

# Spatial variability of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope ratios in an Arctic marine food web

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**ABSTRACT:** Stable isotopes of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) were used to examine trophic structures in an arctic marine food web at small and large spatial scales. Twelve species, from primary consumers to Greenland shark, were sampled at a large spatial scale near the west and east coasts of Greenland. There was a significant positive latitudinal effect on  $\delta^{15}\text{N}$  values, which varied by 2 to 5‰ over the sample range. This latitudinal pattern was also illustrated by the negative correlation between the productive open-water period and baseline  $\delta^{15}\text{N}$  values. At a smaller spatial scale, 8 species from the Nuuk Fjord were compared with species sampled in waters immediately offshore. All values of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  (except for *Calanus finmarchicus*) were more enriched inshore than offshore. The use of *C. finmarchicus*  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values as a baseline explained a portion of the spatial variability in isotopes, attributing some of the variation to physical and biological sources. Hence, significant differences in isotopic signatures on both large and small spatial scales were less related to food web structure than to different physical and biological properties of the water masses. Accordingly, the results illustrate the importance of spatial variability when interpreting trophic structure from stable isotopes.

**KEY WORDS:**  $\delta^{15}\text{N}$  ·  $\delta^{13}\text{C}$  · Greenland · Latitudinal effects · Marine food web · Ecohydrography · Isoscapes

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## INTRODUCTION

Analyses of stable carbon and nitrogen isotopes are commonly used to describe food web structure in marine ecosystems (e.g. Peterson & Fry 1987, Post 2002). The stable isotope ratios of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) provide a time-integrated measure (over weeks to months) of an organism's trophic position and feeding ecology, in contrast to the traditional 'snap-shot' picture provided by stomach content analyses and, furthermore, have the potential to track energy flow through food webs (Hobson & Welch 1992, Hobson et al. 1995, Post 2002). The method is based on the principle that heavier isotopes ( $^{13}\text{C}$  and  $^{15}\text{N}$ ) accumulate from prey to predator (i.e. diet-tissue enrichment,  $\Delta$ ). The lighter isotope

reacts at a faster rate, leading to a higher  $\delta$  value in the remaining substrate relative to the product, with mean fractionation of nitrogen at each trophic level by 3 to 4‰. The trophic fractionation represents the retention of heavy isotopes during assimilation, metabolism and excretion (Post 2002, Søreide et al. 2006a). Thus, stable nitrogen isotopes provide an estimate of a consumer's trophic position given a known baseline  $\delta^{15}\text{N}$ . Trophic fractionation of  $^{13}\text{C}$  is typically about 1‰ (DeNiro & Epstein 1978, Vander Zanden & Rasmussen 2001, Post 2002), and the stable carbon isotope ratio ( $\delta^{13}\text{C}$ ) can be useful when evaluating the sources of primary production in marine systems, as well as general patterns of inshore or benthic versus offshore or pelagic feeding preferences (Hobson et al. 1994, France 1995a). Thus, the

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integrated use of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  can provide valuable information on both food web structure and carbon source.

The trophic level of an organism is estimated relative to a chosen food web baseline ( $\delta^{15}\text{N}_{\text{base}}$ ). This allows for comparison of segregated samples (spatially and/or temporally) despite differences in  $\delta^{15}\text{N}_{\text{base}}$ . Therefore, if a proper  $\delta^{15}\text{N}_{\text{base}}$  estimate is not available, it is not possible to determine whether variation in  $\delta^{15}\text{N}$  values between systems reflects differences in food web structure or baseline variation.  $\delta^{15}\text{N}_{\text{base}}$  values are predominantly influenced by nitrogen limitation (Pennock et al. 1996), interspecific differences in isotope fractionation (Needoba et al. 2003) and form of assimilated nitrogen by the microbial food web (i.e. new primary production [nitrate] vs. regenerated production [ammonium]; Ostrom et al. 1997). Thus, both the baseline and absolute nitrogen values will vary in time and space due to changing chemical and biological conditions (Cabana & Rasmussen 1996, Post 2002). The high turnover rate at the base of the food web (O'Reilly et al. 2002, Post 2002) means such variations are quickly reflected in the tissue.

