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Greenland Shark (*Somniosus microcephalus*) Stomach Contents and Stable Isotope Values Reveal an Ontogenetic Dietary Shift

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Current knowledge on the feeding ecology of the Greenland shark (*Somniosus microcephalus*), a potential top predator in arctic marine ecosystems, is based on small sample sizes as well as narrow size ranges of sharks. Therefore, potential size-related feeding patterns remain poorly documented. Using stomach content data (*N* = 88) and stable isotope values of white muscle tissue (*N* = 40), this study evaluates the diet of sharks ranging in size from 81 to 474 cm (total length). The importance of prey categories (“Fish,” “Mammal,” “Squid,” “Crustacean,” and “Other”) was evaluated based on the reconstructed prey biomass of the stomach contents. Stable isotope values of δ¹³C and δ¹⁵N ranged between −14.4 to −19.9‰ and 11.8 to 17.2‰, respectively. The importance of each prey category was estimated by the Index of Relative Importance (IRI). Our findings suggest that the smallest Greenland sharks (<200 cm) feed on lower trophic level prey, predominantly squids. Larger sharks (>200 cm) mainly feed on higher trophic level prey such as seals, epibenthic and benthic fishes including gadoids (Gadidae), skates (Rajidae), righteye flounders (Pleuronectidae), lumpfish (Cyclopteridae), wolffish (Anarhichadidae), and redfish (Sebastidae). Redfish were, however, only found to be important in the largest sharks sampled (>400 cm). In addition to demonstrating ontogenetic shifts in their feeding preferences, this study supports that Greenland sharks are capable of active predation on fast swimming seals and large fishes.

**Keywords:** Greenland shark, diet, feeding ecology, stomach content, isotopes

**INTRODUCTION**

During the past 10 years, the Greenland shark (*Somniosus microcephalus*) has been subject to increased scientific attention due to its role as a long-lived, highly migratory, and relatively abundant top predator in arctic marine food webs (MacNeil et al., 2012; Campana et al., 2015; Nielsen et al., 2016). The Greenland shark is distributed across the Arctic and in the cold temperate...
waters of the Atlantic and reaches more than 5 m in length. (Compagno, 1984; Mecklenburg et al., 2018). Although they are occasionally reported in shallow waters (<30 m, Harvey-Clark et al., 2005; Eriksen, 2011), Greenland sharks predominantly occur in deep waters (>200 m, Fisk et al., 2012; Campagna et al., 2015), where they have been recorded as deep as 2,992 m near the mid-Atlantic Ridge (Porteiro et al., 2017). In Greenland waters, Greenland sharks are most often encountered at depths of 400–700 m (Nielsen et al., 2014).

Previous studies have investigated the diet and trophic interactions of Greenland sharks by analyzing stomach contents, stable isotopes, and fatty acids (Fisk et al., 2002; Yano et al., 2007; McMeans et al., 2010; Leclerc et al., 2012; McMeans et al., 2013; Nielsen et al., 2014). These studies are mostly based on relatively few individuals (N < 50) from 200 to 400 cm in length, with limited information on larger individuals. Ontogenetic dietary shifts have been documented for other large predatory sharks such as sevengill (Notorynchus cepedianus), white (Carcharodon carcharias), and tiger sharks (Galeocerdo cuvier) (Lowe et al., 1996; Ebert, 2002; Estrada et al., 2006), and preliminary data suggest that small Greenland sharks have a lower trophic position compared to larger sharks (Fisk et al., 2002). Dietary differences across Greenland shark size thus becomes relevant to investigate.

Size distribution of Greenland sharks appears to vary spatially. While sharks <400 cm seem to dominate in the Canadian Arctic, northern Greenland and the Svalbard Archipelago (Norway), larger sharks >400 cm seem to be more common off southern Greenland, Iceland, and Newfoundland (Nielsen et al., 2014; Campagna et al., 2015; Lydersen et al., 2016; Devine et al., 2018).

