largest of 156 Greenland sharks caught was 376 cm (Hansen 1963b).This pattern could be related to size-specific feeding trends, but the current data set does not allow for such conclusions. Furthermore, migratory behavior or spawning migration could cause size-related movement. However, little is known on these aspects of the life history of the Greenland shark.

### Stomach content

Greenland sharks are considered apex predators (MacNeil et al. 2012), but so far, there have been no firsthand observations of Greenland sharks attacking live prey. Studies from Svalbard conclude that Greenland sharks are active predators of fish and seals (Leclerc et al. 2012), and several observations from this study confirm such findings. For example, one wolffish was found with partially swallowed intact prey in its throat, indicating that it had just captured the prey when eaten by the shark. Another example is from two offshore trawl hauls of 2-min duration each on the same position, where two sharks (no. 18 and 19 in Table 1) were caught together with several hundred Atlantic cod. These sharks contained 48 and 35 specimens of Atlantic cod of varying digested stages. No scavenging faunae (e.g., lysianassid amphipods or brittle stars) were identified, which would have been expected if these fish had been found on the sea floor as carcasses (Britton and Morton 1994; Legezynska et al. 2000; Klages et al. 2001; Fisk et al. 2002). Fish prey were generally large (>25 cm in TL, Table 3), which indicates that Greenland sharks prefer or easily detect and catch larger specimens of fish. In support of this is the (almost) complete absence of polar cod in the stomachs. Polar cod is an epibenthic and very abundant species in Greenland waters, and it is an important food source for several marine mammals, birds and fishes (see Welch et al. 1993; Orr and Bowering 1997; Christiansen et al. 2012) and should be one of the most abundant prey items had this been solely a reflection of availability. The majority of prey fishes identified in this and other studies are strictly demersal or epibenthic (see Yano et al. 2007; McMeans et al. 2010; Leclerc et al. 2012), suggesting that hunting for fish mainly is carried out along the sea floor.

Seal remains were observed in 50 % of the stomachs, which is consistent with other studies (see Yano et al. 2007; Leclerc et al. 2012). In stomachs containing freshly ingested seal parts, there was no scavenging fauna or other indications of this being scavenged from a carcass. The majority of observations of scavenging fauna stemmed from sharks caught on baited hooks, and as lysianassid amphipods colonized the bait within a few hours (personal observation), this method of capture obviously complicates the use of such fauna as indicators of recent scavenging events. The largest number of lysianassid amphipods observed in a single stomach was nine, and these were found in the stomach containing tissue from a polar bear (no. 1 in Table 1). As this tissue seemed recently ingested and the shark was caught by trawl, the polar bear was most likely eaten as a carcass. Overall, our findings suggest that seals are caught actively by Greenland sharks, which is consistent with bite marks observed on live seals reported by Canadian inuit hunters (Idrobo and Berkes 2012).

In general, fish were the most important type of prey followed by mammals (Fig. 5a), which is similar to comparable studies by Yano et al. (2007), McMeans et al. (2010) and Leclerc et al. (2012). Within these groups, Atlantic cod, harp seal, skates (most likely thorny ray), and wolffish were most common, which, except for harp seal, have also been found as common prey in Iceland and Svalbard waters (McMeans et al. 2010; Leclerc et al. 2012). The high preference for Atlantic cod is supported by findings of Leclerc et al. (2012) and Rusyaev and Orlov (2013). There are, however, large discrepancies between this study and the only other study on prey composition in Greenland waters, where Greenland halibut, Pinnipedia (seals) and northern shrimp were reported as main prey items (see Yano et al. 2007). These discrepancies might be explained by differences in sampling area. Sampling in this study was conducted all over the Greenland continental margin, whereas Yano et al. (2007) mainly analyzed sharks sampled in deeper offshore waters (>1,000 m). This could well result in different prey availability, different shark size distribution and, consequently, different prey composition. Also, sharks evaluated by Yano et al. (2007) were sampled prior to 1995 in a period when Atlantic cod was virtually absent from Greenland offshore waters (Retzel 2012). This may have caused a shift in shark distribution to deeper waters and a subsequent shift to other prey species such as Greenland halibut. Unfortunately, Yano et al. (2007) do not provide data on fishing effort, making comparison with shark densities of this study impossible. The number of sharks caught since 1988 in bottom trawl during GINR fish surveys is too low to detect any such possible shifts in distribution of Greenland sharks.

