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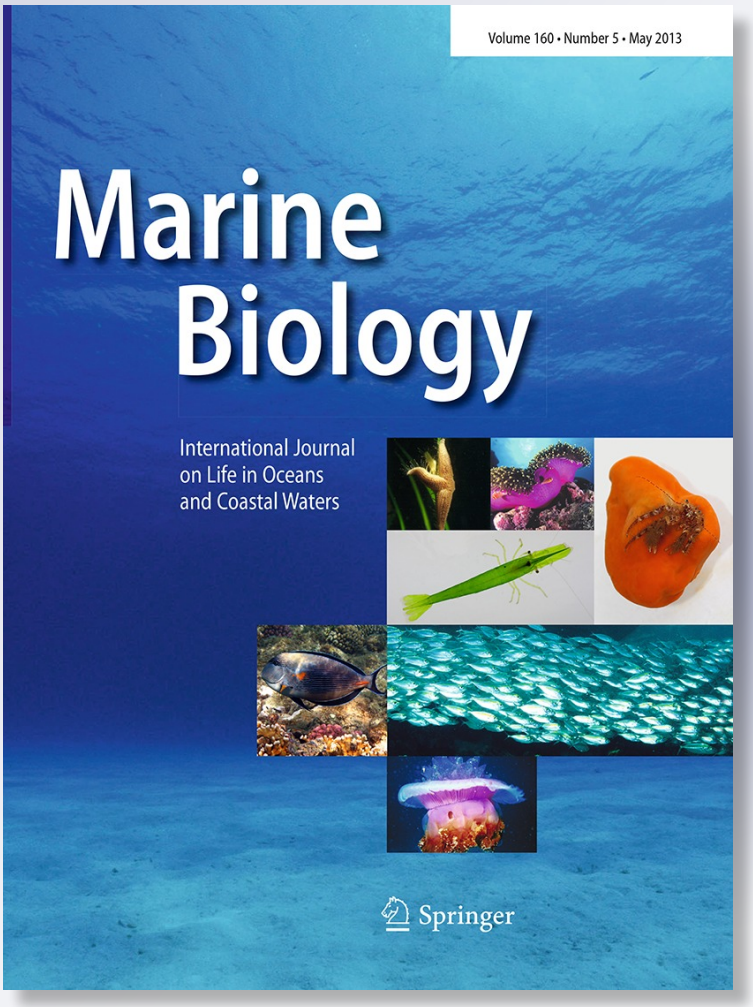

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ORIGINAL PAPER

The role of Greenland sharks (*Somniosus microcephalus*) in an Arctic ecosystem: assessed via stable isotopes and fatty acids

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Abstract The Greenland shark (*Somniosus microcephalus*) is the only shark species known to inhabit ice-covered seas in the North Atlantic, but remains a missing component in most studies of Arctic food webs. In the present study, stable isotopes (SIs) of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) and fatty acids (FAs) were analyzed to identify the role of Greenland sharks (sampled during June 2008–2009) in Kongsfjorden, a productive fjord on the west coast of Svalbard, Norway (~79°N, 12–13°E). The Greenland shark fed at a high trophic position (4.8) based on $\delta^{15}N$ values, and $\delta^{13}C$ confirmed that most (70 %) of their carbon was derived from phytoplankton-based food chains, which is consistent with a heavy reliance on pelagic teleosts and seals. Greenland sharks from Kongsfjorden had fatty acid profiles in both muscle and plasma (e.g., low 20:1n-9, high 22:5n-3) that suggested a low portion of Greenland halibut (*Reinhardtius hippoglossoides*) and high proportion of gadoids and seals in their diet compared to Greenland sharks sampled in Cumberland Sound, Canada, during April 2008, which were previously shown to derive much of their energy from Greenland halibut. The high proportions of seal fatty acids in both slow- (muscle) and fast- (plasma) turnover tissues indicate that trophic interactions between Greenland sharks and seals in Kongsfjorden are a common occurrence. Results from the present study suggest that Greenland sharks likely play a unique and significant role in Arctic marine food webs as a top predator of fishes and marine mammals.

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Introduction

Sharks play important and unique roles in marine ecosystems (Ferretti et al. 2010) and tend to be highly connected in food webs (i.e., involved in many trophic interactions) because they consume a wide variety of prey (Bascompte et al. 2005). They are often the only major predators of other megafauna, including other elasmobranchs, large teleost fishes, and marine mammals, and they can have significant direct (i.e., reduction in numbers) and indirect effects (i.e., predator avoidance behavior) on prey populations (Ferretti et al. 2010). Understanding a shark's feeding ecology is therefore crucial for identifying the impact a particular shark species has on a given food web, as well as for anticipating how a warming climate could alter food web properties. This knowledge is urgently needed because Arctic ecosystems are experiencing shorter periods of seasonal ice cover (Markus et al. 2009) and, as a result, the expansion of southern species into Arctic waters (Drinkwater 2009; Wienerrroither et al. 2011; Renaud et al. 2012).

The Greenland shark (*Somniosus microcephalus*) is the only shark that inhabits seasonally ice-covered North Atlantic seas. Greenland sharks can achieve a large size (at least 6 m, Bigelow and Schroeder 1948), and based on

catch numbers from the liver-oil fishery in the 1940s, they were at least historically abundant (~50,000 sharks landed annually from western and eastern Greenland, Jensen 1948; MacNeil et al. 2012). Stomach content analyses indicate that fishes numerically dominate the diet of Greenland sharks (Fisk et al. 2002; McMeans et al. 2010; Leclerc et al. 2012), and both stomach contents and fatty acid profiles recently supported heavy reliance on a teleost, the Greenland halibut (*Reinhardtius hippoglossoides*), by Greenland sharks from Cumberland Sound, Canada (McMeans et al. 2012a). However, marine mammals are also consumed by Greenland sharks (reviewed by MacNeil et al. 2012). Studies conducted in Kongsfjorden, Svalbard, Norway, for example, revealed that marine mammals were present in >40 % of Greenland shark stomachs that contained food, including tissues from scavenged whales (Leclerc et al. 2011) and both young and adult ringed seals (*Pusa hispida*), as well as lesser quantities of bearded seals (*Erignathus barbatus*) and hooded seals (*Cystophora cristata*) (Leclerc et al. 2012). Given that marine mammals store significant quantities of lipid-rich blubber, they could be an energetically important component of the Greenland sharks' diet (e.g., see Schaufler et al. 2005). Furthermore, given the potentially large numbers of Greenland sharks in Arctic seas, this species could be an important component of Arctic food webs and could have significant effects on prey populations (Leclerc et al. 2012). However, Greenland sharks have only recently been included in food web studies (e.g., Fisk et al. 2002), and their functional role in Arctic ecosystems, their reliance on marine mammals as a source of energy and nutrients, and their effect on prey populations remain unclear.

Kongsfjorden is a productive fjord on the west coast of Svalbard, Norway (Hodal et al. 2012). Both the physical (Svendsen et al. 2002) and the biological (Hop et al. 2002b) components of Kongsfjorden are well studied. Attention has been directed toward the examination of primary producer–zooplankton trophic interactions (Søreide et al. 2006), benthic food web structure (Renaud et al. 2011), and the diet of higher-order predators including seabirds (Wold et al. 2011) and seals (Labansen et al. 2007). The diet of Greenland sharks in Kongsfjorden has only recently been considered (Leclerc et al. 2011, 2012) and there is a need to determine how Greenland sharks "fit" into the Kongsfjorden food web. Because other trophic interactions are reasonably well understood in Kongsfjorden (e.g., Hop et al. 2002b), it is an appropriate location for exploring the role of Greenland sharks in terms of their potential effects on energy and nutrient flow and impact on prey populations.

Previous studies have applied dietary tracers (i.e., stable isotopes [SI] of carbon [$\delta^{13}C$] and nitrogen [$\delta^{15}N$]) to assess resource use and trophic positions (TPs) of Greenland sharks (Fisk et al. 2002; McMeans et al. 2010). However, uncertainty surrounding the appropriate diet-tissue discrimination factor for $\delta^{15}N$ (i.e., $\delta^{15}N_{shark} - \delta^{15}N_{prey}$) is a recognized issue associated with the application of SIs to estimate shark TPs and to reconstruct shark diets using isotope mixing models (reviewed by Hussey et al. 2012). Furthermore, because SI analysis is typically performed on lipid-extracted tissue (i.e., the proteinaceous component), to remove the bias associated with ^{13}C-depleted lipids (Post et al. 2007; Hussey et al. 2012), the application of SI alone can underestimate the contribution of lipid-rich mammal blubber to the diet of predators (Cherry et al. 2010). As long as these concerns are recognized, the application of SIs can lend insight into food web structure and species diets (Søreide et al. 2006). Researchers are advised, however, to combine SIs with additional dietary tracers, like fatty acids (FA), when studying elasmobranch feeding ecology (Hussey et al. 2012).