This study documents the feeding ecology of the Greenland shark, investigated across a large size range, by analyzing stable isotopes and stomach contents. Specifically, we identified prey in stomach contents to the lowest possible taxonomical level, estimated their biomass, and calculated the relative importance of prey through ontogeny. Stable isotopes levels were used to determine whether prey composition was reflected in the 15N signal. Elaborating on the feeding ecology of different sized Greenland shark, currently listed as Near Threatened in the IUCN Red List of Threatened Species and as Data Deficient in the Norwegian Red List (Henriksen and Hilmo, 2015; IUCN, 2018), will allow for a more complete understanding of the species’ role as an important predator in arctic ecosystems.

MATERIALS AND METHODS

Sampling

Greenland sharks (N = 78) from Greenland waters were caught from 2013 to 2017 as part of the international collaboration project “Old and Cold – Biology of the Greenland shark.” Sampling was obtained by the Greenland Institute of Natural Resources (GINR) annual fish surveys (RV Pâmiut, RV Sanna), the TUNU IV and V Expeditions (RV Helmer Hanssen) (Christiansen, 2012), the commercial trawler FV Sisimiut, and targeted Greenland shark expeditions with RV Porsild and RV Sanna. All sampling was carried out in accordance with laws, regulations and authorization from the Government of Greenland (Ministry of Fisheries, Hunting and Agriculture, document number 565466, 935119, 20179208, C-17-129, C-15-17, and C-13-16). Overlap in both sampling area and season (West and East Greenland, inshore and offshore, May–September) allowed us to pool stomach content data with an additional 30 specimens caught in 2012 [reported separately in Nielsen et al. (2014)], increasing the total number of sharks included in this study to 108. All sharks were measured (total length, TL, cm) and the sex determined from the presence (males) or absence (females) of claspers. All shark lengths in this study are reported as TL. To evaluate possible size-related dietary differences, sharks were grouped into six “shark size groups” (TL bins); <200 cm, 201–250 cm, 251–300 cm, 301–350 cm, 351–400 cm, and >400 cm. As in previous studies, data for males and females were combined (see Yano et al., 2007; McMeans et al., 2010; Leclerc et al., 2012; Nielsen et al., 2014). Bin ranges were chosen as “juvenile” sharks of both sexes have previously been defined as those <200 cm (Hussey et al., 2015). In this study (and in general), sharks >400 cm are strictly females and further also potentially mature [cf. Yano et al. (2007) suggesting that males mature at ~300 cm and females mature at >400 cm]. Shark size groups between 200 and 400 cm are thus composed by both immature males and females and potentially mature males.

Stomach Contents

Each stomach was removed and contents examined following the procedure described in Nielsen et al. (2014), with each prey item counted, measured, weighed, and identified to the lowest possible taxonomical level. All prey items were grouped into five prey categories: “Fish,” “Mammal,” “Squid,” “Crustacean,” and “Other.” The “Other” category included birds and all invertebrates except squids and crustaceans. The remaining stomach contents were designated “Non-prey items” and encompassed small rocks/stones, fishing gear, macro algae, metal pieces, fragments of Porifera, small bivalves (<1 cm), and scavenging lyssianassid amphipods. For all “Non-prey items” only frequency of occurrence was calculated.

Reconstructed Biomass

In an attempt to reflect the initial (undigested) quantity of prey consumed, a “reconstructed biomass” was calculated for all prey items (except mammals, see explanation below). For each fish prey item, the reconstructed biomass was calculated from species or genus-specific length-weight relationship acquired from FishBase (Froese and Pauly, 2018). Squid size (pen length) and reconstructed biomass were calculated from beak size according to Zumholz and Frandsen (2006). No attempt was made to reconstruct the initial biomass of any mammal prey items (Nielsen et al., 2014) as it would be unrealistic to assume that an entire large marine mammal, potentially weighing hundreds or thousands of kilogram, was consumed by the shark. Therefore, for calculation purposes, the reconstructed biomass for each mammal prey item was set to be the actual wet mass as this would conservatively reflect the initial quantity consumed. Whenever possible, body morphometrics and wet mass of intact cnidarians (sea anemones), molluscs ( gastropods), crustaceans (amphipods and decapods), echinoderms (sea urchins, sea stars,
bristle stars, and sea cucumbers), and birds were used to estimate initial wet mass of digested specimens. The proportion of reconstructed biomass for each prey category (i.e., “Fish,” “Mammal,” “Squid,” “Crustacean,” and “Other”) was plotted as mean values (± SE) for each of the six shark size groups.

