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ORIGINAL PAPER

Deciphering the structure of the West Greenland marine food web using stable isotopes (δ^{13}C, δ^{15}N)

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Abstract The Arctic is facing major environmental changes impacting marine biodiversity and ecosystem functioning. One way of assessing the responses of an ecosystem to these changes is to quantitatively study food web dynamics. Here, we used stable isotope (δ^{15}N and δ^{13}C) analyses of 39 Arctic marine species to investigate trophic relationships and isotopic niches of the West Greenland food web in 2000–2004. The lowest δ^{15}N values were found for suspension feeding blue mussel (*Mytilus edulis*; 6.1 ‰) and the highest for polar bear (*Ursus maritimus*; 20.2 ‰). For δ^{13}C, copepods (*Calanus* spp.) had the lowest values (−20.4 ‰) and snow crab (*Chionoecetes opilio*) the highest values (−15.8 ‰). Our results show that the three trophic enrichment factor (TEF) approaches used to quantify species trophic positions (fixed TEF of 3.8 and 3.4 ‰ or scaled TEF) did not generally affect trophic modelling and provided similar conclusions. Overall, the findings in this study are in good agreement with previous investigations of other Arctic marine ecosystems. Interestingly, we found little overlap of core isotopic niches used by the four investigated functional groups (mammals, seabirds, fish and invertebrates), except for seabirds and fish where an overlap of 24 % was found. These results provide new insights into species and functional group interactions, as well as into the food web structure and ecosystem functioning of an important Arctic region that can be used as a template to guide future modelling of carbon, energy and contaminant flow in the region.

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Introduction

Marine ecosystems are being affected by the combined effects of climate change (Beaugrand et al. 2002) and anthropogenic influences including fisheries (Halpern et al. 2008), non-native species invasions and release of contaminants (Wiese and Robertson 2004; Hooper et al. 2005). To get a thorough understanding of how an ecosystem reacts to these changes, information is needed on its ecology, functioning and mechanisms of trophic transfer (Thompson et al. 2012). One way of combining these approaches is to study the food web dynamics within a system (Thompson et al. 2012). However, there are major obstacles in deriving long-term information on food web dynamics in marine food webs using conventional approaches such as stomach content analysis (Votier et al. 2003; Polito et al. 2011). A now well-established alternative method to study the trophic structure and dynamics of a community is the application of stable isotope analysis, as stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope ratios in tissues of animals provide information on their source of feeding and their relative trophic position, respectively (e.g. Hobson and Welch 1992; Boecklen et al. 2011; Middelburg 2014).

The marine ecosystem off the coast of West Greenland is one of the most biologically productive areas across the entire Arctic (Smidt 1979; Juul-Pedersen et al. 2015) and supports large populations of fish, seabirds and marine mammals (Born et al. 2003; Boertmann et al. 2004) as well as important spawning and nursery grounds, especially for northern shrimp (*Pandalus borealis*) and Greenlandic halibut (*Reinhardtius hippoglossoides*) (Buch et al. 2004; Simonsen et al. 2006). However, this region is undergoing major environmental changes. For instance, in West Greenland, as well as other parts of the Arctic, global warming has resulted in a reduction in sea ice thickness, distribution and seasonal duration (e.g. Comiso et al. 2008; Kwok and Rothrock 2009; Swart et al. 2015). Locally, the reduction in sea ice, as well as changes in the nutrient balance, has already changed the length and initiation of the growth season for primary producers and the distribution of fish, thereby fundamentally influencing the structure and functioning of the food web (Arrigo et al. 2008; Grebmeier et al. 2006; Wassmann et al. 2011).

Compared to other marine systems in the Arctic, the pelagic food web off West Greenland has been relatively well studied (e.g. Nielsen and Hansen 1995; Munk et al. 2003; Arendt et al. 2010; Kjellerup et al. 2015). However, substantial knowledge gaps remain, in particular on the trophic coupling to the higher trophic levels. The spring phytoplankton bloom develops immediately after the breakup of sea ice (Dünweber et al. 2010). Sea ice conditions are therefore important for the initiation of primary production in spring which, in turn, needs to be matched by the arrival of overwintering copepods of the genus *Calanus*, to get an efficient transfer of energy to higher trophic levels (Swalethorp et al. 2011; Møller et al. 2006, 2016). Current knowledge of marine shellfish and fish in West Greenland is based primarily on single species information (e.g. Møller et al. 2010; Hedeholm et al. 2012) and on research related to fisheries and environmental impact assessments related to hydrocarbon extraction and other anthropogenic activities (e.g. Bergström and Vilhjalmarsson 2007; ABA 2013). Seabird and marine mammal distribution and abundance have similarly been studied in relation to harvest management and planning of oil activities (e.g. Boertmann et al. 2013). However, in general, dietary and trophic information is currently fragmentary in West Greenland, complicating prediction on how species will respond to future environmental changes.

Since climate and anthropogenic changes can readily modify the ecosystem, it is of key importance to acquire baseline knowledge about the trophic structure of this marine ecosystem in order to provide a solid base for detection of the impacts of current and pending environmental change. Furthermore, understanding the ecological niche space occupied by species within an ecosystem, and the extent to which they overlap with other species or functional groups, is key for assessing their role in food web structure and energy transfer (McMeans et al. 2013a; Quillien et al. 2016). Here, we analysed isotopic data from key components of the West Greenland marine food web collected in 2000–2004 to provide a baseline against which current and future isotopic studies can be contrasted. Using these data, we describe the trophic relationships and isotopic niche space from invertebrate to marine mammals and compare our data with that available from other high-latitude marine food webs.

Materials and methods

Sample collections

Thirty-nine species were analysed (Table 1). Invertebrates, fish and seabirds were sampled between 62°00′ and 69°30′N, whereas marine mammals were sampled up to 71°30′N (Fig. 1). Twenty-six of the 39 species were collected during July–October 2003 (northern summer/fall, Table 1). Deviations from this main sampling period by the following species were unavoidable due to seasonal migrations. Copepods (*Calanus* spp.), little auks (*Alle alle*), ringed seals (*Phoca hispida*), hooded seals (*Cystophora cristata*) and polar bear (*Ursus maritimus*) were sampled from March to June (northern spring/summer) in 2003 (polar bear in 2001), while the remaining three species of seabirds [king eider (*Somateria spectabilis*), common

Table 1 Species sampled in the West Greenland marine ecosystem (year; n number of samples, CL carapace length, CW carapace width, ML mantle length, TL total length, ST soft tissue). Values of $\delta^{15}N$, $\delta^{13}C$ and trophic positions (TP) are given as mean $\pm$ SD