Combining SIs with FAs, which reflect the lipid portion of an animal's diet, could provide a more complete view of the Greenland shark's diet. Previous studies have successfully applied FAs to investigate the diets of Kongsfjorden consumers, including zooplankton (Søreide et al. 2008), seabirds (Dahl et al. 2003), seals (Andersen et al. 2004), and polar bear (Grahl-Nielsen et al. 2003). From these studies, it is apparent that differences exist among the FA profiles of potential Greenland shark teleost and marine mammal prey (Andersen et al. 2004). For example, harbor seal (*Phoca vitulina*) blubber FA profiles differed from those of certain teleosts (e.g., polar cod *Boreogadus saida* and Greenland halibut) due to lower mono-unsaturated FAs (MUFA), like 20:1n-9, and higher proportions of certain poly-unsaturated FAs (PUFA), like 22:5n-3, in the seal blubber (Andersen et al. 2004). Teleost muscle and seal blubber from Cumberland Sound also differed in these FAs (McMeans et al. 2012a). Thus, FAs could be particularly useful in determining whether Greenland sharks rely more heavily on marine mammals or teleosts as an energy source, which is important to interpret the sharks' trophic role. Similar to SIs, FAs have the benefit of providing a time-integrated view of diet and are increasingly being applied to study the diet of sharks (Pethybridge et al. 2011; Wai et al. 2011).

The goal of the present study was to identify the role of Greenland sharks in the Kongsfjorden ecosystem, with regard to diet and feeding behavior, based on SI and FA analysis of multiple tissues. Stable isotopes were first used to calculate trophic positions (TPs) and carbon sources for Kongsfjorden Greenland sharks in order to position them within the context of the Kongsfjorden food web. An isotope mixing model was also applied to estimate prey contributions to the Kongsfjorden sharks. Muscle and plasma FAs were then compared between Kongsfjorden

and Cumberland Sound sharks. This comparative method was employed for the FAs because it was expected that the Greenland shark's FA profile would differ from that of their prey due to modification of dietary FA by the sharks (for examples of predator modification of FA, see Grahl-Nielsen et al. 2003, 2011; Andersen et al. 2004; Nordstrom et al. 2008). Because the diet of Cumberland Sound sharks has been previously characterized and found to include large amounts of Greenland halibut (based on stomach contents, stable isotopes and fatty acids, Fisk et al. 2002; McMeans et al. 2012a) and variable amounts of marine mammal (based on stomach contents and contaminants, Fisk et al. 2002), the dominant prey of the Kongsfjorden sharks could be inferred from differences and similarities in their FA profiles relative to that of Cumberland Sound sharks. For example, if Kongsfjorden sharks rely heavily on marine mammal tissue as an energy source, higher proportions of marine mammal FAs would be expected in both plasma and muscle of Kongsfjorden vs Cumberland Sound sharks. However, if Kongsfjorden sharks only sporadically consume marine mammals and also exploit teleost fishes as a major energy source, more similar proportions of marine mammal FAs would be expected between sharks from the two regions.

Materials and methods

Sampling

Greenland sharks were fished using bottom longlines in Kongsfjorden in June 2008 and 2009. Full shark collection and processing procedures are described in Leclerc et al. (2012). Approximately 5 g of dorsal white muscle was sampled from Greenland sharks for SI and FA analysis, posterior to the first dorsal fin. Blood was collected from the ventral vein, centrifuged for 10 min, and the plasma portion was collected using a sterile pipette and transferred to a cryovial for FA analysis. Samples destined for stable isotope and FA analyses were immediately frozen at −20 and −80 °C, respectively.

Stable isotope analysis

Greenland shark muscle was freeze-dried for 48 h, ground with a mortar and pestle, and lipid extracted prior to SI analysis. Lipid extraction was performed following a modified Folch et al. (1957) method, using a 2:1 solution of chloroform: methanol (for detailed lipid extraction procedure see McMeans et al. 2009). Approximately 0.5 mg of each sample was placed in a seamless tin capsule and run on a continuous-flow isotope ratio mass spectrometer (Delta V Advantage, Thermo Electron) at the Great Lakes Institute for Environmental Research, Windsor, Ontario, Canada. SIs are expressed as delta δ values where $\delta X = 1000[R_{\text{sample}} R_{\text{standard}}^{-1}) - 1]$, and $X = {}^{15}\text{N}$ or ${}^{13}\text{C}$ and $R =$ the ratio of ${}^{15}\text{N}:{}^{14}\text{N}$ or ${}^{13}\text{C}:{}^{12}\text{C}$. Replicate analyses of NIST (National Institute of Standards and Technology) standard bovine muscle (NIST 8414, $n = 162$) and internal lab standard (Tilapia muscle, $n = 162$) yielded a precision (i.e., one standard deviation) of 0.13 and 0.20 ‰ for $\delta^{15}\text{N}$ and 0.07 and 0.08 ‰ for $\delta^{13}\text{C}$, respectively.

Fatty acid analysis

Shark muscle and plasma samples were analyzed for FA following the methods detailed in McMeans et al. (2012b). Briefly, lipids were extracted by homogenizing samples in 2 mL of 2:1 (v/v) chloroform:methanol (Folch et al. 1957). Fatty acid methyl esters were generated via addition of a sulfuric-methanol solution (1:100 mixture) and were subsequently analyzed on a Hewlett Packard 6890 GC using splitless injection on a Supelco SP-2560 column and identified using known FA standards. "$\sum$SAFA" is used to indicate the sum of all FA with no double bonds (i.e., saturated FA), "$\sum$MUFA" indicates the sum of all FA with one double bond, and "$\sum$PUFA" indicates the sum of all FA with $\geq$2 double bonds.

Data analysis

Unpublished SI data were available for several benthic and pelagic Kongsfjorden food web components (H. Hop unpubl. data, see Søreide et al. 2006 for SI analytical methods) collected during 1997–2006 (i.e., all stable isotope data provided in Table 1 except for Greenland shark). These data were obtained as part of ongoing studies focused on the Kongsfjorden food web. Copepods (*Calanus glacialis*) were sampled as described in Søreide et al. (2006). Brittle star (*Ophiopholis aculeata*) and wolffish (*Anarhichas lupus*) were collected via hand net, squid (*Gonatus fabricii*) via pelagic trawling, and the remaining fishes via bottom trawling. Marine mammals were harvested in local hunts. TPs for Kongsfjorden Greenland shark and prey were calculated from $\delta^{15}\text{N}$ values using a one-source TP model (Hobson and Welch 1992) as follows:

$$\text{TP}_{\text{consumer}} = 2 + \frac{\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{copepod}}}{\Delta^{15}\text{N}} \quad (1)$$

with copepod (i.e., TP = 2) used as a baseline (Søreide et al. 2008) and 3.4 ‰ used as the diet-tissue discrimination factor ($\Delta^{15}\text{N}$, Søreide et al. 2006). The use of a single $\Delta^{15}\text{N}$ for consumers feeding at different trophic levels is problematic because $\Delta^{15}\text{N}$ decreases with increasing $\delta^{15}\text{N}$ in the diet (Caut et al. 2009), and because large sharks have a lower

Δ^{15}N, of 2.3 ‰ (Hussey et al. 2010), than the commonly applied value of 3.4 ‰ (Post 2002; Søreide et al. 2006). Therefore, an additional TP calculation was performed for Greenland sharks using Atlantic cod (*Gadus morhua*) as a baseline (cod δ^{15}N = 14.0 ‰, TP = 4.0, Table 1), which is a major teleost prey of Kongsfjorden Greenland sharks (Leclerc et al. 2012), and a shark-specific Δ^{15}N of 2.3 ‰ (Hussey et al. 2010). Values of δ^{13}C for copepod (a suspension feeder of phytoplankton, Søreide et al. 2008) and for the benthic brittle star (a deposit feeder of sedimented phytoplankton and detritus, Graeve et al. 1997) were used as baselines to determine fraction of carbon derived from phytoplankton versus benthic carbon and detritus (i.e., α value see below), respectively. A modified two-source model (Post 2002) that accounts for enrichment of ^{13}C at each trophic step was used to calculate α as follows:

$$\alpha = \frac{\delta^{13}C_{consumer} - [\Delta^{13}C \times (TP_{consumer} - 2)] - \delta^{13}C_{brittle\ star}}{\delta^{13}C_{copepod} - \delta^{13}C_{brittle\ star}} \quad (2)$$

where Δ^{13}C was set at 0.6 ‰, a value previously applied in Arctic food web studies (Søreide et al. 2006). $TP_{consumer}$ is the result from the one-source TP calculation Eq. (1).