Index of Relative Importance
The index of relative importance (IRI) for prey items was calculated from the number of prey items (N), the reconstructed biomass of prey items (B) and the frequency of occurrence of prey items (F) expressed as proportions (%), as described in Nielsen et al. (2014). For shark size groups with significantly different $^{15}$N levels (cf. size group <200 cm, see section “Results”) the %IRI was calculated for each prey type. %IRI was also calculated separately for each of the six shark size groups and presented as a summarized %IRI-score for prey categories (“Fish,” “Mammal,” “Squid,” “Crustacean,” and “Other”) as well as at family level within these categories.

Stable Isotopes
Stable isotope analysis of Greenland shark muscle tissue poses two challenges. Firstly, the muscle tissue is lipid rich which demands either chemical lipid extraction or mathematical correction to avoid bias from lipid carbon (Shipley et al., 2017). Secondly, shark muscle contains urea and trimethylamine N-oxide (TMAO), which tend to be depleted in $^{15}$N relative to protein N (Carlisle et al., 2017; Shipley et al., 2017). In order to compare data with the three main studies that present Greenland shark isotope values (Fisk et al., 2002; Hansen et al., 2012; and McMeans et al., 2013), we did not extract the TMAO, but performed lipid extraction. Hence, the $^{13}$C values presented are from lipid extracted samples, whereas the $^{15}$N values are from non-lipid extracted samples, thereby circumventing both the effect of $^{13}$C depleted lipid on $^{13}$C values and the potential effects of lipid extraction on $^{15}$N values.

White muscle tissue (5–10 g) sampled dorsal to the vertebrae and anterior to the first dorsal fin, was dried at 60°C for at least 48 h and split in two aliquots. One sample was lipid extracted using 5 ml of a 2:1 chloroform/methanol mixture which was put into a sealed vial. The sample was allowed to extract for 24 h after which the supernatant was removed. This procedure was repeated three times. The vial and sample was then rinsed with another 5 ml of the chloroform/methanol mixture, and the rinsed sample was allowed to dry for 24 h in a fume hood. Both the lipid extracted and non-lipid extracted samples were pulverized in an agate mortar and 0.4–1 mg replicate samples of both aliquots were packed in tin capsules. The $^{15}$N and $^{13}$C values were standardized using a Gelatine A (Gel-A) standard with known isotopic values of $^{15}$N = 5.4% and $^{13}$C = −21.8%. In order to correct for daily offsets and drift, two or three internal 0.2–0.7 mg Gel-A standards were assayed every nine or ten tissue samples.

All the samples were analyzed at Department of Bioscience, Center for Geomicrobiology, University of Aarhus, Aarhus, Denmark using comparable techniques to previous stable isotope analysis on Greenland sharks (e.g., Fisk et al., 2002). The samples were measured by means of Isotope Ratio Mass Spectrometry in combination with an Element Analyzer and an operational interface (Thermo Electron Corporation Flash EA 1112 series and Thermo Scientific Delta V Plus Isotope Ratio MS). Results are expressed in a δ notation as the deviation from international standards in parts per thousand (‰) according to the formula:

$\delta X = \left[ \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1000$

where X is either $^{13}$C or $^{15}$N, $R_{\text{sample}}$ is $^{13}$C/$^{12}$C or $^{15}$N/$^{14}$N in the sample, and $R_{\text{standard}}$ is the ratio for the given standards. Standards for $^{15}$N were calibrated against atmospheric air. Statistical analysis was carried out in the statistical computing program R (R Development Core Team, 2017). Analysis of variance and post hoc Tukey HSD test were used to evaluate the variation in $^{15}$N and $^{13}$C values between shark size groups. The level of significance was $P < 0.05$.