Common name	Scientific name	Sampling period	Year	Size range	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N	TP (TEF = 3.8‰)	TP (TEF = 3.4‰)	TP Scaled TEF	Niche width (‰²)
Invertebrates												11.4
Blue mussel	*Mytilus edulis*	Sept	2003	1.6–6.1 g ST	12	−18.3 ± 0.4	6.1 ± 0.5	4.0 ± 0.3	1.5 ± 0.1	1.5 ± 0.1	1.6 ± 0.1	0.5
Iceland scallop	*Chlamys islandica*	July	2003	32.6–64.1 g ST	12	−16.9 ± 0.3	7.8 ± 0.2	3.2 ± 0.1	2.0 ± 0.1	2.0 ± 0.1	2.0 ± 0.1	–
Copepod	*Calanus finmarchicus*	May–June	2003	3.4–3.6 mm TL	7	−20.4 ± 0.3	7.9 ± 0.3	3.7 ± 0.1	2.0 ± 0.1	2.0 ± 0.1	2.0 ± 0.1	0.4
Northern Krill	*Meganyctiphanes norvegica*	July	2003	22–35 mm TL	2	−19.0	8.5	–	2.2	2.2	2.1	–
Copepod	*Calanus hyperboreus*	May–June	2003	10.0–10.6 mm TL	5	−18.9 ± 0.6	8.7 ± 0.1	3.6 ± 0.1	2.2 ± 0.0	2.2 ± 0.0	2.2 ± 0.0	0.5
Copepod	*Calanus glacialis*	May–June	2003	3.5–3.6 mm TL	4	−19.2 ± 0.6	9.2 ± 0.1	3.5 ± 0.0	2.3 ± 0.0	2.4 ± 0.0	2.3 ± 0.0	0.3
Northern shrimp	*Pandalus borealis*	July	2003	19–29 mm CL	24	−17.4 ± 0.5	10.0 ± 1.8	3.6 ± 0.3	2.6 ± 0.5	2.6 ± 0.5	2.6 ± 0.5	2.4
Snow crab	*Chionoecetes opilio*	Sept	2003	62–128 mm CW	24	−15.8 ± 0.3	11.0 ± 0.4	3.1 ± 0.1	2.8 ± 0.1	2.9 ± 0.1	2.8 ± 0.1	0.3
Boreoatlantic armhook squid	*Gonatus fabricii*	Aug–Sept	2003	>10 cm ML	26	−18.8 ± 0.5	13.1 ± 1.7	3.3 ± 0.1	3.4 ± 0.5	3.5 ± 0.5	3.5 ± 0.7	2.5
Fish												4.4
Sandeel	*Ammodytes sp.*	July	2003	14–22 cm TL	11	−18.8 ± 0.3	10.0 ± 0.3	3.3 ± 0.2	2.5 ± 0.1	2.6 ± 0.1	2.5 ± 0.1	0.3
Greenland halibut—small	*Reinhardtius hippoglossoides*	Aug–Sept	2003	16–19 cm TL	11	−19.4 ± 0.2	10.5 ± 0.3	3.3 ± 0.1	2.7 ± 0.1	2.8 ± 0.1	2.7 ± 0.1	0.2
Capelin	*Mallotus villosus*	July	2003	13–16 cm TL	12	−19.0 ± 0.6	11.6 ± 1.2	3.3 ± 0.1	3.0 ± 0.3	3.1 ± 0.3	3.0 ± 0.3	1.2
Great silver smelt	*Argentina silus*	July	2003	26 cm TL	1	−17.4	11.8	3.4	3.0	3.2	3.0	–
Greenland halibut—medium	*Reinhardtius hippoglossoides*	Aug–Sept	2003	27–38 cm TL	11	−19.4 ± 0.5	11.9 ± 0.8	3.0 ± 1.6	3.0 ± 0.2	3.2 ± 0.2	3.1 ± 0.3	1.3
Atlantic salmon	*Salmo salar*	Aug–Sept	2003	59–68 cm TL	16	−19.7 ± 0.6	12.1 ± 1.1	–	3.1 ± 0.3	3.2 ± 0.3	3.1 ± 0.4	1.5
Polar cod—small	*Boreogadus saida*	Aug–Sept	2003	8–10 cm TL	14	−18.8 ± 0.3	12.3 ± 0.7	3.3 ± 0.1	3.1 ± 0.2	3.3 ± 0.2	3.2 ± 0.2	0.5
Deepwater redfish	*Sebastes mentella*	July	2003	21–55 cm TL	12	−19.1 ± 0.5	12.6 ± 1.5	3.3 ± 0.1	3.2 ± 0.4	3.4 ± 0.4	3.3 ± 0.6	1.5
Golden redfish	*Sebastes marinus*	July	2003	28–45 cm TL	12	−18.7 ± 0.6	12.9 ± 1.2	3.3 ± 0.1	3.3 ± 0.3	3.5 ± 0.3	3.4 ± 0.4	1.4
American plaice	*Hippoglossoides platessoides*	July	2003	21–32 cm TL	12	−18.0 ± 0.4	12.9 ± 0.7	3.2 ± 0.0	3.3 ± 0.2	3.5 ± 0.2	3.4 ± 0.3	1.1
Haddock	*Melanogrammus aeglefinus*	July	2003	18–24 cm TL	12	−18.0 ± 0.3	13.0 ± 0.5	3.2 ± 0.0	3.3 ± 0.1	3.5 ± 0.1	3.4 ± 0.2	0.3
Atlantic cod—medium	*Gadus morhua*	July–Sept	2003	26–46 cm TL	24	−18.2 ± 0.4	13.1 ± 0.6	3.0 ± 0.9	3.4 ± 0.1	3.5 ± 0.1	3.5 ± 0.2	0.6
Daubed shanny	*Leptoclinus maculatus*	July	2003	13–20 cm TL	12	−17.3 ± 0.5	13.3 ± 0.6	3.2 ± 0.0	3.4 ± 0.2	3.6 ± 0.2	3.5 ± 0.2	0.8
Atlantic wolffish	*Anarhichas lupus*	July–Sept	2003	35–53 cm TL	11	−16.8 ± 1.0	13.6 ± 0.9	3.3 ± 0.1	3.5 ± 0.2	3.7 ± 0.3	3.7 ± 0.4	3.2
Polar cod—medium	*Boreogadus saida*	Aug–Sept	2003	12–15 cm TL	9	−18.9 ± 0.4	13.7 ± 0.5	3.2 ± 0.1	3.5 ± 0.1	3.7 ± 0.2	3.7 ± 0.2	0.6
Greenland halibut—large	*Reinhardtius hippoglossoides*	Aug–Sept	2003	42–55 cm TL	11	−18.7 ± 0.8	14.0 ± 1.1	1.1 ± 1.9	3.6 ± 0.3	3.6 ± 0.3	3.8 ± 0.5	2.7
Spotted wolffish	*Anarhichas minor*	July–Sept	2003	29–88 cm TL	13	−16.4 ± 0.9	14.2 ± 0.6	3.2 ± 0.1	3.7 ± 0.2	3.7 ± 0.2	3.9 ± 0.3	1.3