To further explore relative prey contributions to the diet of Kongsfjorden Greenland sharks, the Bayesian-based SI mixing model SIAR (Parnell et al. 2010) was implemented, which allows the user to input variability around diet-tissue discrimination values. External information about a consumers' diet can also be included as priors to guide the model in calculating dietary proportions. Individual Greenland shark δ^{13}C and δ^{15}N values were included as target values. Means and standard deviations of δ^{13}C and δ^{15}N for known prey, i.e., that were identified in shark stomachs (Leclerc et al. 2012) and for which SI data existed (Table 1), were included as sources in the model (8 prey, listed in Fig. 1). SI values for the smaller ringed seals sampled during 1996 (vs larger seals sampled in 2001, Table 1) were included as the source values for this species because their δ^{15}N was lower than that of the Greenland shark. The proportion of total biomass that each prey species contributed to the sharks' stomachs (Leclerc et al. 2012) was included as a prior to guide model output. Because prey contributions included as priors in the model must sum to 1, the biomass contributions of the eight prey were rounded up or down by a maximum of 0.009 as follows: Atlantic cod, 0.491–0.500; wolffish, 0.201–0.200; ringed seal, 0.177–0.180; haddock (*Melanogrammus aeglefinus*), 0.071–0.080; starry skate (*Amblyraja radiata*), 0.005–0.010; plaice (*Hippoglossoides platessoides*), 0.004–0.010; redfish (*Sebastes mentella*), 0.005–0.010; bearded seal, 0.005–0.010. Subsequent model runs using different rounding schemes produced identical results. SIAR requires a standard deviation to be given for the diet proportion of one source, and we set this value to 0.05 for the Atlantic cod (contributed the most to shark stomach

Table 1 Greenland sharks and potential prey species, tissue(s) analyzed, sample size (*n*), total body length (min–max), and mean ± SD of stable isotope values (δ^{13}C and δ^{15}N, ‰), trophic position (TP), and proportion of pelagic carbon in diet (α), sampled from Kongsfjorden, Svalbard, Norway

Species	Years	Tissue	*n*	Length	δ^{13}C	δ^{15}N	TP_a	α
S. microcephalus	2008, 2009	Muscle	44	245–404	−18.6 ± 0.5	15.9 ± 0.7	4.5 ± 0.2	0.70 ± 0.07
Invertebrates							4.8 ± 0.7[b]	0.72 ± 0.08
O. aculeata	2006	Whole	3	Na	−15.1 ± 0.2	7.9 ± 0.6	2.2 ± 0.2	0.02 ± 0.03
C. glacialis	2006	Whole	3	Na	−22.2 ± 0.4	7.2 ± 0.8	2.0 ± 0.2	1.00 ± 0.07
G. fabricii	2004	Mantle	3	24–45	−18.8 ± 0.2	11.7 ± 0.2	3.3 ± 0.1	0.64 ± 0.02
Fishes								
A. radiata	1997, 2006	Muscle	8	24–45	−18.3 ± 0.6	13.6 ± 0.4	3.9 ± 0.1	0.61 ± 0.09
G. morhua	1997, 2006	Muscle	17	21–56	−19.4 ± 0.4	14.0 ± 0.8	4.0 ± 0.2	0.77 ± 0.06
M. aeglefinus	2006	Muscle	3	16–25	−20.2 ± 0.3	13.0 ± 1.6	3.7 ± 0.5	0.86 ± 0.05
H. platessoides	1997	Muscle	5	31–35	−18.9 ± 0.3	14.8 ± 0.5	4.2 ± 0.1	0.73 ± 0.04
R. hippoglossoides	1997, 2006	Muscle	9	17–47	−19.7 ± 0.5	14.0 ± 0.8	4.0 ± 0.2	0.82 ± 0.06
S. mentella	1997, 2006	Muscle	10	10–23	−20.1 ± 0.7	12.7 ± 1.0	3.6 ± 0.3	0.84 ± 0.08
Anarhichas lupus	1997	Muscle	3	38–44	−17.4 ± 0.3	13.2 ± 0.7	3.8 ± 0.2	0.47 ± 0.06
Mammals								
E. barbatus	2001	Muscle	6	215–226	−18.2 ± 0.4	15.3 ± 0.5	4.4 ± 0.2	0.63 ± 0.06
P. hispida	1996	Muscle	10	111–131	−19.2 ± 0.2	15.1 ± 0.4	4.3 ± 0.1	0.77 ± 0.03
P. hispida	2001	Muscle	7	120–139	−19.0 ± 0.1	16.2 ± 0.7	4.6 ± 0.2	0.77 ± 0.02

[a] TPs calculated using *C. glacialis* (TP = 2) as a baseline and a Δ^{15}N of 3.4 ‰

[b] An additional TP was calculated for the Greenland shark using *G. morhua* as a baseline (TP = 4) and a Δ^{15}N of 2.3 ‰ (Hussey et al. 2010)

contents), which encompasses an approximate 95 % range of biomass contribution to the sharks stomachs from 0.39 to 0.59 (i.e., 0.49 ± 0.1). Values of Δ^{15}N and Δ^{13}C were set to those identified by Hussey et al. (2010) for large sharks (2.3 ± 0.2 ‰ and 0.9 ± 0.3 ‰). This shark-specific Δ^{13}C value differs from the value of 0.6 ‰ used to calculate α for each species in the food web (Eq. 2), the latter value being applied across the food web to maintain consistency with previous Arctic food web studies (Søreide et al. 2006).

Welch's *t* tests were used to investigate the effect of sampling date (i.e., 2008 vs 2009) on Kongsfjorden Greenland shark δ^{13}C, δ^{15}N, and total length. Linear associations between Greenland shark length and δ^{13}C and δ^{15}N were explored using pooled data via Pearson's correlation coefficients.

Fatty acid data for several known and potential Greenland shark prey from waters near Kongsfjorden were obtained from Andersen et al. (2004), including Atlantic cod, plaice, Greenland halibut, and starry skate. Additional FA data from Grahl-Nielsen et al. (2003) for ringed seal and bearded seal were also used. Published data from Cumberland Sound were available for Arctic skate (*Amblyraja hyperborea*), Greenland halibut, and ringed seal (McMeans et al. 2012a). Prey data were sampled in different years (Table 4), but inter-annual variability within-species was smaller than inter-species differences in FA profiles (Budge et al. 2002; Stowasser et al. 2012).

Statistical analyses were performed on 16 FAs, which had mean proportions >1 % in at least one shark tissue (Table 2). Proportions of 18:4n-3 were <1 %, but this FA was included in the analyses because its proportion differed significantly between calanoid copepods from Svalbard and Cumberland Sound waters (McMeans et al. 2012b). First, it was established which of the 16 FAs explained the largest amount of variance among fish and marine mammal prey from both locations using principal component analysis (PCA). Principal component weights for each FA variable were extracted "unscaled" (i.e., scaling = 0) from the PCA, and the loadings were calculated by multiplying the unscaled FA weight by the square root of the eigenvalue for each principal component (McGarigal and Cushman 2000). Proportions of individual FAs that were highly correlated with the first 2 PC axes (i.e., loadings >0.60) (McGarigal and Cushman 2000), and that were important in separating prey species on the PCA, were retained as fish and seal indicator FAs to aid in further exploration of regional differences in the diet of the Greenland shark (see subsequent paragraph). Next, a PCA including the 16 FA proportions was performed on both prey and Greenland shark muscle and plasma from Kongsfjorden and Cumberland Sound to help visualize possible differences in Greenland shark diet between the two locations. All FAs were standardized to a mean of 0 and variance of 1 prior to their inclusion in the PCAs.

The FAs that explained the most variance among prey species, based on the prey PCA, were included in MANOVA analyses (separate MANOVAs were performed for shark muscle and plasma) to test the hypothesis that Kongsfjorden Greenland sharks consumed different prey than Cumberland Sound sharks. Canonical discriminant analysis (DA) was performed following significant MANOVAs to identify which FAs contributed most to the difference between locations. FAs with canonical structure coefficients ≥ 0.6 or ≤ -0.6 (i.e., high correlations between each FA and the canonical function, McGarigal and Cushman 2000) were considered significantly different between groups. DA is appropriate following a significant MANOVA because it maintains the multivariate nature of the data, unlike repeated univariate ANOVAs that ignore interrelationships among variables (Borgen and Seling 1978).

The effects of Kongsfjorden Greenland shark total length and sampling year (2008, 2009) on all 16 FAs in muscle and plasma were determined using simple linear regression and Welch's *t* tests, respectively. ANCOVA was performed (covariate = length, factor = year) when both length and year were significant for a given FA to test for significant difference between years after adjusting for effect of shark length. When a FA that was identified by MANOVA to significantly differ between Cumberland Sound and Kongsfjorden sharks also exhibited a significant relationship with either sampling year or shark length (based on the above comparisons), ANOVA (factor = location, but with Kongsfjorden sharks from 2008 to 2009 coded separately) and ANCOVA (factor = location, covariate = length), respectively, were performed to ensure that a significant location effect remained after accounting for differences in year or length (details provided in Table S1). FAs were first logit-transformed ($\log[FA_i/(1-FA_i)]$) (Warton and Hui 2011) prior to inclusion in the above analyses to meet the assumptions of normality (tested via Shapiro–Wilks tests) and homogeneity of variance (tested via Levene's tests). Also, outliers detected using Mahalanobis distances (2 Kongsfjorden sharks in the muscle and plasma FA matrices and 1 Cumberland Sound shark in the plasma FA matrix) were excluded from all analyses. The significance level was set at 0.05 and all statistical analyses were performed in R (R Development Core Team 2010). The R packages vegan (Oksanen et al. 2010) and candisc (Friendly and Fox 2010) were used for the PCAs and DAs, respectively.

Results

Stable isotopes

Of the four prey species sampled in Kongsfjorden during both 1997 and 2006, Atlantic cod, starry skate, Greenland

halibut, and redfish, Welch's t tests failed to detect significant differences in either $\delta^{15}N$ or $\delta^{13}C$ between sampling years (i.e., all $P < 0.05$), and these data were therefore combined (Table 1). However, $\delta^{15}N$ (Welch's $t_{6.5} = 3.38$, $P < 0.05$) and $\delta^{13}C$ (Welch's $t_{12.3} = 2.90$, $P < 0.05$) were significantly higher in Kongsfjorden ringed seals from 2001 than conspecifics sampled in 1996, and these data are presented separately (Table 1). Neither $\delta^{15}N$ nor $\delta^{13}C$ in Greenland shark muscle were related to sampling year (Welch's t test, $P > 0.05$). Total length of Greenland sharks caught in 2008 and 2009 did not differ (Welch's t test, $P > 0.10$), and values of $\delta^{15}N$ were not significantly correlated with shark total length (Pearson's $r = -0.01$, $P > 0.05$). Values of $\delta^{13}C$ were weakly, positively correlated with shark total length based on Pearson's r (0.33, $P = 0.04$).