RESULTS

Sampling and Stomach Contents
A total of 108 Greenland sharks were sampled from May to September 2012–2017 in inshore and offshore waters (Figure 1). Males measured from 104 to 372 cm ($N = 27$) and females from 81 to 474 cm ($N = 79$) (Supplementary Table S1). Due to wounds inflicted by conspecifics during capture, the sex of two sharks could not be determined. Stomachs were available from 102 specimens. Since fourteen stomachs were empty, 88 stomachs from sharks ranging in size from 81 to 474 cm were included in the stomach content analysis (Table 1 and Supplementary Table S1). The total wet biomass of stomach contents was 462.3 kg and ranged between 0.029 and 52.0 kg for individual stomachs (mean ± SD: 5.3 ± 9.1 kg). In total, 3.5 kg was categorized as “Non-prey items” and of the remaining 458.8 kg of stomach contents, 96.9 % was assigned to one of the following prey categories: “Fish,” “Mammal,” “Squid,” “Crustacean,” or “Other.” The remaining 3.1% was made up by non-identifiable digested biological material. Of the 88 stomachs analyzed, a total of 697 prey items were identified representing 57 different prey types (Table 2).

Reconstructed Prey Biomass and Index of Relative Importance
The total reconstructed biomass was 635.3 kg, adding an additional 176.5 kg to the observed biomass. The reconstructed biomasses for prey categories showed that “Squid” dominated the diet for Greenland sharks <200 cm, whereas “Fish” and “Mammal” were of major importance for all larger size groups (Figure 2). For these (i.e., sharks >200 cm), “Fish” constituted approximately 70% of the reconstructed biomass, and “Mammal” became gradually more prevalent with body length, increasing from 10 to 20% (Figure 2). For sharks <200 cm, armhook squid (Gonatus spp.) was present in all stomachs as the most dominant prey item (%IRI = 93.7, Table 2). For sharks >200 cm, Atlantic cod (Gadus morhua) (%IRI = 26.6) and unknown teleost (%IRI = 17.6) were the main prey followed by Greenland halibut (Reinhardtius
FIGURE 1 | Capture locations for Greenland sharks (N = 108). Color indicates shark size (TL).

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**Stable Isotopes**

Samples for stable isotope analysis were available from 40 sharks measuring between 81 and 474 cm (Supplementary Table S1, Table 1). White muscle $\delta^{13}$C values ranged from $-14.4$ to $-19.9\%_o$ and $\delta^{15}$N between 11.8 and 17.2%o (Supplementary Table S1, Figure 3). While there was no significant difference in $\delta^{13}$C values among size groups (ANOVA, $F_{4,34} = 0.86$, $P = 0.5$), $\delta^{15}$N values differed significantly (ANOVA, $F_{4,34} = 5.8$, $P < 0.05$, Figure 4). Sharks <200 cm had significantly lower $\delta^{15}$N values compared to the three largest size groups (post hoc Tukey HSD test $P < 0.05$) whereas the four largest size groups (251–300 cm, 301–350 cm, 351–400 cm, >400 cm) were not statistically different (Figure 4). As the $\delta^{15}$N value for the 201–250 cm size group was based on only one individual, it was not included in the ANOVA.

**DISCUSSION**

This study investigated the ontogenetic shift of the diet of Greenland sharks and found that the smallest sharks (<200 cm) generally fed at a lower trophic level compared to larger sharks, both in terms of prey items and isotopic $\delta^{15}$N levels. This finding

<table>
<thead>
<tr>
<th>Size bin</th>
<th>Sample size, N</th>
<th>Stomach contents</th>
<th>Stable isotopes</th>
</tr>
</thead>
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<td>&lt;200</td>
<td>8</td>
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<td>8</td>
</tr>
<tr>
<td>201–250</td>
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<td>1</td>
<td>1</td>
</tr>
<tr>
<td>251–300</td>
<td>17</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>301–350</td>
<td>25</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td>351–400</td>
<td>18</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>&gt;400</td>
<td>18</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>Total</td>
<td>88</td>
<td>40</td>
<td>40</td>
</tr>
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</table>

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TABLE 2 | %F = frequency of occurrence, %N = number of prey items, %B = reconstructed biomass, and %IRI = Index of relative importance, for sharks <200 cm (N = 8) and >200 cm (N = 80).