Relative availability has been suggested as an explanation for the difference in composition of prey fishes (and mammals) observed between Svalbard, Iceland and Greenland waters (Leclerc et al. 2012). This is obviously the explanation for the high importance of harp seal found in this study and might explain the difference in the importance of Atlantic cod between the east coast and west coast (Fig. 5b). Biomass estimates from annual surveys can be used as an indicator of seasonal relative availability as Greenland waters are surveyed simultaneously to the shark sampling in this study (see Jørgensen and Treble 2011; Nygaard et al. 2011; Jørgensen 2012; ICES 2013). Redfish are abundant in all the areas, and it is therefore surprising that redfish were not an important prey species (Fig. 5b). Similarly, it is surprising that Greenland halibut appear to be of no importance for sharks caught in 'Northwest' (Fig. 5b), where Greenland halibut is abundant. Whether these findings indicate some degree of prey selectivity is difficult to conclude as the number of sharks of this study is relatively small. However, it might suggest that Greenland sharks have a preference for Atlantic cod, harp seal and wolffish in the investigated areas during summer and early autumn as opposed to redfish, Greenland halibut and northern shrimp which previously have been suggested as main prey items (including seals) in Greenland waters (Yano et al. 2007).

The ecological significance of Greenland shark cannot be fully evaluated without estimates of shark abundance and an understanding of metabolic expenditures. However, taking their ubiquitous presence into consideration, this shark should be considered a key species in the arctic food web.

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## References


Anon (1942) Beretninger vedr. Grønlands Styrelse. Sammendrag af Statistiske Oplysninger om Grønland 1:647–652 (In Danish)

Beck B, Mansfield AW (1969) Observations on the Greenland sharks, *Somniosus microcephalus*, in northern Baffin Island. J Fish Board Can 26:143–145

Bexton S, Thompson D, Brownlow A, Barley J, Milne R, Bidewell C (2012) Unusual mortality of Pinnipeds in the United Kingdom associated with helical (Corkscrew) injuries of anthropogenic origin. Aquatic Mamm 38:229–240

Britton JC, Morton B (1994) Marine carrion and scavengers. Oceanogr Mar Biol Ann Rev 32:369–434

Campana SE (2004) Photographic atlas of fish otoliths of the Northwest Atlantic Ocean. NRC Research Press, Ottawa

Christiansen JS, Hop H, Nilsson EM, Joensen J (2012) Trophic ecology of sympatric Arctic gadoids, *Arctogadus glacialis* (Peters 1872) and *Boreogadus saida* (Lepechin 1774) in NE Greenland. Polar Biol 35:1247–1257. doi:10.1007/s00300-012-1170-y

Clarke MR (1986) A handbook for identification of cephalopod beaks. Oxford Science Publications, Oxford

Cortés E (1997) A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Can J Aquat Sci 54:726–738

Fisk AT, Tittlemier SA, Pranschke JL, Norstrom RJ (2002) Using anthropogenic contaminants and stable isotopes to assess the feeding ecology of Greenland sharks. Ecology 83:2162–2172

Fisk AT, Lydersen C, Kovacs KM (2012) Archival pop-off tag tracking of Greenland sharks *Somniosus microcephalus* in the High Arctic waters of Svalbard, Norway. Mar Ecol Prog Ser 468:255–265. doi:10.3354/meps09962

Frank KT, Petrie B, Shackell NL (2007) The ups and downs of trophic control in continental shelf ecosystems. Trends Ecol Evol 22:236–242. doi:10.1016/j.tree.2007.03.002

Froese R, Pauly D (eds) (2012) FishBase. World Wide Web electronic publication. www.fishbase.org version (10/2012)

Hansen PM (1963a) Tagging experiments with the Greenland shark (*Somniosus microcephalus* (Block and Schneider)) in subarea 1. Int Comm Northwest Atl Fish Special Publ 4:172–175

Hansen PM (1963b) Skrivelse Danmarks Fiskeri-og Havundersøgelse :83–95 (In Danish)

Hansen JH, Hedeholm RB, Sünksen K, Christensen JT, Grønkjær P (2012) Spatial variability of carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N) stable isotope ratios in an Arctic marine food web. Mar Ecol Prog Ser 467:47–59. doi:10.3354/meps09945

Hyslop EJ (1980) Stomach content analysis: a review of methods and their application. J Fish Biol 17:411–429

ICES (2013) Report of the North-Western Working Group (NWWG) 26. April-3.May 2012. ICES Headquarters, Copenhagen. ICES CM 2012/ACOM:07.1425

Idrobo CJ, Berkes F (2012) Pangnirtung inuit and the Greenland shark: co-producing knowledge of a little discussed species. Hum Ecol 40:405–414. doi:10.1007/s10745-012-9490-7

Jørgensen OA (2012) Scientific council meeting—June 2012. Survey for Greenland Halibut in NAFO Division 1C-1D, 2011. NAFO SCR Doc 12/003

Jørgensen OA, Treble MA (2011) Scientific council meeting—June 2011. Assessment of the Greenland Halibut Stock Component in NAFO Subarea 0 + Division 1A Offshore + Division 1B-1F. NAFO SCR Doc 11/027