Among Kongsfjorden prey, copepod and brittle star had the lowest $\delta^{15}N$, and the lowest and highest $\delta^{13}C$, respectively (Table 1). The Kongsfjorden Greenland shark's $\delta^{15}N$ (15.9 ± 0.7) and TP (4.5) were higher than all other species except for the Kongsfjorden ringed seals sampled in 2001 (Table 1). However, when Atlantic cod (instead of copepod) and 2.3 ‰ (instead of 3.4 ‰) were used as the baseline and $\Delta^{15}N$, respectively, to calculate the Greenland sharks' TP (Eq. 2), the value increased to 4.8, which is higher than that of all species for which data are reported (Table 1).

Regarding reliance on phytoplankton vs benthic/detrital carbon sources (i.e., α), haddock, Greenland halibut, and redfish fed predominantly on pelagic prey ($\alpha = 0.86$, 0.82, 0.84, respectively, Table 1), whereas wolffish ($\alpha = 0.47$), starry skate ($\alpha = 0.61$), and squid ($\alpha = 0.64$, Table 1) consumed prey that fed in both benthic/detrital and phytoplankton pathways. Kongsfjorden Greenland sharks ($\alpha = 0.70$, Table 1) and their two most frequently consumed prey in Kongsfjorden, Atlantic cod and ringed seal (both $\alpha = 0.77$, Table 1), fed in both pathways, but relied more heavily on prey whose carbon originated from phytoplankton based on calculated values of α.

SI values for individual Greenland sharks fell within the observed values for the eight prey species including in the isotope mixing model after correcting for isotope enrichment of ^{13}C and ^{15}N (Fig. 1). The relative contributions of these prey to the Greenland shark's diet, as estimated by SIAR, indicated that Atlantic cod contributed the most, followed by haddock, wolffish, and ringed seal (Fig. 1b).

Fatty acids

Fatty acids in muscle of Greenland sharks from Kongsfjorden had 18:1n-9 in the highest proportion, followed by 20:1n-9, 16:0, 22:6n-3, and 20:5n-3 (Table 2). Shark plasma was also dominated by these FAs, but in a different order: 18:1n-9 > 22:6n-3 > 20:5n-3 > 20:1n-9 > 16:0 (Table 2). Percent lipid (on a dry weight basis) of Greenland shark muscle (60.3 %) was higher than that of plasma (17.2 %, Table 2).

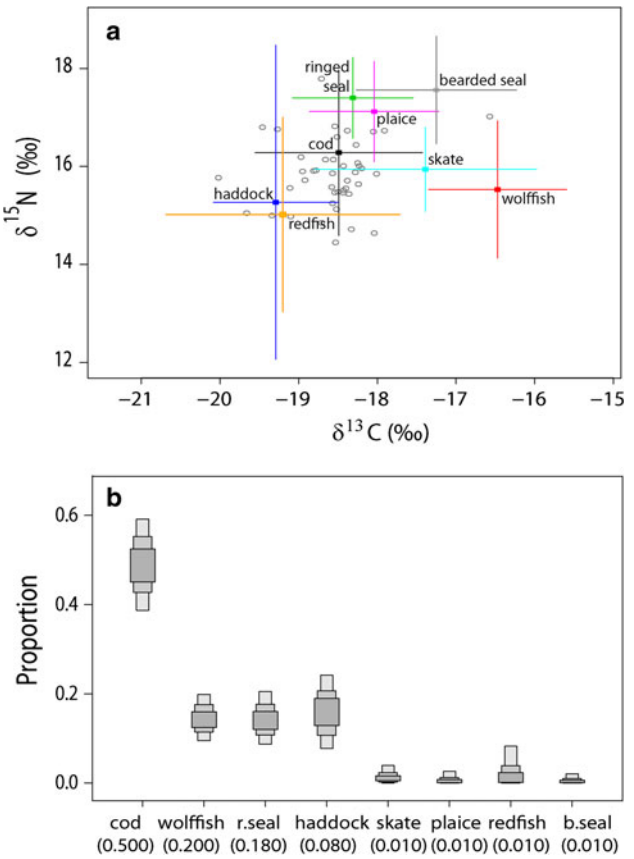

Fig. 1 **a** Stable isotope biplot of individual Kongsfjorden Greenland sharks (*circles*) and mean ± SD of several known prey based on stomach contents. Greenland shark isotopic enrichment factors ($\Delta^{13}C = 0.9$ and $\Delta^{15}N = 2.3$ ‰) were added to prey values before plotting. **b** Relative contributions (25, 75, and 95 % confidence intervals) of prey to Kongsfjorden Greenland sharks as estimated by SIAR. The proportion of total biomass that each prey species contributed to the shark stomachs is shown in parentheses and were included as priors in the model

The first PC axis of the prey FA proportions PCA explained 38.7 % of the variance in the data and separated skates, Atlantic cod, and plaice from Greenland halibut due to higher 20:4n-6, 20:5n-3, and 22:6n-3 in the former and higher 20:1n-9, 22:1n-9, and 22:1n-11 in the latter grouping (Fig. 2a, see Table S2 for FA variable loadings). Marine mammal blubber (i.e., ringed and bearded seal) separated from fish on PC2 (which explained an additional 33.5 % of the variance), due to higher 16:1n-7, 18:1n-9, and 22:5n-3 in the former (Fig. 2a). These nine FAs (i.e., 20:4n-6, 20:5n-3, 22:6n-3, 20:1n-9, 22:1n-9, 22:1n-11, 16:1n-7, 18:1n-9, and 22:5n-3) were used as species-specific indicator FAs (Table 3) to further explore potential differences in Greenland shark diet between locations.

Table 2 Fatty acid proportions (% of total, mean ± SD) of *S. microcephalus* sampled from Kongsfjorden, Svalbard, Norway and Cumberland Sound, Nunavut, Canada

Fatty acid	Svalbard		Cumberland sound[a]	
	Plasma	Muscle	Plasma	Muscle
n	45	45	12	18
16:0	9.3 ± 1.1	11.2 ± 0.8	8.8 ± 1.4	10.1 ± 0.8
16:1n-7	5.2 ± 2.4	6.5 ± 0.9	4.3 ± 1.0	6.7 ± 1.3
18:0	2.3 ± 0.5	1.7 ± 0.2	2.4 ± 2.2	1.3 ± 0.3
18:1n-9	16.8 ± 1.2	19.6 ± 2.3	15.3 ± 2.1	19.8 ± 2.1
18:1n-7	6.4 ± 1.2	7.1 ± 0.9	4.5 ± 1.4	7.1 ± 1
18:2n-6	1.4 ± 0.3	1.3 ± 0.1	1.1 ± 0.3	1.1 ± 0.1
18:3n-3	0.3 ± 0.2	0.3 ± 0.2	0.5 ± 0.7	1.5 ± 0.6
18:4n-3	0.5 ± 0.4	0.5 ± 0.3	0.3 ± 0.2	0.2 ± 0.1
20:1n-9	11.0 ± 2.6	14.7 ± 1.8	16.4 ± 3.4	17.9 ± 2.9
20:4n-6	2.4 ± 0.9	1.6 ± 0.4	2.4 ± 0.7	1.6 ± 0.3
20:5n-3	11.0 ± 1.6	7.4 ± 1	9.1 ± 1.8	5.6 ± 0.9
22:1n-11	6.2 ± 2.0	6.4 ± 2.1	9.9 ± 3.1	9.5 ± 2.1
22:1n-9	1.8 ± 0.5	1.6 ± 0.3	2.9 ± 0.6	2.0 ± 0.2
22:5n-3	4.0 ± 0.9	3.0 ± 0.6	2.7 ± 1.7	1.7 ± 0.4
22:6n-3	12.8 ± 2.1	11.0 ± 1.3	10.6 ± 2.1	8.8 ± 1.3
24:1n-9	1.3 ± 0.5	0.7 ± 0.1	1.5 ± 0.3	0.8 ± 0.1
∑SAFA	13.9 ± 1.7	14.7 ± 0.9	12.9 ± 4.3	12.7 ± 0.8
∑MUFA	51.1 ± 4	58.6 ± 2.9	58.9 ± 5.8	65.4 ± 2.2
∑PUFA	35.0 ± 4	26.6 ± 2.7	28.2 ± 3.7	21.8 ± 2.2
% lipid	17.2 ± 6.4	60.3 ± 5.2	14.4 ± 4.8	56.8 ± 5.9

[a] McMeans et al. (2012a)

Inspection of the mean FA values for the prey (Table 4) supports the differences indicated by PCA. Proportions of 18:2n-6 loaded significantly on PC1 (Table S1), but this FA was not included as a prey indicator FA because it varied little among prey species (a maximum mean difference of 1.1 %, Table 4) and has previously been shown to be ineffective for tracing resource use in upper trophic levels (Hall et al. 2006). Little geographic variation was apparent in prey FA profiles because species sampled from both Kongsfjorden and Cumberland sound (i.e., skates, Greenland halibut, ringed seal) grouped together on the prey PCA (Fig. 2a) and exhibited similar FA proportions (Table 4). One exception is 18:4n-3, which was higher in prey from Svalbard waters (Table 4).