Greenland has an extensive north–south directed coastline, with a number of large fjord systems influenced by glacier run-off (Mortensen et al. 2011). The offshore water masses in the coastal areas around Greenland are complex and consist of 2 main currents. These are the cold, low-saline East Greenland Current from the Arctic Ocean and the temperate, saline Irminger Current, originating in the Atlantic Ocean. The 2 currents meet at the southern part of the Greenland east coast, with the heavier Irminger Current subducting the relatively low-saline East Greenland Current. The water masses turn north at Cape Farewell, forming the West Greenland Current in which the 2 water masses gradually mix as they flow north along the western coast (Ribergaard 2011) (Fig. 1). This suggests that water masses around Greenland have different physical and biological properties, resulting in concurrent changes in the isotopic baseline depending on the degree of mixing between water masses. This, in turn, can be affected by large-scale circulation patterns and local-area bathymetry such as sill fjords. For example, Petursdottir et al. (2008) found that the  $\delta^{15}\text{N}$  value of *Calanus finmarchicus*

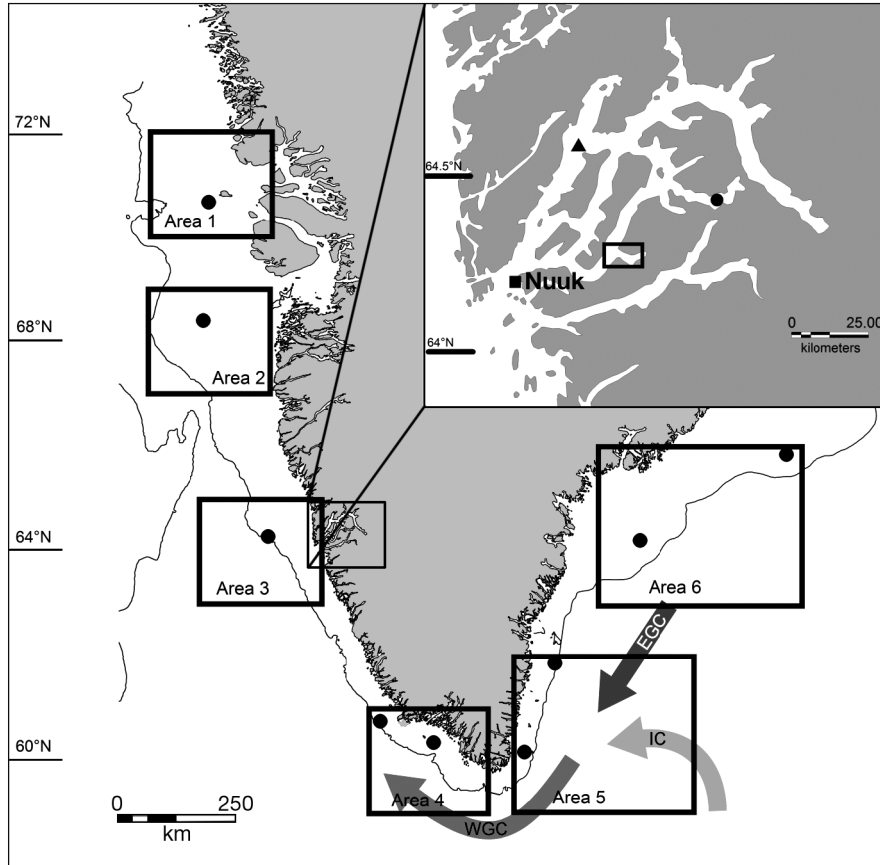


Fig. 1. Southern Greenland. Off-shore squares represent the study areas in which all fish species were sampled. Circles mark the stations where shrimp, krill and *Calanus finmarchicus* were sampled. The 500 m depth contour (i.e. shelf edge) is also shown. The dominant currents and their directions of flow are indicated with arrows: East Greenland Current (EGC), Irminger Current (IC) and West Greenland Current (WGC). The different shading of arrows indicates the mixing of EGC and IC as they form the WGC. Inset: The Nuuk fjord system is shown with Nuuk city and sampling sites for fish (except Greenland halibut; □), the sampling station for *C. finmarchicus* and krill (●), and the sampling site for Greenland halibut (▲)

caught in the Irminger Current of the Reykjanes Ridge south of Iceland was  $3.5 \pm 0.1\text{‰}$  (mean  $\pm$  SE), while Søreide et al. (2006a) found a  $\delta^{15}\text{N}$  value of  $6.4 \pm 0.2\text{‰}$  for *C. finmarchicus* in the Fram Strait west of Svalbard. Hence, the coastal ecosystem around Greenland is an ideal place to study isotopic baseline shifts and the effects of geographical separation on food web structure.

The main objectives of this study were (1) to assess isotopic baseline differences over a large spatial scale along the Greenland coast, considering 12 different species from various trophic levels and habitats, (2) to assess isotopic baseline shifts between the Nuuk Fjord and an adjacent offshore area and (3) to use this information to explore potential spatial differences in food web structure in Greenlandic coastal ecosystems.