Table 1 continued

Common name	Scientific name	Sampling period	Year	Size range	n	δ^{13}C (‰)	δ^{15}N (‰)	C:N	TP (TEF = 3.8 ‰)	TP (TEF = 3.4 ‰)	TP Scaled TEF	Niche width (‰²)
Atlantic cod—large	*Gadus morhua*	July–Sept	2003	51- 70 cm TL	15	−17.6 ± 0.5	14.7 ± 0.8	1.7 ± 1.7	3.8 ± 0.2	4.0 ± 0.2	4.1 ± 0.4	1.4
Shorthorn sculpin	*Myoxocephalus scorpius*	Sept	2003	30–40 cm TL	6	−16.8 ± 0.6	15.3 ± 0.8	1.2 ± 1.8	3.9 ± 0.2	4.2 ± 0.2	4.4 ± 0.4	1.5
Greenland shark	*Somniosus microcephalus*	July	2003	Appr. 400 cm TL	1	−19.5	17.0	4.8	4.4	4.7	5.3	–
Seabirds												3.4
King eider	*Somateria spectabilis*	Jan	2004	1.52–1.83 kg	9	−17.7 ± 0.3	11.3 ± 0.3	3.4 ± 0.1	2.9 ± 0.1	3.0 ± 0.1	2.9 ± 0.1	0.4
Common eider	*Somateria molissima*	Jan	2004	1.48–2.16 kg	32	−17.3 ± 0.8	11.4 ± 0.6	3.4 ± 0.1	2.9 ± 0.2	3.0 ± 0.2	2.9 ± 0.2	1.3
Little auk	*Alle alle*	March	2003	0.15–0.22 kg	19	−19.5 ± 0.3	11.7 ± 0.4	–	3.0 ± 0.1	3.1 ± 0.1	3.0 ± 0.1	0.4
Brünnich's guillemot	*Uria lomvia*	Nov	2003	0.85–1.03 kg	12	−19.3 ± 0.4	12.0 ± 0.5	3.5 ± 0.2	3.1 ± 0.1	3.2 ± 0.1	3.1 ± 0.1	0.5
Kittiwake	*Rissa tridactyla*	Sept	2003	0.33–0.45 kg	12	−19.5 ± 0.4	12.1 ± 0.8	3.6 ± 0.2	3.1 ± 0.2	3.2 ± 0.2	3.1 ± 0.2	1.1
Black guillemot	*Cepphus grylle*	Sept	2003	no data	20	−19.2 ± 0.6	13.8 ± 0.3	–	3.5 ± 0.1	3.7 ± 0.1	3.7 ± 0.1	0.6
Marine mammals												3.3
Minke whale	*Balaenoptera acuto-rostrata*	Sept	2003	appr. 450–550 cm TL	6	−19.0 ± 1.1	12.0 ± 0.5	3.6 ± 0.4	3.1 ± 0.1	3.2 ± 0.1	3.1 ± 0.2	2.0
Harp seal	*Pagophilus groenlandicus*	Aug–Sept	2003	100–140 cm TL	10	−18.6 ± 0.2	13.8 ± 0.8	3.4 ± 0.1	3.5 ± 0.2	3.7 ± 0.2	3.7 ± 0.3	0.4
Walrus	*Odobenus rosmarus*	Jan	2002	250 cm TL	1	−19.5	14.0	4.1	3.6	3.8	3.8	–
Ringed seal	*Phoca hispida*	April	2003	91–108 cm TL	10	−18.8 ± 0.2	15.4 ± 0.4	3.5 ± 0.1	4.0 ± 0.1	4.2 ± 0.1	4.4 ± 0.2	0.3
Beluga	*Delphinapterus leucas*	Dec	2000	292–487 cm TL	18	−18.3 ± 0.3	15.9 ± 0.4	3.4 ± 0.1	4.1 ± 0.1	4.4 ± 0.1	4.7 ± 0.2	0.4
Narwhal	*Monodon monoceros*	Nov	2000	no data	7	−18.3 ± 0.3	16.1 ± 0.3	3.4 ± 0.0	4.2 ± 0.1	4.4 ± 0.1	4.8 ± 0.1	0.3
Hooded seal	*Cystophora cristata*	April–May	2003	240–386 cm TL	7	−16.9 ± 0.3	16.9 ± 0.7	3.0 ± 1.3	4.4 ± 0.2	4.6 ± 0.2	5.3 ± 0.5	0.8
Polar bear	*Ursus maritimus*	May	2001	appr. 220 cm TL	1	−16.8	20.2	3.3	5.2	5.6	8.6	–

eider (*Somateria molissima*) and Brünnich's guillemot (*Uria lomvia*)] were sampled during November–January (northern winter) 2003/2004, and three species of marine mammals [walrus (*Odobenus rosmarus*), beluga (*Delphinapterus leucas*) and narwhal (*Monodon monoceros*)] were sampled during November–January (northern winter) in 2000/2002.

Copepods were sampled from the research vessel R.V. Porsild (University of Copenhagen) at a permanent station located 1 nautical mile off Qeqertarsuaq (69°15′N, 53°33′W) (Hansen et al. 2012b) and collected in the upper 50 m of the water column using a WP-2 net (mesh size 200 μm). Samples were diluted in surface water in a 100-L thermo box and brought to the laboratory where the dominating *Calanus* species (*Calanus hyperboreus*, *C. glacialis* and *C. finmarchicus*) were carefully sorted and rinsed in filtered surface water before being transferred to a test tube and deep frozen (−28 °C).

Samples of snow crab were collected during a routine pot survey using squid as bait (Carl and Burmeister 2006). Samples of northern shrimp, northern krill (*Meganyctiphanes norvegica*), Boreoatlantic armhook squid (*Gonatus fabricii*), capelin (*Mallotus villosus*), polar cod (*Boreogadus saida*), sandeel (*Ammodytes* sp.), deepwater redfish (*Sebastes mentella*), golden redfish (*Sebastes marinus*), Greenland halibut, great silver smelt (*Argentina silus*), American plaice (*Hippoglossoides platessoides*), haddock (*Melanogrammus aeglefinus*), Atlantic cod, daubed shanny (*Leptoclinus maculatus*), Atlantic wolffish (*Anarhichas lupus*), spotted wolffish (*Anarhichas minor*) and shorthorn sculpin (*Myoxocephalus scorpius*) were collected by a 3000/20-mesh Skjervøy bottom trawl (Kanneworff and Wieland 2003). All samples taken were deep frozen (−50 °C) on board immediately after collection.

Samples of additional invertebrates [blue mussel (*Mytilus edulis*), Iceland scallop (*Chlamys islandica*)], fish [Atlantic salmon (*Salmo salar*)], seabirds [Brünnich's guillemot, black-legged kittiwake (*Rissa tridactyla*), common eider, king eider, black guillemot (*Cepphus grylle*)] and marine mammals [harp seal (*Pagophilus groenlandicus*) and minke whale (*Balaenoptera acutorostrata*)] along with supplementary samples of spotted wolffish and Atlantic wolffish were collected from coastal Inuit subsistence catches. For marine mammals, tissue samples were deep frozen (−28 °C/− 50 °C) 6–24 h postmortem.

All necessary permits to collect samples from the different species of animals were obtained from the Ministry of Fisheries, Hunting and Agriculture (APNN) in Greenland.