Based on the Greenland shark-only PCA, tissue type appeared to explain more variance in the data than location because plasma of both Kongsfjorden and Cumberland Sound sharks separated from muscle on PC1 due to higher loadings of 18:0, 20:4n-6, 20:5n-3, 22:5n-3, and 22:6n-3 (Fig. 2b, Table S2). Kongsfjorden shark muscle and plasma tended to separate from Cumberland Sound samples on PC2 due to higher 16:0 and 16:1n-7 and lower 22:1n-9, 22:1n-11, and 24:1n-9 in the former, although overlap existed among locations (Fig. 2b).

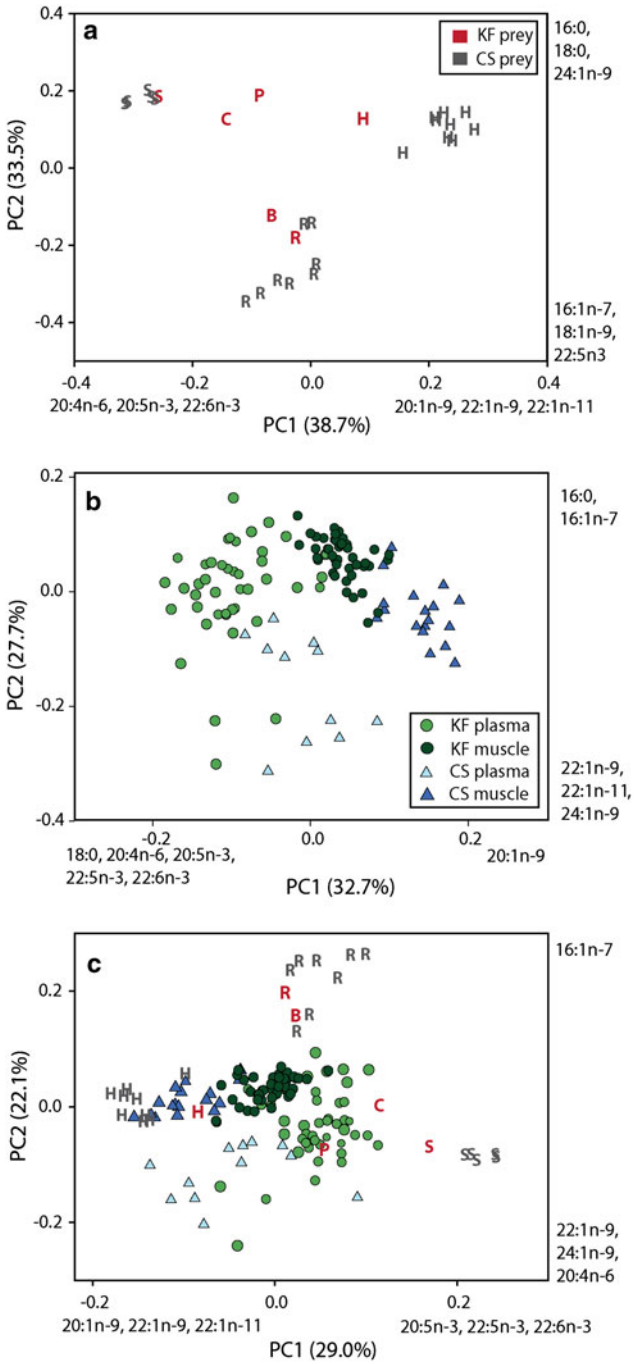

Fig. 2 Principal component analyses performed on: **a** prey, **b** Greenland shark (muscle and plasma), and **c** prey and Greenland shark fatty acid proportions from Kongsfjorden, Svalbard, Norway (KF) and Cumberland Sound, Canada (CS; McMeans et al. 2012a). The amount of variance explained and fatty acids that loaded significantly (i.e., >0.60) on each PC axis are shown

The first two PC axes extracted from the Greenland shark and prey PCA explained 51.1 % of the variance in the FA proportions (Fig. 2c; Table S2). Cumberland Sound muscle and plasma values were closer to Greenland halibut on PC1, whereas Kongsfjorden sharks were closer to

Atlantic cod, skate, and plaice (Fig. 2c). On PC2, Kongsfjorden plasma samples were closer to marine mammal blubber than Cumberland Sound plasma (Fig. 2c).

MANOVA revealed that Kongsfjorden and Cumberland Sound Greenland sharks significantly differed in the proportions of prey indicator FA (Table 3) in both muscle ($F_{(9,59)} = 20.36$, Pillai = 0.782, $P < 0.001$) and plasma ($F_{(9,52)} = 11.88$, Pillai = 0.709, $P < 0.001$). DA revealed that six of the nine indicator FAs contributed significantly to this difference (Table 3, see Table S3 for canonical structure coefficients), with Kongsfjorden Greenland sharks having higher proportions of one of the three seal markers (22:5n-3) and lower proportions of the three Greenland halibut markers (20:1n-9, 22:1n-9 and 22:1n-11) in both muscle and plasma compared to Cumberland Sound sharks (Table 3). Kongsfjorden shark muscle and plasma also had significantly higher proportions of one of the three Atlantic cod, plaice, skate markers (20:5n-3, Table 4).

Several muscle FAs were significantly related to Kongsfjorden shark total length based on linear regression (16:1n-7, 18:0, 22:1n-9, 22:1n-11, 24:1n-9, 22:5n-3; Table 5, see Fig. 3 for plots of the strongest negative and strongest positive relationships based on r^2 values). No plasma FA was related to shark length (Table 5). Based on Welch's t tests, proportions of several FAs differed significantly between 2008 and 2009 in Kongsfjorden Greenland shark muscle (16:0, 18:1n-7, 18:4n-3, 22:1n-11, 20:4n-6, 20:5n-3, 22:6n-3) and plasma (16:0, 18:1n-7, 18:1n-9, 18:4n-3, 20:5n-3, Table 5). Only one FA, muscle 22:1n-11, exhibited a significant effect of both length and year, and ANCOVA identified that values of 22:1n-11 still differed between 2008 and 2009 even after adjusting for the length effect (Table 5). The length:date interaction term was not significant (i.e., $P > 0.05$) and the ANCOVA was therefore run without this term.

Table 3 Fatty acid indicators for *S. microcephalus* prey identified using principal component analysis. MANOVA was performed to identify differences between Kongsfjorden and Cumberland Sound Greenland shark in the proportions of the nine prey indicator fatty acids (one MANOVA each for shark muscle and plasma)

Species	Fatty acids
Prey	Indicator
Skate, Atlantic cod	High 20:4n-6, 20:5n-3, 22:6n-3
Greenland halibut	High 20:1n-9, 22:1n-9, 22:1n-11
Seal blubber	High 16:1n-7, 18:1n-9, 22:5n-3
Greenland shark	Significant differences
Kongsfjorden muscle	Higher 20:5n-3, 22:5n-3, 22:6n-3
	Lower 20:1n-9, 22:1n-9, 22:1n-11
Kongsfjorden plasma	Higher 20:5n-3, 22:5n-3
	Lower 20:1n-9, 22:1n-9, 22:1n-11

Significant differences of each individual fatty acid between locations were determined via canonical discriminant analysis (fatty acids with canonical structure coefficients ≥ 0.6 or ≤ -0.6 were considered significant)

skate: *Amblyraja* spp., Atlantic cod (*G. morhua*), Greenland halibut (*R. hippoglossoides*), seal blubber: ringed seal (*P. hispida)* and bearded seal (*E. barbatus*)

Table 4 Mean fatty acid proportions for prey species of *S. microcephalus* sampled from Kongsfjorden (KF) or Cumberland Sound (CS). Prey were analyzed for fatty acids either whole (W), as muscle (M) or as blubber (B). Percent (%) lipid is on a dry weight basis.