## MATERIALS AND METHODS

The study includes sampling offshore at sites along the Greenland coast, as well as inshore in Nuuk Fjord. The species and size categories sampled at all locations were chosen based on their wide-spread occurrence and ecological relevance to the Greenland ecosystem, as well as to maximize the trophic range sampled.

### Offshore field sampling

All samples along the Greenland coast were collected from the trawler RV 'Pâmiut' from June to August 2010 during the annual stratified-random bottom trawl surveys carried out by the Greenland Institute of Natural Resources in Greenlandic waters. Samples included copepods *Calanus finmarchicus*, krill *Thysanoessa raschii*, shrimp *Pandalus borealis* and 8 teleost fish species: wolffish *Anarhichas lupus* and *A. minor*, Atlantic cod *Gadus morhua* (small and large), polar cod *Boreogadus saida*, American plaice *Hippoglossoides platessoides*, capelin *Mallotus villosus*, Greenland halibut *Reinhardtius hippoglossoides*, redfish *Sebastes mentella* (small and large) and Greenland shark *Somniosus microcephalus*, resulting in a total of 13 sample groups (Table 1).

All fish species, shrimps and krill were sampled in 6 predetermined areas at depths of between 88 and 1446 m along the Greenlandic coast from 72°N in the west to 66°N in the east (Fig. 1). Five individuals of each group were sampled from each

area when possible (Table 1). To obtain the best representation of within-area variation, individuals were sampled from as many hauls within each area as possible. Whenever a Greenland shark was caught (regardless of the predetermined areas) total length, weight and sex were determined and a muscle sample was taken near the dorsal fin before it was released.

*Calanus finmarchicus* were sampled at each sampling area using a 500  $\mu\text{m}$  plankton net. The plankton net was lowered to 150 m and then slowly retrieved ( $20\text{ m min}^{-1}$ ) while the vessel was moving at 1 knot. The contents from the cod-end were filtered first through a 2 cm sieve and afterwards through a 200  $\mu\text{m}$  sieve to remove jellyfish and other large organisms and retain the larger copepods. *C. finmarchicus* were sampled in the evening to minimize gut content (Lampert & Taylor 1985, Head & Harris 1987) and kept frozen on a filter at  $-20^{\circ}\text{C}$  until further analysis.

### Inshore field sampling

Samples were collected in Nuuk Fjord (64°N; Fig. 1) in June and July 2010 and included *Calanus finmarchicus* and krill as well as 5 teleost fish species: Atlantic cod (small and large), redfish (large), American plaice, Greenland halibut and capelin (Table 1). Fish species (except Greenland halibut) were sampled at the same location, but logistics required that *C. finmarchicus* and krill were sampled at a different site within the fjord (Fig. 1). Most fish species were caught using fishing rods, whereas undigested capelin were taken from cod stomachs immediately upon capture. Greenland halibut were caught in the fjord by the local commercial fishery using a long-line set at 300 to 500 m depth. *C. finmarchicus* and krill were collected in the inner part of the fjord with a MIK net (2 m in diameter; 600  $\mu\text{m}$  mesh size) and a MultiNet (Hydrobios) equipped with five 300  $\mu\text{m}$  nets.

### Sample preparation

Total length, weight and sex of the fish were determined in the laboratory. Length of shrimp and krill were measured from the post-orbital notch to the posterior margin of the carapace and posterior end of the uropods, respectively. The weights of shrimp, krill and *Calanus finmarchicus* were estimated.

Table 1. Species sampled in 6 areas along the Greenland coast and in the Nuuk Fjord (Fig. 1). Total length (cm) is given for each species; values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (mean  $\pm$  SE) and number (N) sampled are given for each species per area. Empty cells indicate no species caught in the respective area. Copepods were not measured. Similar letters (a to e) indicate statistically similar stable isotope values of each species among areas. Asterisk indicates significant difference (significance level  $p \leq 0.05$ ) between the Nuuk Fjord and Area 3