<table>
<thead>
<tr>
<th>Family</th>
<th>Common name</th>
<th>% F &lt;200 cm</th>
<th>% N &lt;200 cm</th>
<th>% B &lt;200 cm</th>
<th>% IRI &lt;200 cm</th>
<th>% F &gt;200 cm</th>
<th>% N &gt;200 cm</th>
<th>% B &gt;200 cm</th>
<th>% IRI &gt;200 cm</th>
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</thead>
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<td>Fish</td>
<td></td>
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<tr>
<td>Gadus morhua</td>
<td>Gadidae Gadoids</td>
<td>26.3</td>
<td>20.0</td>
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<td>26.6</td>
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<td>Gadidae Gadoids</td>
<td>18.8</td>
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<td>4.2</td>
<td></td>
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<td>Boreogadus saida</td>
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<td>2.1</td>
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<td>Gadus ogac</td>
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<tr>
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<td>3.7</td>
<td>17.6</td>
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<td>Rajidae</td>
<td>Rajidae Skates</td>
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<td>5.8</td>
<td>3.3</td>
<td>8.5</td>
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<td>Rajidae, egg case</td>
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<td>Anarchichadidae Wolfish</td>
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<td>0.0</td>
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<td>Macrourus berglax</td>
<td>Macrouridae Grenadiers</td>
<td>1.3</td>
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<tr>
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<td>16.3</td>
<td>2.2</td>
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<td>2.0</td>
<td>0.5</td>
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<tr>
<td>Squid</td>
<td></td>
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<tr>
<td>Gonatus spp.</td>
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<td>100</td>
<td>22.5</td>
<td>80.0</td>
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(Continued)
TABLE 2 | Continued

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<th>Family</th>
<th>Common name</th>
<th>% F &lt;200 cm</th>
<th>% N &lt;200 cm</th>
<th>% B &lt;200 cm</th>
<th>% IRI &lt;200 cm</th>
<th>% F &gt;200 cm</th>
<th>% N &gt;200 cm</th>
<th>% B &gt;200 cm</th>
<th>% IRI &gt;200 cm</th>
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<tr>
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<tr>
<td><strong>Infraorder</strong></td>
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<td>Eurythenes gryllus</td>
<td>Lysianassida</td>
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<td>2.8</td>
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<td><em>Hyas</em> spp.</td>
<td>Brachyura</td>
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<td>2.4</td>
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<td>0.6</td>
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<td>Chionoecetes opilio</td>
<td>Brachyura</td>
<td>Crab</td>
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<td>0.1</td>
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<tr>
<td>Lithodes maja</td>
<td>Brachyura</td>
<td>Crab</td>
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<tr>
<td>Pandalus borealis</td>
<td>Caridea</td>
<td>Shrimp</td>
<td>1.3</td>
<td>0.2</td>
<td>0.0</td>
<td>&lt;0.01</td>
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</tr>
<tr>
<td>Pandalus spp.</td>
<td>Caridea</td>
<td>Shrimp</td>
<td>12.5</td>
<td>1.3</td>
<td>2.2</td>
<td>&lt;0.1</td>
<td>0.2</td>
<td>0.0</td>
<td>&lt;0.01</td>
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<tr>
<td>Sclerocrangon boreas</td>
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<td>Shrimp</td>
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<td>0.0</td>
<td>&lt;0.01</td>
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<tr>
<td>Pasiphaea spp.</td>
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<td>0.5</td>
<td>0.0</td>
<td>&lt;0.01</td>
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<td>Colossendeis proboscidea</td>
<td>Colossendeidae</td>
<td>Marine sea spider</td>
<td>12.5</td>
<td>2.2</td>
<td>&lt;0.1</td>
<td>0.2</td>
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<tr>
<td><strong>Other</strong></td>
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<td></td>
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<tr>
<td>Unknown auk</td>
<td>Auk</td>
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<td>0.3</td>
<td>0.2</td>
<td>&lt;0.01</td>
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<tr>
<td>Ophiuroidea</td>
<td>Brittle star</td>
<td>Sea cucumber</td>
<td>8.8</td>
<td>0.1</td>
<td>0.1</td>
<td>&lt;0.01</td>
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<tr>
<td>Holothuroidea</td>
<td>Sea anemone</td>
<td>Seaurchin</td>
<td>1.3</td>
<td>0.1</td>
<td>2.0</td>
<td>&lt;0.01</td>
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<tr>
<td>Arctinia</td>
<td>Sun star</td>
<td>1.3</td>
<td>0.2</td>
<td>0.2</td>
<td>&lt;0.01</td>
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<tr>
<td>Echinoidae</td>
<td>Starfish</td>
<td>3.8</td>
<td>0.2</td>
<td>0.2</td>
<td>&lt;0.01</td>
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<tr>
<td>Solasteridiae</td>
<td>Snail</td>
<td>17.5</td>
<td>0.1</td>
<td>0.0</td>
<td>&lt;0.01</td>
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</tr>
</tbody>
</table>