Species	Sskate	Askate	Cod	Halibut		Plaice	Ringed		Bearded
Location	KF[a]	CS[b]	KF[a]	KF[a]	CS[b]	KF[a]	KF[c]	CS[b]	KF[c]
Years	1998	2008	1999	1999	2008	1998	1999	2008	1999
Tissue	W	M	W	W	M	W	B	B	B
Fatty acid									
16:0	16.5	18.1	14.0	12.7	10.0	14.5	8.0	5.5	9.0
16:1n-7	7.8	3.0	8.4	12.2	10.5	10.7	19.0	21.3	17.0
18:0	4.0	4.4	3.1	2.8	2.0	3.1	0.8	0.7	1.7
18:1n-9	12.3	8.1	11.9	15.8	15.5	12.1	19.0	18.5	17.0
18:1n-7	10.5	6.3	5.2	3.9	6.6	6.6	5.0	7.2	6.0
18:2n-6	1.2	1.5	1.1	0.6	0.9	0.9	1.2	1.7	1.5
18:3n-3	0.3	0.3	0.9	0.3	0.9	0.3	0.7	0.4	0.6
18:4n-3	1.1	0.3	2.5	1.7	0.7	1.0	2.1	0.4	1.5
20:1n-9	2.1	4.4	6.7	15.0	17.7	9.3	9.0	7.8	10.0
20:4n-6	5.0	3.3	0.8	0.4	0.4	3.0	0.4	0.5	0.8
20:5n-3	10.9	10.3	14.5	8.1	3.7	11.0	9.0	8.5	7.0
22:1n-11	0.7	0.8	2.1	9.7	16.2	5.4	2.0	2.3	2.0
22:1n-9	1.1	0.5	0.4	1.9	2.3	1.2	0.4	0.5	0.6
22:5n-3	1.8	2.2	1.0	1.4	0.6	2.5	4.9	5.4	4.3
22:6n-3	20.0	30.5	22.3	8.7	4.8	11.9	9.0	9.5	12.0
24:1n-9	1.0	0.3	0.7	0.6	0.7	1.5	0.1	0.1	0.2

Sskate: *A. radiata*, Askate: *A. hyperborea*, Cod: *G. morhua*, Halibut: *R. hippoglossoides*, Plaice: *H. platessoides*, Ringed: *P. hispida*, Bearded: *E. barbatus*

[a] Andersen et al. (2004)

[b] McMeans et al. (2012a, b)

[c] Grahl-Nielsen et al. (2003)

Table 5 Effects of body length and sampling year (2008 or 2009) on logit-transformed fatty acid proportions of Greenland shark muscle and plasma sampled from Kongfjorden, Svalbard based on simple linear regression and Welch's *t* tests, respectively

Fatty acid	Length				Sampling year			
Muscle	Slope	Intercept	r^2	*P*	Statistic	*P*	2008 $n = 30$	2009 $n = 13$
16:0	ns			>0.05	$t_{41} = 3.51$	<0.01	11.4 ± 0.6	10.7 ± 0.6
16:1n-7	0.002	−3.32	0.22	<0.001	ns	>0.05		
18:0	0.001	−4.40	0.11	<0.05	ns			
18:1n7	ns			>0.05	$t_{41} = 2.32$	<0.05	7.3 ± 0.9	6.6 ± 0.8
18.4n3	ns			>0.05	$t_{41} = 8.91$	<0.0001	0.6 ± 0.2	0.1 ± 0.1
22:1n-9	−0.003	−3.33	0.33	<0.0001	ns	>0.05		
22:1n-11	−0.005	−1.10 (2008) −1.35 (2009)	0.62	<0.0001	$F_{1,40} = 24.5$	<0.0001	7.2 ± 2.0	4.8 ± 1.0
24:1n-9	−0.002	1.27	0.34	<0.001	ns	>0.05		
20:4n-6	ns			>0.05	$t_{41} = -2.098$	<0.05	1.6 ± 0.3	1.8 ± 0.2
22:5n-3	0.003	−4.40	0.24	<0.001	ns	>0.05		
20:5n-3	ns			>0.05	$t_{41} = -2.36$	<0.05	7.2 ± 1.0	7.9 ± 1.0
22:6n-3	ns			>0.05	$t_{41} = -2.46$	<0.05	10.7 ± 1.2	11.7 ± 1.2
Plasma								
16:0	ns			>0.05	$t_{41} = -23.23$	<0.01	9.6 ± 1.0	8.5 ± 0.9
18:1n7	ns			>0.05	$t_{41} = -3.92$	<0.001	6.1 ± 0.8	7.4 ± 1.2
18:1n9	ns			>0.05	$t_{41} = 2.88$	<0.01	17.1 ± 1.1	16.0 ± 1.1
18:4n3	ns			>0.05	$t_{41} = 7.10$	<0.001	0.7 ± 0.4	0.1 ± 0.0
20:5n-3	ns			>0.05	$t_{41} = -2.76$	<0.01	10.8 ± 1.3	12.1 ± 1.6

Because both length and year affected 22:1n-11, interannual differences were tested subsequent to the removal of the length effect using ANCOVA, after ensuring that the length:22:1n-11 interaction term was not significant. Mean ± SD for each sampling year is provided for fatty acids with a significant year effect ‰

ns not significant

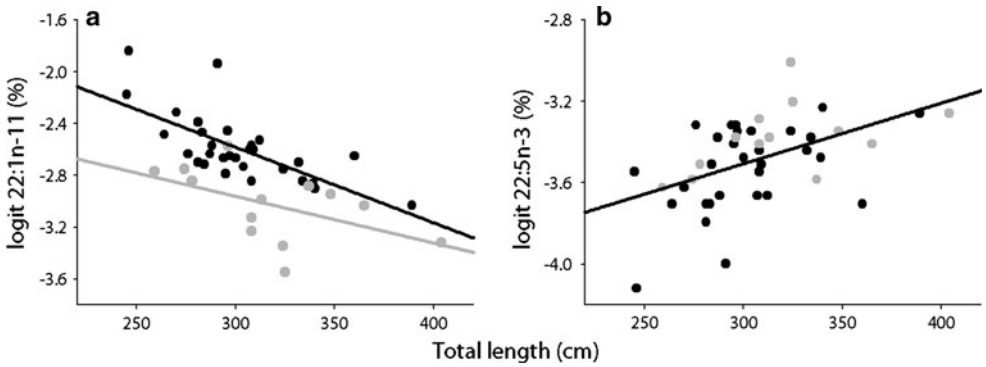

Fig. 3 Linear relationships between logit-transformed proportions of muscle 22:1n-11 (**a**) and 22:5n-3 (**b**) versus total length of Greenland sharks sampled in Kongsfjorden, Svalbard, Norway in June 2008 (*gray*) and 2009 (*black*). Analysis of covariance indicated that sampling year significantly affected 22:1n-11 (but not 22:5n-3), but the slope of the length vs 22:1n-11 relationship was similar between 2008 and 2009 (i.e., the length:date interaction was not significant at $P = 0.05$). Regression coefficients for all significant length relationships are provided in Table 5

Several indicator FAs that were identified by MANOVA to differ between locations (i.e., Table 3) also exhibited a significant effect of sampling year (muscle 22:1n-11, 20:5n-3, 22:6n-3; plasma 20:5n-3) or length (muscle 22:1n-9, 22:1n-11, 22:5n-3) in Kongsfjorden sharks, based on the above comparisons. Neither of these effects altered the results of our location comparison, however, because Kongsfjorden sharks from both 2008 and 2009 had significantly higher 20:5n-3 (in muscle and plasma) and 22:6n-3 (in muscle, based on ANOVA, Table S3) and

lower 22:1n-11 (after adjusting for the effect of length via ANCOVA, Table S3) than Cumberland Sound sharks. Kongsfjorden sharks also had significantly lower muscle 22:1n-9 and higher 22:5n-3 than Cumberland Sound sharks after accounting for the effect of shark length (based on ANCOVA, Table S3).

Discussion

Greenland sharks in Kongsfjorden fed at a high TP based on $\delta^{15}N$ and relied heavily on prey that feed in phytoplankton-*Calanus* energy pathways, based on $\delta^{13}C$-calculated values of α. The stomach contents of the Kongsfjorden Greenland sharks support the SI results because they contained a substantial amount of upper TP prey including marine mammals and benthic/pelagic teleost fishes including Atlantic cod (although benthic species like *Anarhichus* were also present, Leclerc et al. 2012). Fatty acid analysis further revealed that Kongsfjorden Greenland sharks had significantly lower proportions of Greenland halibut indicator FAs and higher proportions of seal and skate/Atlantic cod indicator FAs than Cumberland Sound sharks in both long- (muscle) and short-term turnover tissues (plasma). This suggests that Greenland sharks from Kongsfjorden routinely feed in the water column and consume teleosts like Atlantic cod, as well as marine mammal blubber, indicating that the high occurrence of marine mammals identified in the stomachs of these sharks (Leclerc et al. 2012) is not a chance occurrence, but rather reflects a common trophic interaction. Based on our results, Greenland sharks fit into the Kongsfjorden food web as a top TP consumer of piscivorous predators and acquire a substantial amount of their energy from benthic/pelagic teleosts and marine mammals.

Trophic position and carbon sources

The $\delta^{15}N$-based TPs calculated herein generally support existing knowledge for the diet of Kongsfjorden food web components (reviewed by Hop et al. 2002b). For example, Atlantic cod from the Barents Sea, measuring between 20 and 50 cm in length, heavily consume zooplanktivorous capelin (*Mallotus villosus*) (Mehl 1991), which supports the TP of 4.0 calculated for similar-sized cod reported here. The $\delta^{15}N$ and TP of the Kongsfjorden ringed seals sampled in 1996 (15.1 ‰ and 4.3, respectively) is in agreement with consumption of TP 3, or higher, prey, including carnivorous zooplankton like adult *Themisto libellula* and zooplanktivorous polar cod (Weslawski et al. 1994). The ringed seals sampled in 2001 had higher $\delta^{15}N$ and TP values (16.2 and 4.6 ‰, respectively), and included larger individuals (length range of 120–139 cm) than conspecifics from 1996 (length range 111–130 cm). The larger ringed seals sampled in 2001 could have been consuming higher TP fish like Atlantic cod, in addition to zooplankton and polar cod (Labansen et al. 2007), based on their calculated TP of 4.6. However, Atlantic cod has not been identified in ringed seal stomachs to date, though such a trophic interaction is possible considering the abundance of Atlantic cod in Kongsfjorden in recent years (Hop et al. 2002b).