Species	Common name	Size interval (cm)	Area 1, 70–72°N, west coast, 1–5 Jul		Area 2, 67–69°N, west coast, 16 Jun–11 Jul		Area 3, 63–65°N, west coast, 11 Jun–21 Jul			
			$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$		
<i>Anarhichas</i> spp.	Wolffish	30–60	-18.5 $\pm$ 0.2 <sup>a</sup>	16.1 $\pm$ 0.2 <sup>a</sup>	-18.2 $\pm$ 0.1 <sup>a</sup>	15.2 $\pm$ 0.0 <sup>a</sup>	-16.8 $\pm$ 0.1 <sup>b</sup>	13.2 $\pm$ 0.3 <sup>b,d</sup>		
<i>Boreogadus saida</i>	Polar cod	5–20	-20.4 $\pm$ 0.1 <sup>a</sup>	12.2 $\pm$ 0.2 <sup>a</sup>	-20.5 $\pm$ 0.1 <sup>a</sup>	12.0 $\pm$ 0.1 <sup>ab,b</sup>	-19.7 $\pm$ 0.1 <sup>b</sup>	12.3 $\pm$ 0.1 <sup>a</sup>		
<i>Calanus finmarchicus</i>	Copepod		-22.1 $\pm$ 0.1 <sup>a</sup>	9.7 $\pm$ 0.0 <sup>a</sup>	-22.1 $\pm$ 0.1 <sup>a</sup>	8.9 $\pm$ 0.1 <sup>ab,b</sup>	-20.3 $\pm$ 0.1 <sup>b</sup>	7.3 $\pm$ 0.3 <sup>ab,b</sup>		
<i>Gadus morhua</i> (small)	Atlantic cod	25–35				13.4 $\pm$ 0.1 <sup>a</sup>	-19.2 $\pm$ 0.2 <sup>a</sup>	12.9 $\pm$ 0.2 <sup>ab,b</sup>		
<i>Gadus morhua</i> (large)		45–55				14.5 $\pm$ 0.2 <sup>a</sup>	-18.7 $\pm$ 0.1 <sup>a</sup>	12.9 $\pm$ 0.3 <sup>b</sup>		
<i>Hippoglossoides platessoides</i>	American plaice	20–40	-19.5 $\pm$ 0.0 <sup>a</sup>	14.4 $\pm$ 0.4 <sup>a</sup>	-18.8 $\pm$ 0.1 <sup>b</sup>	14.3 $\pm$ 0.2 <sup>a</sup>	-18.9 $\pm$ 0.1 <sup>b,c</sup>	12.7 $\pm$ 0.3 <sup>b</sup>		
<i>Mallotus villosus</i>	Capelin	10–15	-20.5 $\pm$ 0.0 <sup>a</sup>	12.9 $\pm$ 0.1 <sup>a</sup>	-20.3 $\pm$ 0.2 <sup>a</sup>	12.4 $\pm$ 0.0 <sup>a</sup>	-20.5 $\pm$ 0.3 <sup>a</sup>	10.0 $\pm$ 0.4 <sup>b</sup>		
<i>Pandalus borealis</i>	Shrimp	2–3	-18.7 $\pm$ 0.1 <sup>a,b,d</sup>	11.6 $\pm$ 0.2 <sup>a</sup>	-18.5 $\pm$ 0.3 <sup>a,c</sup>	11.0 $\pm$ 0.2 <sup>ad</sup>	-18.2 $\pm$ 0.1 <sup>a</sup>	10.5 $\pm$ 0.2 <sup>b,d</sup>		
<i>Reinhardtius hippoglossoides</i>	Greenland halibut	35–45	-21.2 $\pm$ 0.1 <sup>a</sup>	13.8 $\pm$ 0.2 <sup>a</sup>	-20.1 $\pm$ 0.3 <sup>ab,b</sup>	13.1 $\pm$ 0.2 <sup>ab,b</sup>	-19.4 $\pm$ 0.2 <sup>b,c</sup>	12.8 $\pm$ 0.3 <sup>ab,b</sup>		
<i>Sebastes mentella</i> (small)	Redfish	15–25	-20.4 $\pm$ 0.0 <sup>a</sup>	12.7 $\pm$ 0.1 <sup>a</sup>	-20.3 $\pm$ 0.0 <sup>a</sup>	12.1 $\pm$ 0.2 <sup>ab,b</sup>	-20.5 $\pm$ 0.3 <sup>a</sup>	11.0 $\pm$ 0.4 <sup>b,d,e</sup>		
<i>Sebastes mentella</i> (large)		35–45	-19.4 $\pm$ 0.3 <sup>a</sup>	15.1 $\pm$ 0.2 <sup>a</sup>	-20.3 $\pm$ 0.4 <sup>a</sup>	13.6 $\pm$ 0.9 <sup>ab,b</sup>	-19.7 $\pm$ 0.4 <sup>a</sup>	11.9 $\pm$ 0.7 <sup>b,c</sup>		
<i>Somniosus microcephalus</i>	Greenland shark	270–473	-16.4 $\pm$ 0.0 <sup>a</sup>	17.2 $\pm$ 0.0 <sup>a</sup>			-15.2 $\pm$ 0.0 <sup>a</sup>	16.5 $\pm$ 0.0 <sup>a</sup>		
<i>Thysanoessa raschii</i>	Krill	1–2	-20.8 $\pm$ 0.1 <sup>ab,b</sup>	11.1 $\pm$ 0.4 <sup>a</sup>	-20.2 $\pm$ 0.2 <sup>b</sup>	9.3 $\pm$ 0.2 <sup>b</sup>	-20.6 $\pm$ 0.1 <sup>ab,b</sup>	8.9 $\pm$ 0.5 <sup>b,c</sup>		