Stable isotope analysis

Muscle samples from all species [except blue mussels, copepods and northern krill where the whole animal (minus

shell) was used] were prepared for $\delta^{13}C$ and $\delta^{15}N$ analyses by the isotope laboratory at the Department of Soil Science, University of Saskatchewan, Saskatoon, Canada. Samples were washed in distilled water, freeze-dried, powdered and treated with a 2:1 chloroform–methanol solution to remove lipids. Our approach was to normalize sample measurements in this way in order to compare our data with other major isotopic food web studies conducted in the region (e.g. the North Water Polynya and the Canadian Arctic, Hobson et al. 1995, 2002a). We recognize that such lipid extractions while controlling for differential lipid content in order to make $\delta^{13}C$ measurements more easily interpreted, can have small (0 ‰) to moderate (0.5 ‰) effects on tissue $\delta^{15}N$ values (Søreide et al. 2006). However, we favoured our approach over the use of calibrations based on the elemental C:N ratios which have not been developed specifically for our food web of interest. Our approach thus provides key information on protein pathways and not necessarily on lipid pathways and should be interpreted as such. Samples were then dried under a fume hood. Additionally, zooplankton were soaked in 0.1 N HCl to remove carbonates and then dried without rinsing. Homogenized samples of 1 mg were loaded into tin cups and combusted at 1200 °C in a Robo-Prep elemental analyser. Resultant CO_2 and N_2 gases were then analysed using an interfaced Europa 20:20 continuous-flow isotope ratio mass spectrometer (CFIRMS), with every five samples separated by two laboratory standards (Bowhead whale baleen and egg albumen). Stable isotope abundances were expressed in the δ-notation as the deviation from standards in parts per thousand (‰) according to the following equation:

$$\delta X = \left(\left(R_{sample} / R_{standard} \right) - 1 \right) * 1000 \tag{1}$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The $R_{standard}$ values were based on the PeeDee Belemnite for ^{13}C and atmospheric N_2 for ^{15}N. Replicate measurements of internal laboratory standards of similar matrix (Bowhead whale baleen and egg albumin) indicate within-run ($n = 6$) measurement errors of ±0.1 ‰ and ±0.3 ‰ for $\delta^{13}C$ and $\delta^{15}N$ values, respectively.

Estimations of trophic positions

Stable isotope analysis has, over the past 20 years, increasingly been used to study animal diets and trophic positions (see review by Boecklen et al. 2011). One very important aspect of using stable isotopes to describe the food web structure of a community is determining the diet–tissue discrimination factor ($\Delta^{15}N$) or trophic enrichment factor (TEF), namely the isotopic offset between a consumer tissues and its diet (Hobson and Clark 1992; Post 2002). It remains a challenge to choose the most appropriate TEF value for any given system, especially those involving a
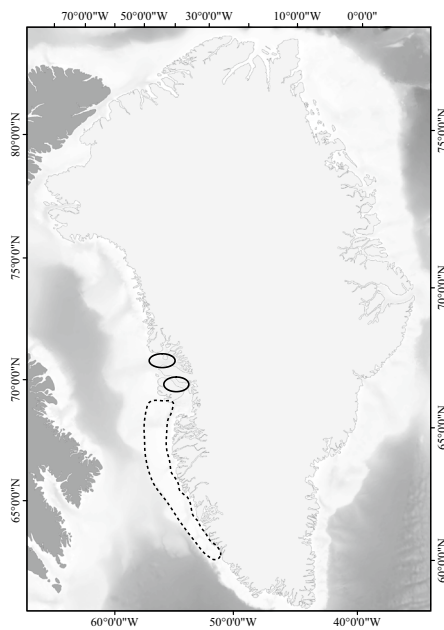
Fig. 1 The sampling area in West Greenland. Invertebrates, fish and seabirds were sampled between 62° and 69°30′N (*dashed area*), whereas marine mammals had a sampling range up to 71°30′N (*dashed* and *solid line areas*). Projection: equidistant conic with a central meridian of −60 degrees

wide variety of trophic positions and taxa. A meta-analysis conducted by Post (2002) suggests that a TEF of 3.4 ‰ is a reasonable estimate (see also Minagawa and Wada 1984). However, for Arctic marine systems, modelling based on extensive food web isotopic assays suggests that a TEF of 3.8 ‰ is more appropriate (Hobson and Welch 1992; Hobson et al. 1994, 2002a, 2002b; Hobson and Bond 2012). More recently, the idea of varying TEF values (Olive et al. 2003; Olin et al. 2013) has resulted in the suggestion of using a scaled approach (Hussey et al. 2014a). Our primary motivation was to produce a dataset that could be readily compared with previous work (i.e. by using a TEF of 3.8 ‰). However, we also modelled our trophic positions based on the generalized TEF value of 3.4 ‰ and the scaled approach suggested by Hussey et al. (2014a).

Trophic positions (TP) using the generalized estimated TEF values were calculated according to the formula:

$$TP_{consumer} = TP_{primary\ consumer}$$
$$+ \left(\delta^{15}N_{consumer} - \delta^{15}N_{primary\ consumer}\right) \Big/ TEF \tag{2}$$

We assigned the copepod *Calanus finmarchicus* (average $\delta^{15}N$ value 7.92 ‰ in our study area) to the second trophic level (i.e. $TP_{primary\ consumer} = 2.0$).

To apply the scaled trophic estimates we used the formula (see Hussey et al. 2014a, b for details):

$$TP = \frac{\log\left(\delta^{15}N_{lim} - \delta^{15}N_{primary\ consumer}\right) - \log\left(\delta^{15}N_{lim} - \delta^{15}N_{TP}\right)}{k}$$
$$+ TP_{primary\ consumer} \tag{3}$$

where

$$k = -\log\left(\frac{\beta_0 - \delta^{15}N_{lim}}{-\delta^{15}N_{lim}}\right) \tag{4}$$

$$\delta^{15}N_{lim} = \frac{-\beta_0}{\beta 1} \tag{5}$$

Values of β_0 (5.92) and β_1 (−0.27) were taken from Hussey et al. (2014a, p. 243). Again we assigned copepod *Calanus finmarchicus* (average $\delta^{15}N$ value 7.92 ‰ in our study area) to the second trophic level (i.e. TP = 2.0).

Niche width and overlap

The position of a species in the δ-space is mainly driven by resource use and foraging habitats. The isotopic niche width (‰²) was measured for each species by calculating the standard ellipse area SEA (40 %, SIAR default), corrected for small sample sizes (SEA_C) following Jackson et al. (2011). The individual isotope niche width (SEA_C) was calculated for all species except northern krill, great silver smelt, Greenland shark, walrus and polar bear due to too small sample sizes (Table 1). In addition, niche widths and (semi-quantitative) niche overlaps were calculated for the four functional groups (invertebrates, fish, seabirds and marine mammals). Niche overlap is given as the proportion of the overlapping area between the niches of groups A and B out of the summed niche area of A and B. All analyses were done using the package SIAR in R (R Development Core Team 2011).

Results

Stable isotopes

The lowest $\delta^{15}N$ values sampled in our study were for the suspension feeding blue mussel (6.1 ± 0.5 ‰ SD), and the highest were for polar bear (20.2 ‰) (Table 1, Electronic Supplementary Material Figure S1). Groups of invertebrates, fish, seabirds and marine mammals had mean $\delta^{15}N$ values ranging from 6.1 to 13.1 ‰, 10.0 to 17.0 ‰, 11.3 to 13.8 ‰ and 12.0 to 20.2 ‰, respectively (Table 1; Figs. 2, 3, 4, 5). Species having the lowest $\delta^{15}N$ values generally also had the lowest $\delta^{13}C$ values, except for marine mammals, where the opposite was the case. The lowest $\delta^{13}C$ values were observed in *Calanus finmarchicus* (−20.4 ± 0.3 ‰ SD) and the highest in the snow

crab (-15.8 ± 0.3 ‰ SD). Groups of invertebrates, fish, seabirds and marine mammals had mean $\delta^{13}C$ values ranging from -20.4 to -15.8 ‰, -19.7 to -16.4 ‰, -19.5 to -17.3 ‰ and -19.5 to -16.8 ‰, respectively (Table 1; Electronic Supplementary Material Figure S1).