Non-prey items (%F): <200 cm: Amphipods 25; >200 cm: Macro algae 11.3, Bivalvia 5.0, Portifera 3.8, amphipod 26.3, rock 21.3, fishing equipment 8.8, metal 2.5 For sharks <200 cm, reconstructed biomass is 10.8 kg for 45 prey items. For sharks >200 cm, reconstructed biomass is 624.5 kg for 652 prey items.

FIGURE 2 | Proportional composition of reconstructed biomass of prey categories (“Fish,” “Mammal,” “Squid,” “Crustacean,” and “Other”) in the different shark size categories, for the 88 sharks with non-empty stomachs. Reconstructed biomass of each prey category is plotted as mean ± SE and the sample size (N) is given for each shark size category.

mirrors observations by Fisk et al. (2002), who reported lower $\delta^{15}N$ values in two 135 cm sharks compared to fifteen specimens >250 cm. We also observed that the stomach contents of the <200 cm sharks were mainly armhook squid and the $\delta^{15}N$ values were similar to that of other squid-feeding predators of the North Atlantic (Hooker et al., 2001; Mendes et al., 2007). The $\delta^{15}N$ values of larger sharks >200 cm indicated a diet consisting of higher trophic level prey such as large piscivorous fishes and seals corresponding with stomach content results for these size classes, which primarily consisted of Atlantic cod, Greenland halibut and seals (see stable isotope values for Greenlandic marine food webs in Hansen et al., 2012). Taken together, the stomach contents and $\delta^{15}N$ analyses suggests an ontogenetic shift from small (<200 cm), primarily squid-eating sharks, to larger (>200 cm), fish and mammal-eating sharks. However, sample size was limited for sharks from 201 to 250 cm, making it challenging to determine at which exact size the ontogenetic shift occurs.