Species	Size interval (cm)		Area 4, 59–61°N, west coast, 25–31 Jul		Area 5, 59–62°N, east coast, 5–8 Aug		Area 6, 63–66°N, east coast, 10–29 August		Nuuk Fjord, 64°N, west coast, 29 Jun–8 Jul	
			$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<i>Anarhichas</i> spp.	30–60	-17.9 $\pm$ 0.1 <sup>a</sup>	11.8 $\pm$ 0.5 <sup>b,c</sup>	5	-17.9 $\pm$ 0 <sup>ab,b</sup>	12.5 $\pm$ 0.0 <sup>c,d</sup>	1	-18.5 $\pm$ 0.3 <sup>a</sup>	11.3 $\pm$ 0.3 <sup>c</sup>	4
<i>Boreogadus saida</i>	5–20	-21.2 $\pm$ 0.2 <sup>c</sup>	10.9 $\pm$ 0.5 <sup>b,c</sup>	5	-22.4 $\pm$ 0 <sup>d</sup>	11.5 $\pm$ 0.0 <sup>ab,c</sup>	1	-22.6 $\pm$ 0.1 <sup>d</sup>	10.4 $\pm$ 0.3 <sup>c</sup>	5
<i>Calanus finmarchicus</i>	25–35	-20.5 $\pm$ 0.1 <sup>b</sup>	6.5 $\pm$ 0.6 <sup>ab,b</sup>	6	-21.3 $\pm$ 0.0 <sup>d</sup>	6.1 $\pm$ 1.2 <sup>b</sup>	6	-21.2 $\pm$ 0.1 <sup>d</sup>	8.1 $\pm$ 0.2 <sup>ab,b</sup>	6
<i>Gadus morhua</i> (small)	45–55	-20.1 $\pm$ 0.1 <sup>b,c</sup>	10.6 $\pm$ 0.3 <sup>b</sup>	5	-19.9 $\pm$ 0.1 <sup>b,c</sup>	12.2 $\pm$ 0.3 <sup>c</sup>	5	-20.3 $\pm$ 0.0 <sup>c</sup>	9.5 $\pm$ 0.3 <sup>d</sup>	5
<i>Gadus morhua</i> (large)	20–40	-19.7 $\pm$ 0.1 <sup>b</sup>	12.3 $\pm$ 0.4 <sup>bb,c</sup>	5	19.8 $\pm$ 0.1 <sup>b</sup>	11.2 $\pm$ 0.3 <sup>c</sup>	5	-20.0 $\pm$ 0.2 <sup>b</sup>	11.2 $\pm$ 0.4 <sup>c</sup>	5
<i>Hippoglossoides platessoides</i>	10–15	-19.1 $\pm$ 0.1 <sup>ab,b</sup>	11.6 $\pm$ 0.4 <sup>b,c</sup>	5	-19.6 $\pm$ 0.2 <sup>ac</sup>	10.2 $\pm$ 0.4 <sup>c</sup>	5	-19.4 $\pm$ 0.1 <sup>ac</sup>	11.4 $\pm$ 0.1 <sup>b,c</sup>	5
<i>Mallotus villosus</i>	2–3	-20.6 $\pm$ 0.3 <sup>a</sup>	9.6 $\pm$ 0.3 <sup>b</sup>	5	-20.7 $\pm$ 0.1 <sup>a</sup>	9.0 $\pm$ 0.2 <sup>b</sup>	5	-20.7 $\pm$ 0.2 <sup>a</sup>	9.7 $\pm$ 0.4 <sup>b</sup>	5
<i>Pandalus borealis</i>	35–45	-19.0 $\pm$ 0.1 <sup>b,c,e</sup>	9.6 $\pm$ 0.1 <sup>b,c</sup>	5	-19.0 $\pm$ 0.1 <sup>de</sup>	9.6 $\pm$ 0.2 <sup>c</sup>	10	-19.3 $\pm$ 0.1 <sup>e</sup>	10.2 $\pm$ 0.1 <sup>c,d</sup>	10
<i>Reinhardtius hippoglossoides</i>	15–25	-19.9 $\pm$ 0.3 <sup>ac</sup>	11.3 $\pm$ 0.6 <sup>b</sup>	4	-19.7 $\pm$ 0.8 <sup>ab</sup>	13.9 $\pm$ 0.8 <sup>ab</sup>	5	-21.4 $\pm$ 0.7 <sup>a</sup>	12.3 $\pm$ 0.7 <sup>ab,b</sup>	5
<i>Sebastes mentella</i> (small)	35–45	-21.2 $\pm$ 0.4 <sup>a</sup>	9.4 $\pm$ 0.2 <sup>c</sup>	5	-20.6 $\pm$ 0.0 <sup>a</sup>	10.3 $\pm$ 0.4 <sup>ce</sup>	5	-20.6 $\pm$ 0.1 <sup>a</sup>	10.5 $\pm$ 0.1 <sup>d</sup>	5
<i>Sebastes mentella</i> (large)	270–473	-19.4 $\pm$ 0.2 <sup>a</sup>	12.7 $\pm$ 0.5 <sup>ab,d</sup>	5	-20.3 $\pm$ 0.1 <sup>a</sup>	9.3 $\pm$ 0.1 <sup>e</sup>	5	-20.6 $\pm$ 0.2 <sup>a</sup>	11.3 $\pm$ 0.4 <sup>c,d,e</sup>	5
<i>Somniosus microcephalus</i>	1–2	-15.3 $\pm$ 0.4 <sup>a</sup>	16.4 $\pm$ 0.2 <sup>a</sup>	6	-21.0 $\pm$ 0.2 <sup>a</sup>	7.7 $\pm$ 0.3 <sup>c</sup>	10	-20.9 $\pm$ 0.1 <sup>a</sup>	9.2 $\pm$ 0.5 <sup>b</sup>	5