Food web length

With a TEF of 3.8 ‰ the mean TPs of all organisms ranged from 1.5 to 5.2 indicating a food web in West Greenland spanning 5 trophic levels (Table 1; Fig. 6). A TEF of 3.4 ‰ showed similar results with mean TPs of organisms ranging from 1.5 to 5.6, also indicating a food web of 5 trophic levels (Table 1). Using a scaled TEF mean TPs ranged from 1.6 to 8.6 indicating a food web with 8 trophic levels (Table 1).

Isotopic niche width and overlap

The isotopic niche width of all individual invertebrate species ranged from 0.3 ‰^{2} (*Calanus glacialis* and snow crab) to 2.5 ‰^{2} (Boreoatlantic armhook squid), with an overall width for the group of 11.4 ‰^{2}. The niche width of the individual fish species ranged from 0.2 ‰^{2} (Greenland halibut – small) to 3.2 ‰^{2} (Atlantic wolffish) with a group niche width of 4.4 ‰^{2}. The individual seabird species ranged in niche width from 0.4 ‰^{2} (king eider) to 1.3 ‰^{2} (common eider) and an overall group width of 3.4 ‰^{2}. The individual marine mammal species ranged in isotopic niche width from 0.3 ‰^{2} (ringed seal and narwhal) to 2.0 ‰^{2} (minke whale) and had a group size of 3.3 ‰^{2}.

We found the core isotopic niche areas used by seabirds and fish to have an overlap of 24.3 % (Table 2; Fig. 7). Seabird and invertebrate niches had an overlap of 9.9 % and fish and invertebrate niches an overlap of 3.0 % (Table 2; Fig. 7). The isotopic niche area of marine mammals and fish had an overlap of 1.2 % (Table 2; Fig. 7), whereas no overlap was found between the core niche areas of marine mammals and invertebrates. However, looking exclusively at the Boreoatlantic armhook squid, where the wide niche width is driven by high $\delta^{15}N$ values, we found the total niche area of squid and marine mammals to have an overlap of 10.3 %.

Discussion

Our isotopic analysis of the marine food web of West Greenland has provided a trophic model describing relationships among diverse organisms from herbivorous zooplankton to polar bears. Our work based on a TEF of 3.8 ‰ contributes to the circumpolar understanding by allowing direct comparisons with models developed for other Arctic regions such as the North Water Polynya (Hobson et al. 2002a), North East Water Polynya (Hobson
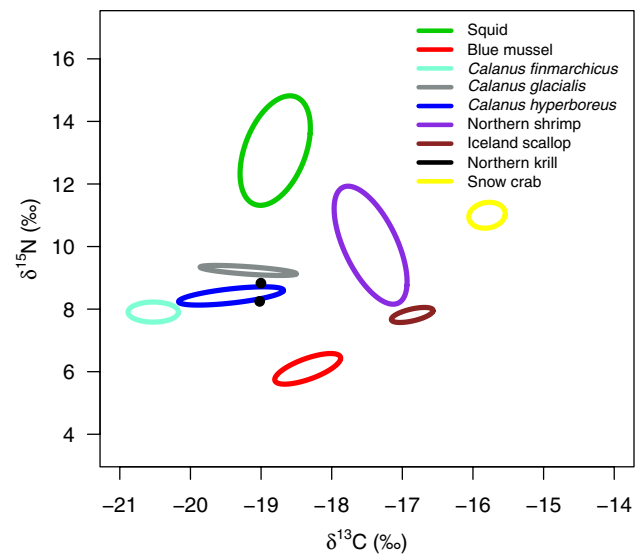

Fig. 2 Stable isotope biplot illustrating the isotopic niche of the invertebrate community in West Greenland. *Ellipses* represent the isotopic niche width of 40 % (SIAR default) corrected for small sample size (Jackson et al. 2011)

et al. 1995), Lancaster Sound (Hobson and Welch 1992) and the sub-Arctic Gulf of Alaska (Hobson et al. 1997). We acknowledge that our choice of TEF can clearly influence our interpretations of food web structure and so also applied two other approaches. However, we found that a trophic model using a TEF of 3.4 ‰ and the scaling approach advocated by Hussey et al. (2014a) did not result in substantial differences in our trophic estimates with the exception of marine mammals. Polar bear, especially, where the scaling approach estimated this species at a TP of 8.6, while this value was 5.2 and 5.6 with TEF 3.8 ‰ and 3.4 ‰, respectively, seems to be clearly overestimated. However, considering we only had one polar bear sample, this needs further investigation. To a lesser degree, we also found the scaling approach provided higher TP estimates for ringed seal (range between TEF 3.8 ‰ and scaling method: 4.0–4.4), beluga (4.1–4.7), narwhal (4.2–4.8) and hooded seal (4.8–5.3). With these exceptions noted, our study confirmed an expected 5–5.5 trophic-level system with considerable overlap between isotopic niches of species at each level, as illustrated from other Arctic areas, such as the North East Water Polynya (Hobson et al. 1995) and Lancaster Sound (Hobson and Welch 1992). While we fully recognize that the isotopic niche is not necessarily equivalent to the ecological niche, the derivation of isotopic niches can greatly assist in understanding food web structure and function (Newsone et al. 2007).

The relationships described here can now be used to examine the existing structure within the food web and serve as a template and baseline with which to compare