When investigating the feeding ecology of a species, it is important to combine data of stomach contents and stable isotopes because stable isotopes provide an integrated and long-term estimate of trophic position that cannot be inferred from stomach content (Hobson and Welch, 1992; Christiansen et al., 2012). Although, stomach content analysis enables prey species identification and provides a detailed snapshot of recently ingested prey, regurgitation during capture and varying rates of digestion can skew the stomach content results leading to spurious conclusions, especially when sample size is small (Wetherbee et al., 2012). In this study, armhook squid was the single most important prey for the smallest sharks (<200 cm, %IRI = 97.6, Table 2), and was also relatively important in sharks >200 cm (%IRI = 6.8, Table 2), and more specifically, for 351–400 cm sharks (%IRI = 27.1, Table 3). For the
<table>
<thead>
<tr>
<th>Size Category</th>
<th>Recons. Biomass</th>
<th>No. Prey Items</th>
<th>Fish (%IRI)</th>
<th>Righteye Flounders</th>
<th>Wolfish</th>
<th>Squid (%IRI)</th>
<th>Crustacean (%IRI)</th>
<th>Other (%IRI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt; 200, N = 8</td>
<td>10.8 kg</td>
<td>45</td>
<td>0.3</td>
<td>0.4</td>
<td>0.2</td>
<td>0.4</td>
<td>3.9</td>
<td>0.2</td>
</tr>
<tr>
<td>201–250, N = 2</td>
<td>2.9 kg</td>
<td>41</td>
<td>20.6</td>
<td>1.1</td>
<td>0.2</td>
<td>11.8</td>
<td>0.2</td>
<td>3.8</td>
</tr>
<tr>
<td>251–300 cm, N = 17</td>
<td>83.3 kg</td>
<td>109</td>
<td>29.8</td>
<td>21.5</td>
<td>1.1</td>
<td>8.6</td>
<td>14.7</td>
<td>0.4</td>
</tr>
<tr>
<td>301–350 cm, N = 25</td>
<td>153.0 kg</td>
<td>137</td>
<td>19.8</td>
<td>Unidentified</td>
<td>0.2</td>
<td>12.8</td>
<td>Eurythenes grylls</td>
<td>0.2</td>
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<tr>
<td>351–400 cm, N = 18</td>
<td>96.2 kg</td>
<td>127</td>
<td>16.7</td>
<td>Unidentified</td>
<td>0.2</td>
<td>17.8</td>
<td>Large amphipod</td>
<td>0.2</td>
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<tr>
<td>&gt; 400 cm, N = 18</td>
<td>289.1 kg</td>
<td>238</td>
<td>16.7</td>
<td>Unidentified</td>
<td>0.2</td>
<td>27.1</td>
<td>Crab</td>
<td>0.2</td>
</tr>
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</table>

(Continued)
TABLE 3 | Continued

<table>
<thead>
<tr>
<th>Size Category</th>
<th>Main Prey Items (%)IRI &gt; 5</th>
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<tbody>
<tr>
<td>&gt;400 cm, N = 18</td>
<td>Armhook squid, unidentified</td>
</tr>
<tr>
<td>351–400 cm, N = 25</td>
<td>unidentified, unidentified</td>
</tr>
<tr>
<td>301–350 cm, N = 17</td>
<td>unidentified, unidentified, unidentified</td>
</tr>
<tr>
<td>201–250 cm, N = 2</td>
<td>unidentified, unidentified, unidentified</td>
</tr>
<tr>
<td>&lt;200 cm, N = 8</td>
<td>unidentified, unidentified, unidentified</td>
</tr>
</tbody>
</table>

Reconstructed biomass and number of prey items within each shark size category is presented together with the most important individual prey groups.

reasons described below, we are not convinced that IRI-levels accurately reflect the importance of squids for larger sharks >200 cm. Firstly, one Greenland shark of 351 cm (GS17, Table 1) contained 32 squid beaks making this single observation accountable for 29% of all armhook squid observations in sharks >200 cm. Secondly, the contribution of the reconstructed biomass to the squid IRI-score is minimal but driven by a high frequency of occurrence (F) and numerical abundance (N) which is different from sharks <200 cm where all IRI parameters (F, N, and B) were high for squids. Thirdly, squids were much smaller (pen length mean ± SD: 16.8 ± 6.88 cm, N = 88) than prey items of >200 cm Greenland sharks typically measuring 21.3–68.8 cm in length (Nielsen et al., 2014). Lastly, the vast majority of squid observations were based on hard-to-digest chitin beaks, which, for large sharks, especially, are prone to be derived from secondary stomach contents of large fully swallowed and digested prey like seal, Greenland halibut and Atlantic cod (a “matrijoska effect”). Based on the arguments outlined above, we believe that the importance of squids for sharks >200 cm is overestimated by our IRI calculations. In contrast, however, we believe that squids are very important for <200 cm sharks as indicated by their numerical abundance, frequency of occurrence, reconstructed biomass, and by δ15N values. The prominence of Atlantic cod (%IRI = 26.6) in the diet of sharks >200 cm was to some extent, also driven by observations from only few sharks, with 69% of all cod observations (87 of 127 specimens) being present in only two stomachs. However, Atlantic cod were recorded in 26% of all stomachs and are (in contrast to squids) very unlikely to be consumed secondarily. Thus the generally high importance of Atlantic cod seems a reasonable conclusion, which together with skates, seals, Greenland halibut, lumpfish, and wolffish are the most important prey for sharks >200 cm.