### Stable isotope preparation and analysis

Fish samples were prepared by removing white muscle tissue ( $10.31 \pm 4.26$  g wet weight, mean  $\pm$  SD) dorsally from both sides of the fish, posterior to the dorsal fin, which ensured no bones were present in the sample. All skin was subsequently removed. White muscle tissue was used for stable isotope analysis because of its low tissue turnover rate (Rounick & Hicks 1985, Hesslein et al. 1993) and because muscle is the primary food source for higher trophic levels and does not require the removal of inorganic carbonates (Pinnegar & Polunin 1999). Muscle tissue was also dissected from shrimp and krill after the chitinous exoskeleton and gut were removed. Lipids were extracted from the lipid-rich *Calanus finmarchicus* (Lee et al. 2006) using a chloroform-methanol solution (2:1) according to Søreide et al. (2006b). All samples were freeze-dried (freeze dryer ALPHA 1-2/LD plus) to constant mass at  $-60^\circ\text{C}$  for 24 h. The dried samples were kept in a desiccating cabinet containing silica gel until further analysis.

Dried muscle tissues from shark, fish, shrimp and krill were homogenized using a mortar and pestle. Approximately 1 mg (dry mass, DM) of sample ( $1.14 \pm 0.10$  DM, mean  $\pm$  SD) was weighed into pre-weighed tin capsules ( $5 \times 9$  mm). *Calanus finmarchicus* with no visible stomach contents were selected and transferred into tin capsules as whole individuals. Several copepods collected at the same location were pooled into one sample to obtain sufficient material for isotopic analysis.

A total of 388 samples were analyzed (Table 1). Stable carbon and nitrogen isotope analyses were performed at the University of California Davis Stable Isotope Facility in California, USA. Samples were combusted in a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd.). The crimped tin capsules were introduced via a solid autosampler and combusted at  $1000^\circ\text{C}$  in a reactor packed with chromium oxide and silvered cobaltous/cobaltic oxide. Following combustion, oxides were removed in a reduction reactor (reduced copper at  $650^\circ\text{C}$ ). A post-reactor gas chromatography column was kept at  $65^\circ\text{C}$  for separation of evolved  $\text{N}_2$  and  $\text{CO}_2$  before entering the isotope ratio mass spectrometer. Isotope ratios are expressed in conventional  $\delta$  notation in parts per thousand (‰) as a measure of heavy to light isotope using:

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

where  $X$  is  $^{13}\text{C}$  or  $^{15}\text{N}$  and  $R$  is the corresponding ratio,  $^{13}\text{C}:^{12}\text{C}$  or  $^{15}\text{N}:^{14}\text{N}$ .