Fig. 3 Stable isotope biplot illustrating the isotopic niche of the fish community in West Greenland. *Ellipses* represent the isotopic niche width of 40 % (SIAR default) corrected for small sample size (Jackson et al. 2011)
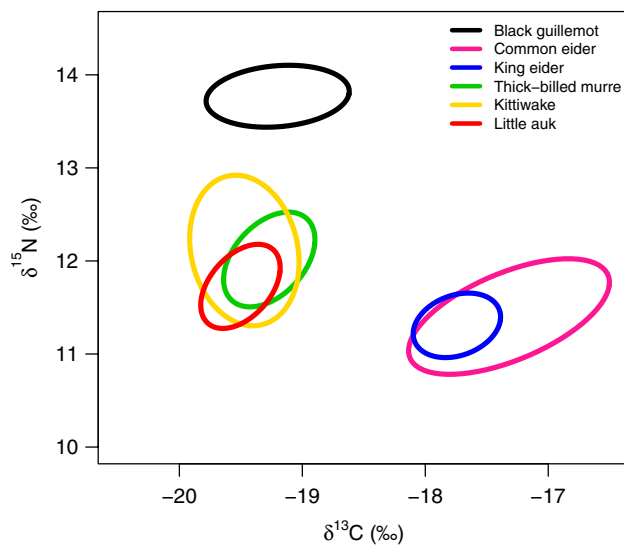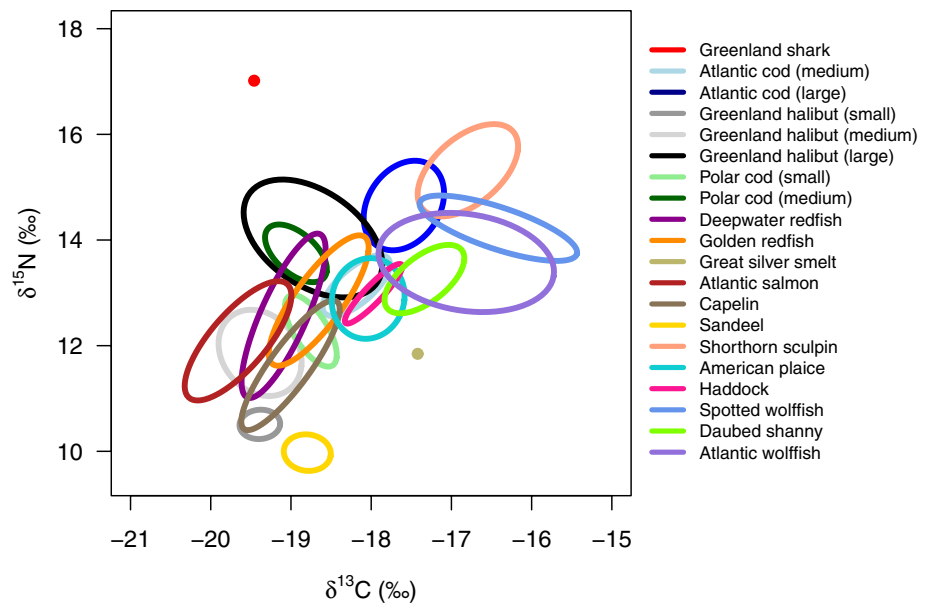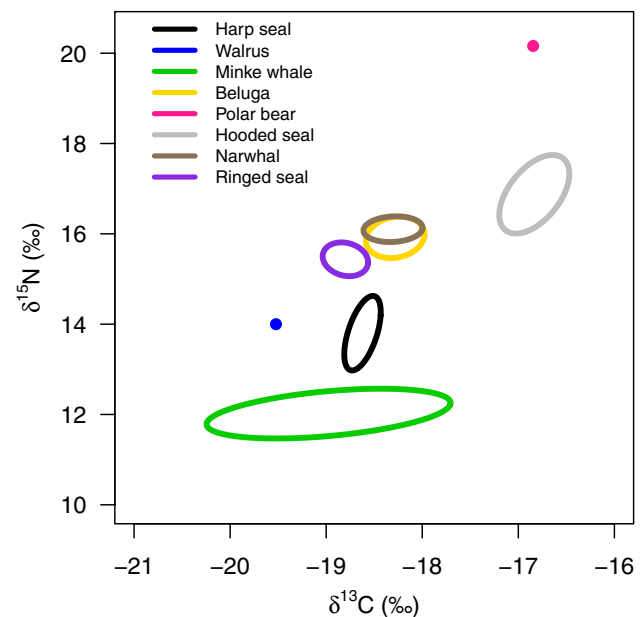

Fig. 4 Stable isotope biplot illustrating the isotopic niche of the seabird community in West Greenland. *Ellipses* represent the isotopic niche width of 40 % (SIAR default) corrected for small sample size (Jackson et al. 2011)

Fig. 5 Stable isotope biplot illustrating the isotopic niche of the marine mammal (including shark) community in West Greenland. *Ellipses* represent the isotopic niche width of 40 % (SIAR default) corrected for small sample size (Jackson et al. 2011)

with other Arctic marine food webs and monitor the effects of environmental changes underway in this and other regions (e.g. Vizzini and Mazzola 2004). We advocate the continued use of a generalized TEF value of 3.8 ‰ because this makes for direct comparisons with other high Arctic marine food webs. However, we recognize that for monitoring purposes, consistency is required and encourage researchers to continually strive to improve TP estimates based on the stable isotope approach.

West Greenland is continuously experiencing major environmental challenges which affect the trophic ecology

of organisms (diet and habitat) and could thereby impact the whole marine food web structure. For instance, Greenland has experienced a warming of the sea along its west coast and a subsequent regime shift in the fish community in the marine system in the 1920s and 1930s (Drinkwater 2006). The shift resulted in the retreat of cold-water fish species to the north and at the same time in an expansion of boreal species (most noticeably the Atlantic cod).
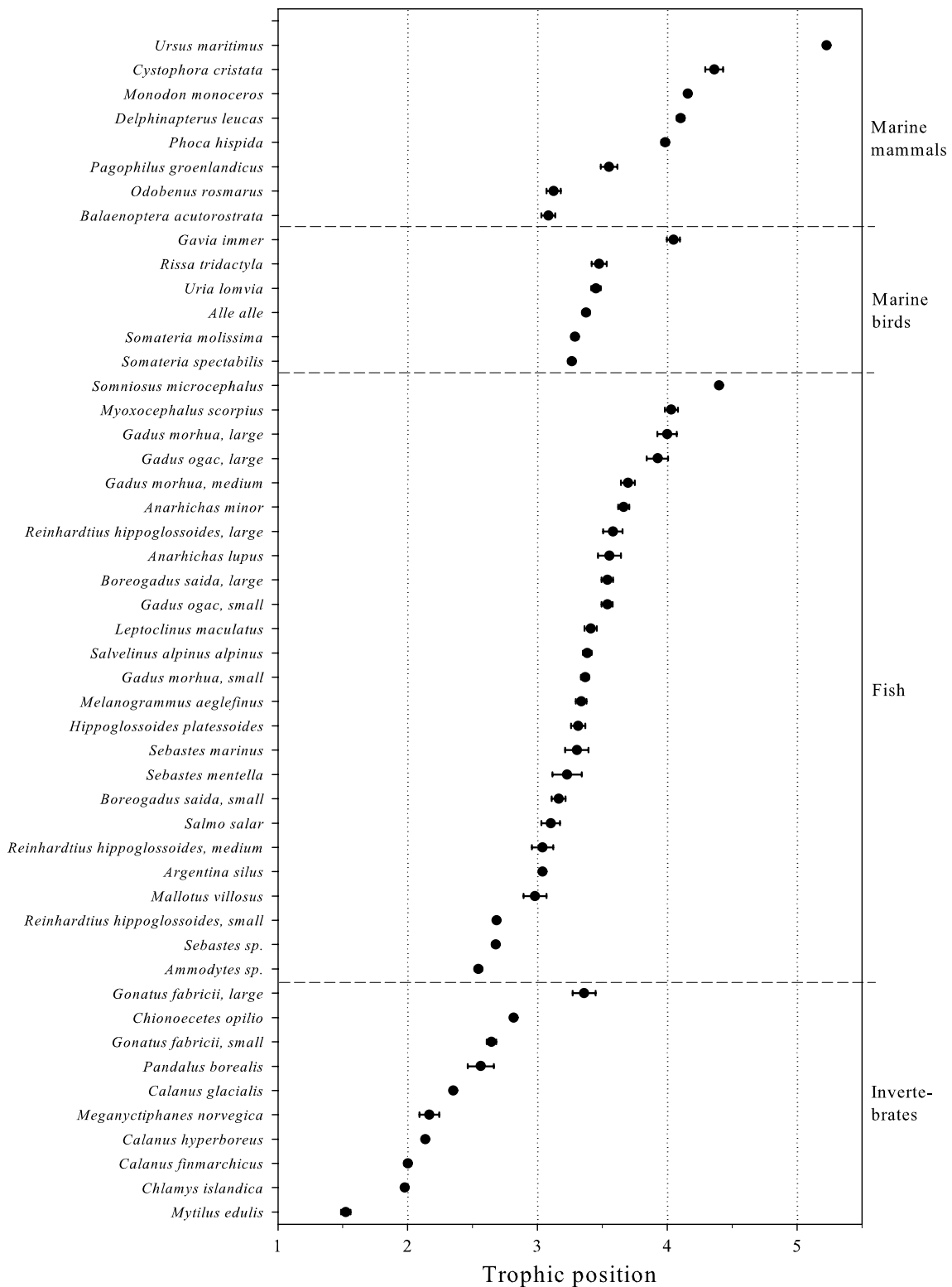
Fig. 6 Food web model for the West Greenland ecosystem based on trophic position (mean ± SD) and using a trophic enrichment factor (TEF) of 3.8 ‰. Species within groups (invertebrates, fish, seabirds and marine mammals) are sorted in ascending order according to trophic position within each group