The relative TPs reported for Greenland sharks in the present study are the first for Kongsfjorden. They were calculated in two ways, using a literature-derived value of 3.4 ‰ and a shark-specific value of 2.3 ‰. Relative to known prey species like Atlantic cod and ringed seal (from 1996), Greenland sharks were enriched in ^{15}N by 1.9 and 0.8 ‰, respectively, which supports the suggestion by previous authors that sharks have lower $\Delta^{15}N$ than the commonly applied enrichment value of 3.4 ‰ (Hussey et al. 2010). Because piscivores (i.e., TP = 4), like Atlantic cod, were a more important component of the Kongsfjorden Greenland sharks' stomachs than zooplanktivores (i.e., TP = 3), like squid (Leclerc et al. 2012), the calculated TP for Greenland sharks of 4.8 using a $\Delta^{15}N$ of 2.3 ‰ is more consistent with the sharks' stomach contents than the value of 4.5, calculated using 3.4 ‰ as the $\Delta^{15}N$. Of course, applying a $\Delta^{15}N$ value of 3.4 ‰ to all species except the Greenland shark does not fully address the problem of uncertainty around $\Delta^{15}N$ for the other species (Caut et al. 2009). For example, an individual harp seal was experimentally shown to have a muscle $\Delta^{15}N$ values of 2.4 ‰ (Hobson et al. 1996). Increased understanding of $\Delta^{15}N$ values in sharks (Hussey et al. 2012) and other food web components will help us arrive at more accurate $\delta^{15}N$-based TP estimates. However, it is clear from our SI data that the Greenland shark is a top TP predator in Kongsfjorden.

Carbon source calculations revealed that Greenland sharks and most of their prey relied heavily on phytoplankton-based food chains. The dominance of phytoplankton as a carbon source to both pelagic (Tamelander et al. 2006) and benthic (Renaud et al. 2011) components of Arctic food webs is well known. Based on our results, even benthic fishes in Kongsfjorden, like the Greenland halibut ($\alpha = 0.77$), obtain energy that originates in the overlying water column. Therefore, the α value of 0.70 for Kongsfjorden Greenland sharks indicates feeding in predominantly pelagic carbon pathways, but not necessarily exclusively on pelagic fishes. The dominance of phytoplankton in Arctic food webs makes it difficult to separate the reliance of upper trophic levels on pelagic vs benthic prey, but $\delta^{13}C$ was still useful in the present study for identifying that phytoplankton fuels the food chains that ultimately support large, top consumers like Greenland sharks in Kongsfjorden.

Stable isotope mixing model

Estimated prey contributions from the isotope mixing model generally agreed with stomach content information (e.g., Atlantic cod was the main contributor, Leclerc et al. 2012), which could be at least partially attributed to the inclusion of stomach content–derived prey biomass contributions as priors in the model. We included these priors to help guide the model in its output because our number of sources was high (8), and model performance decreases with increasing number of sources (Parnell et al. 2010), including prior information seemed more reasonable than, for example, dropping sources that contributed little to stomach contents. For example, haddock, which contributed only 7.1 % to the Greenland sharks stomachs (Leclerc et al. 2012), contributed ~20 % to the sharks diet based on the isotope mixing model, and this species could therefore be a more important diet component to the sharks than reflected by stomach contents. Although the mixing model-estimated contribution of ringed seal (10–20 %) agreed with the reported contribution of this species to the sharks' stomach contents (Leclerc et al. 2012), it is nonetheless important to consider that the isotopic information obtained by the Greenland shark from marine mammal blubber will be lost during the lipid extraction process. Greenland sharks consume marine mammal in the form of whole seal pups or as large chunks of blubber, skin, and muscle (Leclerc et al. 2012; McMeans et al. 2012a), or in the special case of carrion feeding on discards from whaling operations in Svalbard (Leclerc et al. 2011), as pure blubber strips. In any case, blubber is likely the tissue with most biomass (and energy) in the shark diet from marine mammal sources. We therefore suspect that the actual contribution of marine mammal to the Greenland sharks' diet may be underestimated by the lipid-extracted SI values reported here, which has also been suggested by previous researchers (Fisk et al. 2002). These concerns were anticipated and were part of the motivation behind coupling SI with FA analysis.

Inferring Greenland shark diet from fatty acid profiles

As expected, Greenland sharks and prey exhibited species-specific FA profiles because conspecific individuals grouped together on the PCAs. Seal blubber from Kongsfjorden and Cumberland Sound differed from fish muscle in FAs like 16:1n-7 and 22:5n-3, which agrees with previous observations (Andersen et al. 2004). Results from the present study therefore support previous conclusions that a given species' FA profile reflects a combination of both diet and metabolism (Grahl-Nielsen et al. 2003). Also, in support of previous observations (McMeans et al. 2012a), Greenland shark tissues differed in their FA profile based on the shark-only PCA; sharks from both locations had higher proportions of several PUFA (i.e., 20:4n-6, 20:5n-3, 22:5n-3, 22:6n-3) in plasma than muscle. Tissue-specificity in Greenland shark FA profiles could reflect different lipid composition (e.g., higher contribution of PUFA-rich polar lipids in plasma) and function (e.g., plasma used for transport, muscle used for storage) between muscle and plasma (McMeans et al. 2012a). In recognition that Greenland shark FA profiles would differ from those of prey and that the extent of this difference would depend on the shark tissue sampled (based on tissue-specific shark FA profiles, Pethybridge et al. 2011; McMeans et al. 2012a), we used a comparative method of two tissues (plasma, muscle) between Cumberland Sound and Kongsfjorden. This approach assumes that if Greenland sharks from both locations have similar physiologies and that prey species exhibit low geographic FA variability, then differences in shark FAs in each tissue between locations can confidently be attributed to dietary differences and be used to infer the sharks' trophic role.

The conservative structure of FAs combined with the unique origin of certain FAs (i.e., *de novo* biosynthesis of FAs mostly occurs in primary producers and some herbivorous zooplankton [e.g., *Calanus*]) has made FAs a useful tool for studying food web structure (Dalsgaard et al. 2003; Budge et al. 2006; Iverson 2009; Wold et al. 2011). Because higher trophic level organisms are generally limited in their capability to synthesize or modify certain long-chain MUFA and PUFA, these FAs produced at the bottom of the food chain be traced up the food web (Dalsgaard et al. 2003; Falk-Petersen et al. 2009). Specifically, the high proportions of 20:5n3 and 22:6n3 indicate that FAs in Greenland sharks originated from a mixture of diatoms and dinoflagellates or *Phaeocystis pouchetii* (Graeve et al. 1994; Falk-Petersen et al. 2009). The higher proportions of 20:1 and 22:1 ("*Calanus* markers"—see for example Falk-Petersen et al. 2009) in Cumberland Sound vs Kongsfjorden sharks suggest that Cumberland Sound sharks prey on species that directly or indirectly consume large amounts of *Calanus* copepods. The *Calanus* FAs are likely transferred through the pelagic food chain via carnivorous zooplankton or pelagic fishes (e.g., polar cod). Both groups are known to prey heavily on *Calanus* copepods (Hop et al. 2002a; Søreide et al. 2006; Falk-Petersen et al. 2009), and polar cod also prey to a large extent on pelagic amphipods (Hop and Gjosæter 2013). Similar FA profiles between Cumberland Sound and Kongsfjorden prey species support our assumption of low geographic prey variability and indicate that observed differences in FAs of Greenland sharks between these locations most likely arose from differences in diet. Based on the above arguments, Kongsfjorden Greenland sharks were obtaining lower C_{20}–C_{22} MUFA and higher 20:5n-3, 22:5n-3 and 22:6n-3

in their diet, relative to Cumberland Sound sharks, which is consistent with lower consumption of Greenland halibut and higher consumption of other prey like skate, Atlantic cod or ringed seal. Based on stomach contents, Atlantic cod and ringed seals were the most common teleost and marine mammal consumed by the Kongsfjorden Greenland sharks (Leclerc et al. 2012). The presence of Atlantic cod and ringed seal in the Greenland shark's stomachs (Leclerc et al. 2012) supports the interpretation that high 20:5n-3, 22:5n-3, and 22:6n-3 in Kongsfjorden sharks arose from predator–prey interactions with these species, instead of via shared resources (see Budge et al. 2006).

An additional concern when inferring a predator's diet from indicator FAs is that the same FA can be available in multiple prey types. For example, multiple teleosts had high proportions of 20:5n-3 and 22:6n-3 (skate, cod, plaice) in the present study. However, Greenland halibut had higher MUFA, like 20:1n-9, by >5 % relative to the other teleosts and marine mammals. As such, lower C_{20}–C_{22} MUFA in Kongsfjorden Greenland sharks can more confidently be attributed to lower consumption of a particular prey species: Greenland halibut. The lack of this species in the Kongsfjorden sharks' stomachs (Leclerc et al. 2012) further supports the conclusion that lower proportions of C_{20}–C_{22} MUFA in Kongsfjorden sharks arose from a lower consumption of Greenland halibut relative to Cumberland Sound sharks. Selective retention or metabolism by the Greenland sharks could also alter the efficacy of certain prey indicator FAs and could explain why only one of the three seal indicator FAs differed between regions based on MANOVA (i.e., 16:1n-7 and 18:1n-9 were similar and only 22:5n-3 differed between locations). Controlled FA feeding studies, which are currently lacking for sharks, will help identify which FAs are the most reflective of dietary vs metabolic processes and how FAs are selectively allocated to or mobilized from different tissues. Finally, it is important to consider that Greenland sharks are opportunistic feeders and that sharks from both Kongsfjorden (Leclerc et al. 2011) and Cumberland Sound (Fisk et al. 2002) will, for example, scavenge marine mammal tissues when available. Thus, the exact makeup of the Greenland sharks' diet, with regard to relative prey contributions, is likely variable with space and time.