Standards for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were calibrated against USGS-40, USGS-41, IAEA-N1, IAEA-N2 and IAEA-N3. The long-term standard deviation at the facility is 0.2‰ for  $^{13}\text{C}$  and 0.3‰ for  $^{15}\text{N}$ .

### Estimation of baseline-corrected values

The isotopic baseline (i.e. copepods) in carbon was removed from estimates of stable carbon isotope ratios as:

$$\Delta\delta^{13}\text{C} = \text{mean } \delta^{13}\text{C}_{\text{species}} - \text{mean } \delta^{13}\text{C}_{\text{baseline}} \quad (2)$$

### Estimation of relative trophic level

Relative trophic level ( $\text{RTL}_{\text{N}}$ ) was estimated for all groups based on the following formula:

$$\text{RTL}_{\text{N}} = \frac{\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{base}}}{\Delta\delta^{15}\text{N}} + \text{TL}_{\text{base}} \quad (3)$$

where  $\delta^{15}\text{N}_{\text{consumer}}$  is the  $\delta^{15}\text{N}$  of the species in question,  $\Delta\delta^{15}\text{N}$  is the diet-tissue enrichment in  $\delta^{15}\text{N}$  per trophic level,  $\delta^{15}\text{N}_{\text{base}}$  is the average  $\delta^{15}\text{N}$  of the group chosen as the base of the food web and  $\text{TL}_{\text{base}}$  is the trophic level of that group. *Calanus finmarchicus* were chosen as the base assuming a herbivorous diet (i.e.  $\text{TL}_{\text{base}} = 2$ ; Hobson & Welch 1992, Søreide et al. 2006a, Nilsen et al. 2008). Although omnivory has been observed in *C. finmarchicus* (De Laender et al. 2010, Kürten et al. in press), *C. finmarchicus* in other arctic regions have been shown to be almost exclusively herbivorous (Søreide et al. 2008), prompting a similar simplifying assumption in previous studies (e.g. Nilsen et al. 2008). A  $\Delta\delta^{15}\text{N}$  of 3.4 and 3.2‰ was used for invertebrates and fish, respectively (Søreide et al. 2006a, Sweeting et al. 2007). The different enrichment factors indirectly indicate variations in enrichment correlated to body size, diet (Fry et al. 1999), growth rate (Trueman et al. 2005) and tissue turnover (Kurlle & Worthy 2001, Olive et al. 2003).

### Statistical analyses

All analyses were carried out using the statistical computing program R (R Development Core Team 2011) or SPSS 19.0 (Statistical Package of Social Sciences). Parametric tests were preceded by tests for assumptions. When these were violated, the data



were either transformed (squared) or non-parametric statistics were applied. One-way ANOVA or Kruskal-Wallis tests were used to analyze the variation in  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , relative trophic level and baseline-corrected  $\delta^{13}\text{C}$  for each species among areas. Due to heteroscedasticity in the data the differences were tested for each species separately. The latitudinal differences in baseline species (*Calanus finmarchicus* and krill) among areas were compared using ANCOVA.

## RESULTS

A total of 388 samples were taken from offshore sites along the Greenland coast (N = 359) and inshore Nuuk Fjord (N = 29) during June to August 2010 (Table 1).

### Large spatial scale study

There were considerable latitudinal differences in  $\delta^{15}\text{N}$  values among the 6 study areas along the Greenlandic coast (Fig. 2). Species-specific tests showed a significant effect of area on  $\delta^{15}\text{N}$  in all species (ANOVA,  $F_{4-5, 18-34} \geq 11.6$ ,  $p \leq 0.001$ , Kruskal-Wallis,  $\chi^2 \geq 14.6$ , N = 26 to 30 all  $p < 0.03$ ; Table 1). Greenland shark were not included in these tests due to the limited number of catches (N = 7; Table 1). For most species the  $\delta^{15}\text{N}$  values decreased from north (Area 1) to south (Area 4) on the west coast and increased slightly northwards on the east coast (Areas 5 and 6; Fig. 2). A clear example of this typical pattern was seen in shrimp (Fig. 3), with west coast values decreasing 2.0‰ and east coast values increasing 0.6‰. A few species (small cod, capelin, polar cod and wolffish) diverged from this general pattern. For instance, the  $\delta^{15}\text{N}$  values of polar cod and capelin did not decline gradually from north to south. Rather, the  $\delta^{15}\text{N}$  value (mean  $\pm$  SD) of capelin declined abruptly from a high value in Areas 1 and 2 ( $12.6 \pm 0.1\text{‰}$ ) to a lower mean value in Areas 3, 4, 5 and 6 ( $9.6 \pm 0.8\text{‰}$ ) (Kruskal-Wallis,  $\chi^2 = 19.01$ , N = 30,  $p < 0.0001$ ).  $\delta^{15}\text{N}$  values of wolffish and small cod did not increase on the east coast, but continued to decline from high values (mean  $\pm$  SD) in the most northern area on the west coast ( $16.1 \pm 0.4\text{‰}$  and  $13.5 \pm 0.3\text{‰}$ ) to the lowest value in the most northern area on the east coast ( $11.3 \pm 0.5\text{‰}$  and  $9.5 \pm 0.7\text{‰}$ ).