Klages M, Vopel K, Bluhm H, Brey T, Soltwedel T, Arntz WE (2001) Deep-sea food falls: first observation of a natural event in the Arctic Ocean. Polar Biol 24:292–295. doi:10.1007/s003000000199

Leclerc LM, Lydersen C, Haug T, Glover KA, Fisk AT, Kovacs KM (2011) Greenland shark (*Somniosus microcephalus*) scavenge offal from minke (*Balaenoptera acutorostrata*) whaling operations in Svalbard (Norway). Polar Res 30:7342. doi:10.3402/polar.v30i0.7342

Leclerc LME, Lydersen C, Haug T, Bachmann L, Fisk AT, Kovacs KM (2012) A missing piece in the Arctic food web puzzle? Stomach contents of Greenland sharks sampled in Svalbard, Norway. Polar Biol 35:1197–1208. doi:10.1007/s00300-012-1166-7

Legezynska J, Weslawski JM, Presler P (2000) Benthic scavengers collected by baited traps in the high Arctic. Polar Biol 23:539–544

Lucas ZN, Natanson LJ (2010) Two shark species involved in predation on seals at sable Island, Nova Scotia, Canada. Proc Nova Scotian Instit Sci 45:64–88

Lucas Z, Stobo WT (2000) Shark-inflicted mortality on a population of harbour seals (*Phoca vitulina*) at Sable Island, Nova Scotia. J Zool 252:405–414

MacNeil MA, McMeans BC, Hussey NE, Vecsei P, Svavarsson J, Kovacs KM, Lydersen C, Treble MA, Skomal GB, Ramsey M, Fisk AT (2012) Biology of the Greenland shark *Somniosus microcephalus*. J Fish Biol 80:991–1018. doi:10.1111/j.1095-8649.2012.03257.x

McMeans BC, Svarvarsson J, Dennard S, Fisk AT (2010) Diet and resource use among Greenland sharks (*Somniosus microcephalus*) and teleosts sampled in Iceland waters, using $\delta^{13}$C, $\delta^{15}$N, and mercury. Can J Fish Aquat Sci 67:1428–1438. doi:10.1139/F10-072

Nielsen JG, Bertelsen E (1992) Fisk i grønlandske farvande. Atuakkiorfik, Nuuk (In Danish)

Nygaard R, Fock H, Stransky C (2011) Scientific council meeting—June 2011. Assessment of Demersal Redfish in NAFO Subarea 1. NAFO SCR Doc 11/40

Orr DC, Bowering WR (1997) A multivariate analysis of food and feeding trends among Greenland halibut (*Reinhardtius hippoglossoides*) sampled in Davis Strait during 1986. ICES J Mar Sci 54:819–829

Pedersen PM (2011) Grønlands havalger. Forlaget Epsilon.dk (in Danish)

Pinkas LM, Oliphant S, Iverson ILK (1971) Food habits of albacore, bluefin tuna and bonito in Californian waters. Cal Fish Game 152:1–105

Retzel A (2012) Greenland commercial data for Atlantic cod in Greenland offshore waters for 2011. ICES North Western Working Group, 26. April 3. May 2012. Working doc 17

Ridgway SH, Harrison RJ (1981) Handbook of marine mammals, vol 2. Academic Press, Toronto

RStudio (2012) RStudio: Integrated development environment for R (Version 0.96.122) [Computer software]. Boston, MA. Retrieved October 2012. Available from http://www.rstudio.org/

Rusyaev SM, Orlov AM (2013) Bycatches of the Greenland shark *Somniosus microcephalus* (Squaliformes, Chondrichthyes) in the Barents sea and adjacent waters under bottom trawling data. Journal of Ichthyology 53:111–115. doi:10.1134/S0032945213010128

Stokesbury MJW, Harvey-Clark C, Gallant J, Block BA, Myers RA (2005) Movement and environmental preferences of Greenland sharks (*Somniosus microcephalus*) electronically tagged in the St. Lawrence Estuary, Canada. Mar Biol 148:159–165

Welch HE, Crawford RE, Hop H (1993) Occurrence of Arctic cod (*Boreogadus saida*) schools and their vulnerability to predation in the Canadian High Arctic. Arctic 46:331–339

Yano K, Stevens JD, Compagno LJV (2007) Distribution, reproduction and feeding of the Greenland shark *Somniosus* (*Somniosus*) *microcephalus*, with notes on two other sleeper sharks, *Somniosus* (*Somniosus*) *pacificus* and *Somniosus* (*Somniosus*) *antarcticus*. JFish Biol 70:374–390. doi:10.1111/j.1095-8649.2007.01308.x

Zumholz K, Frandsen RP (2006) New information on the life history of cephalopods off west Greenland. Polar Biol 29:169–178. doi:10.1007/s00300-005-0036-y