Following this warm period, the last three decades of the 1900s experienced a series of anomalous cold years (Buch et al. 2004; Drinkwater 2004; Stein 2004, 2005) before a new regime shift during 1997 in Disko Bay. This latter resulted in a noticeable change in water characteristics and a change to a general warming trend in this century (Hansen et al. 2012b; Cappelen and Vinther 2014). Accordingly, a change in the diet of Greenland halibut has been observed during the period 1978–2003 with increasing importance of invertebrates (Dwyer et al. 2010). Similarly, Falk and Durinck (1993) studied stomach contents in Brünnich's guillemots during the winter 1988–89 and found that they fed almost exclusively on fish from October to December. Brünnich's guillemots are opportunistic feeders favouring fish when readily available. A TP of 3.1 for Brünnich's guillemots sampled in November 2003 in this study suggests a diet mainly consisting of zooplankton in the preceding month. This contrasts to the study from 1988 to 1989, possibly indicating a change in the availability of fish. Conversely, little auks sampled for this study had a TP of 3.0 and a similar TP value was found for little auks wintering off Nuuk in 2007 (Fort et al. 2010a), suggesting that the base of the food web had not changed considerably between 2003 and 2007.

Invertebrates

The nine species of invertebrates analysed from West Greenland showed a wide range of both $\delta^{15}N$ and $\delta^{13}C$ values, reflected by a large isotopic niche width for this group in comparison with fish, seabirds and marine mammals. This result confirms that invertebrates show a wide range of trophic ecologies, occupying various habitats and feeding at several trophic levels. Furthermore, the calculated 40 % isotopic niches for the different species of invertebrates did not overlap, indicating a group mostly made up of specialists segregating in their environment. However, we need to acknowledge that an absence of overlap between species in this group could also be a result of a lack of species sampled. Values of $\delta^{15}N$ for copepods ranged from 7.9 ‰ (TP 2) for *Calanus finmarchicus* to 9.2 ‰ for *C. glacialis*, suggesting that *C. finmarchicus* were primarily herbivorous
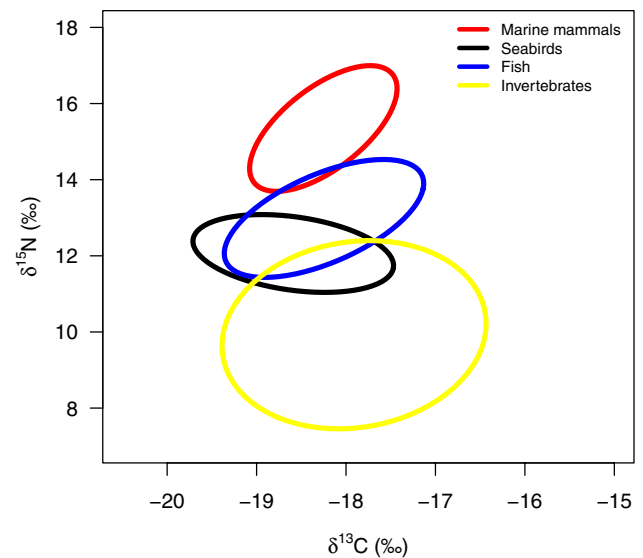

Fig. 7 Stable isotope biplot illustrating the isotopic niche of the four functional groups (invertebrates, fish, seabirds and marine mammals) in West Greenland. *Ellipses* represent the isotopic niche width of 40 % (SIAR default) corrected for small sample size (SEAc; Jackson et al. 2011)

during the sampling period and supporting findings by Stevens et al. (2004) and Campbell et al. (2009). This result also supports our choice of this species as representative of a primary herbivore at TP 2.

Being filter feeders, blue mussels play an important role in harvesting the plankton and seston in the water column, and thus we would have expected blue mussels to occupy the same trophic level as *C. finmarchicus* and Iceland scallop (*Chlamys islandica*) (i.e. at TP 2). Our model with a TEF of 3.8 ‰ (as well as a TEF of 3.4 ‰ and the scaled TEF), however, produced a TP of 1.5 (1.5 and 1.6, respectively) for blue mussel, which is below that expected for a filter feeder. Our model did not consider organisms that void nitrogenous wastes in different ways and could therefore be inappropriate for these organisms. As reviewed by Vanderklift and Ponsard (2003), molluscs and detritivores show the lowest diet–tissue isotopic discrimination for $\delta^{15}N$. This is related to their excretion of ammonia. Such lower discrimination would result in lower tissue $\delta^{15}N$ values and hence lower TP estimates. Future refinements of marine TP models using $\delta^{15}N$ values should consider the form of nitrogenous excretion and the relative dependence of some organisms on detritus (Vanderklift and Ponsard 2003).

As expected, the predator Boreoatlantic armhook squid foraged at the highest trophic level among invertebrates. For some individuals, these levels reached those occupied by some piscivorous marine mammals. In that respect, we found the total niche area of squids and marine mammals

Table 2 Isotopic niche overlap (%) between the four functional groups in the West Greenland marine ecosystem expressed as the proportion of the overlapping area between niches of groups A and B out of the summed niche areas of A and B

	Marine mammals	Seabirds	Fish	Invertebrates
Marine mammals		0	1.2	0
Seabirds			24.3	9.9
Fish				3

to have an overlap of 10.3 %. All squid individuals sampled were larger than 10 cm, which corresponds to an age of 1 year or older (Kristensen 1984). As with other predators, the diet of Boreoatlantic armhook squids has been found to change with size, with larger individuals having a more piscivorous diet (Wiborg 1980; Kristensen 1984). We did not have accurate information on individual size, but the large range in $\delta^{15}N$ values (10.7–16.5 ‰) could be explained by large difference in individual size. Future studies should aim at collecting more species/age specific details in order for us to improve our understanding of interactions at lower trophic levels.

Fish

The fish community in West Greenland is characterized by demersal species. These include Greenland halibut, Atlantic and spotted wolffish, deepwater and golden redfish in the deeper waters, whereas, on the banks, sandeel is more prominent (Pedersen and Kanneworff 1995). Based on the $\delta^{13}C$ data, the demersal species did not exclusively feed on benthic organisms, except for the two most ^{13}C-enriched species of wolffish and shorthorn sculpin (Pedersen and Zeller 2001, Fig. 3; Table 1). As discussed for Boreoatlantic armhook squids, isotope results for Greenland halibut, polar cod and Atlantic cod showed these species to change their diet with increasing size from crustaceans towards a higher proportion of fish (Fig. 3, Pedersen and Riget 1993; Hovde et al. 2002; Ramsvatn and Pedersen 2012).