Our findings also show that prey fishes differ between shark size groups. For example, righteye flounder (mainly Greenland halibut, Table 3) were among the most important prey for sharks between 251 and 350 cm, but of limited importance to larger sharks (i.e., 351–400 and >400 cm). Furthermore, despite redfish being abundant across the Greenland continental shelf (ICES, 2017), they were only an important part of the diet among the largest sharks (>400 cm). Females this size from Iceland shelf waters have also been reported to feed predominantly on redfish (McMeans et al., 2010) suggesting some degree of prey selectivity. For sharks >400 cm, the scarcity or complete lack of deep sea fishes such as Greenland halibut, grenadiers and slickheads (Alepocephalidae) in the stomachs is noteworthy and is supported by depth records from a recent tagging study in Greenland waters (Nielsen, 2018), which found that >400 cm females do not spend much time at depths >800 m. Instead, females this size seem to mainly occupy and forage on the continental shelf and the upper part of the continental slope.

The apparent shift in diet between small and large sharks was corroborated by significantly lower δ15N values in sharks of <200 cm compared to sharks >200 cm. As noted in the Section “Materials and Methods” we did not attempt to extract
TMAO and urea from the samples, though these compounds have been shown to lower the δ¹⁵N values to a variable extent (Carlisle et al., 2017). As we primarily used the isotopic values to compare between shark size groups, we believe any TMAO and urea produced bias in δ¹⁵N would be expected to have a similar effect across size groups. Hansen et al. (2012) analyzed Greenland shark samples from the same areas around Greenland (lengths 270 to 473 cm) and found average δ¹⁵N values of 16.7‰ which is similar to our values. Greenland sharks from Svalbard (lengths 245 to 404 cm) were reported by McMeans et al. (2013) to have average values of 15.9 (δ¹⁵N) and −18.6 (δ¹³C), which are also very similar to the ones reported here. In contrast, the δ¹³C values found by Hansen et al. (2012) were approximately 2‰ higher (−15.6‰ compared to −17.6‰ in our study). While the reason for the discrepancy between the two values is not clear, it could be due to varying isotopic baselines in different areas of Greenland.
Carlisle, A. B., Litvin, S. Y., Madigan, D. J., Lyons, K., Bigman, J. S., Ibarra, M.,
and MacNeil et al., 2012). Furthermore, two intact and freshly
swimming marine mammals (Figure 5c, Idrobo and Berkes, 2012
and MacNeil et al., 2012). Furthermore, two intact and freshly
ingested seals were found without any scavenging fauna common
for carcasses (Figure 5b) suggesting that the seals had been
swallowed during a recent hunting event (Leclerc et al., 2012).
How Greenland shark catch fast swimming prey such as seals
remains to be resolved (Edwards et al., in press), but is has been
suggested that predation occurs on seals sleeping in the water
(column (Leclerc et al., 2012).

In conclusion, Greenland shark display a marked ontogenetic
shift in trophic relationships from a squid diet in small sharks
(<200 cm) to a diet dominated by fishes and seals in larger
sharks (>200 cm). As the diet reflects available prey for given
graphic areas and depths, how may we define Greenland
shark in terms of feeding behavior? The squid diet for juvenile
Greenland sharks is interesting and suggests a specialized feeding
behavior where younger animals actively select squid, whereas
larger animals appear generalists mainly feeding on demersal
fishes and seals in addition to a minor proportion of benthic
invertebrates. Clearly better information on the distribution,
behavior and environments occupied by Greenland shark of
different size and age is needed to clarify the understanding of the
trophic relationships for this migratory and long-lived species.

AUTHOR CONTRIBUTIONS
JN coordinated this work. JN, HK, PB, KP, and JS collected the
stomachs. JN and RH analyzed the stomach contents. HK, PG,
and RH analyzed the stable isotopes. JN, JC, and RH designed the
project and wrote the manuscript. All authors revised, reviewed,
and finally approved the work.

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Greenland shark”) which was financially supported by the Danish
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The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars. 2019.00125/full#supplementary-material

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