Due to the wide range of prey types consumed by Greenland sharks (MacNeil et al. 2012), it was not feasible to obtain data for all known or potential shark prey inhabiting Kongsfjorden and Cumberland Sound. However, the prey species included in the FA analyses in the present study were the most frequently identified in, or those that contributed the most on a biomass basis to, the sharks' stomach contents (i.e., Atlantic cod and ringed seal in Kongsfjorden, Leclerc et al. 2012; Greenland halibut and ringed seal in Cumberland Sound, McMeans et al. 2012a). Species that were not included here, but that are consumed in relatively large quantities by Greenland sharks, include the squid and wolffish in Kongsfjorden (identified in 27.3 and 18.2 % of sharks, respectively, Leclerc et al. 2012) and shorthorn sculpin (*Myoxocephalus scorpius*) in Cumberland Sound (identified in 27.8 % of Cumberland Sound sharks; McMeans et al. 2012a). FA data for Kongsfjorden haddock were not available in the literature (this species has arrived only recently to the Archipelago), although this species contributed ~20 % to the Kongsfjorden shark's diet based on the isotope mixing model. Exclusion of species listed above likely did not affect our FA results in any major way because available data for squid (Prince William Sound, Alaska, Iverson et al. 2002), wolffish, and haddock (Icelandic waters, Sigurgisladóttir and Pálmadóttir 1993) and shorthorn sculpin from Cumberland Sound (B.C. McMeans, M.T. Arts, A.T. Fisk, unpubl. data) reveal that these species have a more similar FA profile to the teleosts sampled in the present study than the marine mammals. For example, mean proportions of 22:5n-3 in armhook squid (Gonatidae), wolffish, haddock, and sculpin were 0.5, 1.0, 1.9, and 1.8 %, respectively, which agrees with the other teleosts sampled and is lower than proportions found in seal blubber (Table 4). Furthermore, proportions of 20:1n-9 in these species were 2.8, 0.8, 0.5, and 5.7 %, respectively, which are lower than values observed for Greenland halibut. Consumption of these species, therefore, does not explain the high C_{20} MUFA in Cumberland Sound Greenland sharks. Lower proportions of Greenland halibut indicator FAs (e.g., 20:1n-9) and higher proportions of the seal indicator FA 22:5n-3 in Kongsfjorden sharks are also not explained by scavenging on minke whale (*Balaenoptera acutorostrata*) blubber because this material is higher in 20:1n-9 and lower in 22:5n-3 (Olsen and Grahl-Nielsen 2003) than seals (Table 4). Recognizing that stomach contents give an incomplete representation of a predators diet breadth, we nonetheless sampled the major known prey of Greenland sharks from both Kongsfjorden and Cumberland Sound and are not aware of other species that would explain the observed differences in Greenland shark FAs between locations.

The FA profiles of Kongsfjorden Greenland sharks were generally similar between June 2008 and 2009. However, significant differences in several FAs indicate moderate inter-annual variability in both muscle and plasma, which could be attributed to variable feeding behavior over time. This is consistent with the fact that in 2008, many sharks had consumed minke whale offal (Leclerc et al. 2011), whereas this prey was not detected in the sharks sampled in 2009. Shark total length did not differ between sampling years and therefore does not explain the observed inter-annual variability in specific FAs. However, shark length did appear to explain some of the variation in certain prey

indicator FAs among individual sharks' muscle, based on the significantly negative relationships between shark length and 22:1n-9 and 22:1n-11 (which are high in Greenland halibut) and positive correlations with 16:1n-7 and 22:5n-3 (which are high in seal blubber, Table 3). These results could suggest that larger Greenland sharks consumed more marine mammal blubber and less Greenland halibut than smaller sharks in Kongsfjorden and support previous reports of diet-driven shifts in FA profiles with fish length (Iverson et al. 2002). Even though length was not related to either plasma FA or to $\delta^{15}N$, the weak trend toward increasing $\delta^{13}C$ in larger sharks is also consistent with greater consumption of seal or benthic teleosts (e.g., wolffish) that had more enriched ^{13}C relative to pelagic teleosts like Atlantic cod and haddock (Table 1). The lack of length relationships with plasma FAs could be attributed to the dynamic nature of this tissue, because fish plasma FA profiles are highly sensitive to, for example, the timing since the last meal (Alkanani et al. 2005).

Ecological role of Greenland sharks

The present analysis of SI and FA in Greenland sharks is the first for Norwegian waters and raises several points about the potential role of Greenland sharks in marine ecosystems. The Greenland shark is clearly a flexible feeder that consumes a wide range of prey based on the observation that several different prey items are found in the stomach of any one individual (e.g., Fisk et al. 2002; Leclerc et al. 2012). Polar bears are also predators of seals (Grahl-Nielsen et al. 2003), and seals are predators of fish (Labansen et al. 2011), but no other resident predator has a diet composed of both large teleosts and marine mammals. Therefore, individual Greenland sharks would exhibit low diet overlap with other resident predators in Kongsfjorden. The Greenland shark is the only large predatory fish in Kongsfjorden and other Arctic areas. The impact of a given shark on its ecosystem is difficult to predict due to the complexity of trophic interactions in marine food webs (Stevens et al. 2000). However, the greatest effect of a shark species on its prey populations likely arises when there is little diet overlap among sharks and other predators (because there is less chance for compensatory responses from other predators following changes in shark abundance, Kitchell et al. 2002; Schindler et al. 2002). Due to low diet overlap among Greenland sharks and other predators in Kongsfjorden, combined with their potentially large abundance (Jensen 1948; MacNeil et al. 2012), the role filled by the Greenland shark, and its effect on prey populations in Arctic food webs, could be significant.

Sharks can also have indirect effects on prey populations by altering their behavior (Ferretti et al. 2010). For example, Alaskan harbor seals (*Phoca vitulina richardsi*) in Prince William Sound experience predation risk from killer whales (*Orcinus orca*) in shallow surface waters and from Pacific sleeper sharks in deeper water, which affects their prey selection and feeding habitat (Frid et al. 2007). The situation in Kongsfjorden and other Arctic fjords could be similar, with polar bears acting as predators of ice-associated seals at the surface in ice-covered waters and Greenland sharks as predators in the water column. One obvious limitation to robustly concluding that Greenland sharks have a significant effect on seals is the uncertainty regarding the sharks' ability to actively capture seals. Even though Greenland sharks are slower swimmers than other sharks that prey on pinnipeds (Skomal and Benz 2004), they might be capable of capturing fast moving prey like seals while they sleep in the water column (see discussion in Leclerc et al. 2012). Corkscrew shaped wounds observed on Sable Island seals are thought to be caused by Greenland sharks (Lucas and Natanson 2010) and provide further evidence that these lethargic sharks can attack seals in open water. High proportions of seal FA markers in both muscle and plasma suggest routine consumption of marine mammals by Kongsfjorden sharks, which would be consistent with the ability of these sharks to actively capture marine mammals. More sporadic reliance on marine mammals, on the other hand, which could be indicated by lower proportions of seal FAs in Kongsfjorden relative to Cumberland Sound sharks in one or both tissues, would be more consistent with the sharks accessing this prey via opportunistic scavenging. The stomachs of Kongsfjorden Greenland sharks showed little evidence of scavenging seals (i.e., few necrophageous amphipods), which lends additional support to the contention that Kongsfjorden sharks are able to take live prey (Leclerc et al. 2012). The positive correlations between seal indicator FAs and shark length observed herein further indicate that larger sharks have either a higher preference for seals or a greater ability to capture or consume them. Direct observations of Greenland sharks actively capturing marine mammals are obviously difficult to obtain. However, continued work involving satellite tracking and the deployment of accelerometers and video cameras could lend further insight into the extent of seal predation events by Greenland sharks in Kongsfjorden.

Conclusions

In conclusion, Greenland sharks in Kongsfjorden consistently consume teleosts like Atlantic cod and marine mammals like ringed seals, based on SIs and FAs. The reason that Greenland sharks in Kongsfjorden exploited more of these prey and less of the bottom-dwelling Greenland halibut than Cumberland Sound sharks cannot

be assessed completely here because few prey or shark abundance data exist for comparison of these two locations. Greenland sharks are considered opportunistic, so that geographic differences in feeding behavior might be attributed to differences in prey abundance and/or prey distributions. Further work is required to address this idea. However, results of the present study provide the first evidence to suggest that the diet, and therefore the potential role, of Greenland sharks can vary between Arctic marine ecosystems and that both teleosts and marine mammals are likely significant sources of energy for Greenland sharks in Kongsfjorden.

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