Sharks play an important role in food webs as apex predators by interacting at several trophic positions (Ferretti et al. 2010). The Greenland shark in this study had a TP of 4.4. This position is similar to findings by McMeans et al. (2013b) which revealed that Atlantic cod make up a large proportion of the diet of Greenland sharks from Kongsfjorden (Svalbard). Stable isotope results from our study (Fig. 3; Table 1) suggest that this is likely the case in West Greenland as well.

The sixteen species of fish analysed also showed a wide range of both $\delta^{15}N$ and $\delta^{13}C$ values. However, the core isotopic niche width for the group was considerably smaller than that of invertebrates and similar to that of marine mammals and seabirds, indicating a lower diversity of habitats and feeding ecologies. In contrast to the invertebrate group, all species except sandeel (and possibly great silver smelt) overlapped in their isotopic niche area with other species. This indicates a group consisting of many generalists and confirms a highly productive West Greenland ecosystem. Indeed, a higher degree of niche segregation would have been expected in a nutrient poor system to reduce competition between species. Such information is essential as it demonstrates that environmental change,

if modifying specific habitats or specific prey species like *Calanus* copepods, could highly impact higher trophic levels and the entire food chain.

Seabirds

Large numbers of common eiders, king eiders, Brünnich's guillemots, black guillemots and little auks winter in the open water of the West Greenland ecosystem (Merkel et al. 2002; Boertmann et al. 2004, 2013) where species were sampled in this study. The seabird community sampled showed a high degree of grouping in their isotopic niche areas (Fig. 4).

King and common eiders grouped together in their isotopic niches. They both occupied a TP of 2.9 and the most benthic position compared to the four other seabird species in West Greenland. Given the low TP found for mussels in this study, the diet of the eiders suggests a mixed diet such as polychaetes, echinoderms and crustaceans as found by Merkel et al. (2007a; 2007b) in Southwest Greenland and in West Iceland by Kristjansson et al. (2013). This is also supported by the isotopic niche area for common eider, which was the largest in the seabird group.

Little auks, Brünnich's guillemots and black-legged kittiwakes all overlapped in their isotopic niche area, but with kittiwakes having a broader diet (according to the isotopic niche width). The little auk feeds predominantly on copepods during spring and summer (Stempniewicz 2001), but has, based on stomach analyses, been found to feed predominantly on krill during winter in Southwest Greenland (Rosing-Asvid et al. 2013), while isotopic analysis in another study suggested that copepods were still important during winter (Fort et al. 2010b). Little auks in our study were collected in March, during the copepod feeding phase, and our estimate of a TP of 3.0 supports this expectation. Similar results have been found in the North Water Polynya (TP 3.2, Hobson et al. 2002a) and in West Greenland (TP 3.2 using Eq. 3, Fort et al. 2010a). A TP of 3.1 found for Brünnich's guillemots (November) and black-legged kittiwakes (September) in contrast to the higher values found in the North Water Polynya (Hobson et al. 2002a; Karnovsky et al. 2008), suggests a mixed diet of fish and crustaceans with more fish in the North Water Polynya.

The diet of black guillemots generally consists of a variety of fish and invertebrates (predominantly benthic species, Ewins 1990; Byers et al. 2010). The TP of 3.5, and the fact that the isotopic niche area of black guillemots did not overlap with any of the other species, is in agreement with a diet consisting of a higher percentage of fish than the other birds collected in this study. However, the $\delta^{13}C$ data indicated little use of benthic fish

species in West Greenland. This is in accordance with the winter and spring occurrence of black guillemots dispersed in the offshore pack ice (Mosbech and Johnson 1999) feeding mainly on polar cod (Bradstreet and Brown 1985).

Marine mammals

Due to the high productivity of West Greenland fjords, banks and shelves (Smidt 1979; Juul-Pedersen et al. 2015), this region is an important feeding area for marine mammals with seasonal occurrence of high-quality food patches (Heide-Jørgensen and Teilmann 1994). In addition to polar bear and walrus, at least 14 species of whale and five species of seals occur in the area (Boertmann et al. 2013). In this study we only sampled three whale species; thus, this group is highly underrepresented. This could possibly be an explanation for why we measured a relatively small isotopic niche width for the group and only a small or no overlap with the fish and seabird groups. Only narwhal and beluga overlapped in their isotopic niche area, but, in general, we expect that greater dietary overlap exist among marine mammals excluding polar bears and encourage more extensive sampling of this group.

Minke whale, harp seal and walrus were found to occupy the lowest TP in the marine mammal group. Capelin and sandeel have been found to be important food items for minke whales (Larsen and Kapel 1981) and harp seals (Kapel and Angantyr 1991; Boertmann et al. 2013) in West Greenland waters. However, a TP of 3.5 for harp seals and 3.1 for minke whales suggests a mixed diet of small schooling fish and crustaceans, also found by Boertmann et al. (2013). A TP of 3.6 is higher than expected for walruses if their sole diet was herbivorous clams but could be explained by walruses occasionally feeding on vertebrates like seals, birds and fish (Muir et al. 1995, Born 1997).

Ringed seals TP (4.0) was in good agreement with prior estimates of diet consisting of polar cod, Arctic cod, *Liparis* spp. and amphipods (Siegstad et al. 1998). Beluga (TP = 4.1) and narwhals (TP = 4.2) were also in good agreement as they are known to predominantly feed on fish (polar cod and Greenland halibut, respectively). Squid and shrimp have been found to contribute to their diet (Heide-Jørgensen and Teilmann 1994; Laidre and Heide-Jørgensen 2005); however, during the sampling period of this study fish appear to be the main prey items. Hooded seals occupied a TP of 4.4 also suggesting forage fish to be the main diet of the sampled individuals. A previous study analysing stomach contents indicated that capelin was the most important prey (ca. 93 % by weight) for hooded seals in Southwest Greenland (Kapel 2000). Our data support a diet consisting of capelin and/or other forage fish.

Implications and future perspectives

Our study, to our knowledge, is the first extensive investigation of the West Greenland marine food web structure. In this respect, our model is important in assisting future studies of the effects of climatic and anthropogenic stressors on West Greenland marine ecosystems, potentially causing changes in the structure of marine food webs. Nonetheless, future and expanded studies focused on additional species should provide complementary data and allow long-term investigations of modifications of Arctic marine food web structure under rapid environmental change. Moreover, it is well recognized that baseline isotopic values for primary production can vary spatially and seasonally in isotopic signals (e.g. Hansen et al. 2012a) and should be taken into account, or the variance in resulting trophic estimates modelled. To some degree, this can be accomplished by investigating a variety of tissues representing different periods of dietary integration (Hobson 1993; Hobson et al. 2002a; Hobson and Bond 2012). We recommend a generalized approach where more species and especially those representing lower trophic levels (i.e. invertebrates) are included, as they play a key role in transferring energy from primary producers to upper-level predators in marine ecosystems (McMeans et al. 2013a). An example is the amphipod *Themisto libellula* that, through SI modelling, is considered a keystone in the North Water Polynya high Arctic system (Hobson et al. 2002a). Likewise, organisms involved in the microbial loop (unicellular grazers such as ciliates and dinoflagellates) are potential key species in marine Arctic ecosystems (Levinsen and Nielsen 2002) and should therefore be considered in future investigations. In addition, we recommend carefully designed collection schemes where standard biological data (i.e. total length, weight, age, sexual status) are recorded in order to allow for a full interpretation of species stage-dependent diet within and between regions.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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