Similar to  $\delta^{15}\text{N}$  values there was a significant effect of area on  $\delta^{13}\text{C}$  values in most species (ANOVA,  $F_{4-5, 20-34} \geq 2.8$ ,  $p \leq 0.04$ , Kruskal-Wallis,  $\chi^2 \geq 14.0$ , N = 24 to 39,  $p < 0.002$ ; Table 1), except capelin (ANOVA,

$F_{5,24} = 0.53$ ,  $p = 0.75$ ) and small redfish (ANOVA,  $F_{5,24} = 1.6$ ,  $p = 0.20$ ). However, no clear latitudinal pattern of  $\delta^{13}\text{C}$  values was found in the 6 study areas (Fig. 2).

The baseline species, *Calanus finmarchicus* and the krill *Thysanoessa raschii*, showed parallel increasing  $\delta^{15}\text{N}$  values with latitude (ANCOVA,  $F_{1,64} = 54.1$ ,  $p < 0.001$ ), but krill had a mean marginally higher (1.2‰) than *C. finmarchicus* (ANCOVA,  $F_{1,64} = 16.8$ ,  $p < 0.001$ ). In contrast,  $\delta^{13}\text{C}$  values of both *C. finmarchicus* and krill showed no general pattern with latitude and also differed from each other. Mean  $\delta^{13}\text{C}$  values of *C. finmarchicus* differed among areas (ANOVA,  $F_{5,21} = 30.9$ ,  $p < 0.001$ ) and were grouped in pairs, with Areas 1 and 2, 3 and 4, and 5 and 6 being similar (Tukey's post hoc test,  $p < 0.05$ ). The  $\delta^{13}\text{C}$  values of krill in Area 2 differed from those in Areas 4, 5 and 6 (ANOVA,  $F_{5,34} = 3.7$ ,  $p = 0.009$ , Tukey's post hoc test,  $p < 0.05$ ; Fig. 4). Interestingly, the  $\delta^{13}\text{C}$  values of *C. finmarchicus* were more depleted than those of krill in eastern areas (5 and 6), whereas the opposite pattern was found at the same latitudes on the west coast (Areas 3 and 4).

The clear latitudinal trend observed in  $\delta^{15}\text{N}$  values disappeared when these were converted to relative trophic level (RTL) using *Calanus finmarchicus* baseline values. There were still differences among areas in all species except krill (ANOVA,  $F_{5,34} = 1.46$ ,  $p = 0.23$ ), but significant differences were primarily driven by low RTL in Area 6 (Tukey's post hoc test,  $p < 0.05$ ). The clearest patterns in RTL among areas were seen in shrimp, polar cod and small cod, all exhibiting a higher RTL in more southern areas (3 to 5) compared to northern areas. The RTL of polar cod and shrimp were both higher in Areas 3 and 4 compared to Areas 1 and 2 (Tukey's post hoc test,  $p < 0.05$ ). Small cod in Areas 3 and 5 had a higher relative trophic level compared to that in Areas 2, 4 and 6 (Tukey's post hoc test,  $p < 0.05$ ; Fig. 5).

The baseline-corrected  $\delta^{13}\text{C}$  values differed among areas in all species (ANOVA,  $F_{4-5, 20-34} \geq 3.1$ ,  $p \leq 0.03$ , Kruskal-Wallis,  $\chi^2 \geq 12.9$ , N = 24 to 39,  $p < 0.03$ ). This was especially pronounced in the low RTL species. In general the values were highest in Areas 1 and 2, lowest in Areas 3 and 4 and increased again in Areas 5 and 6 (Fig. 5).

### Inshore-offshore comparison

There was a significant area effect (i.e. in- vs. offshore) with both  $\delta^{13}\text{C}$  (ANOVA,  $F_{1,51} = 70.0$ ,  $p < 0.001$ ) and  $\delta^{15}\text{N}$  values (ANOVA,  $F_{1,51} = 63.5$ ,  $p <$

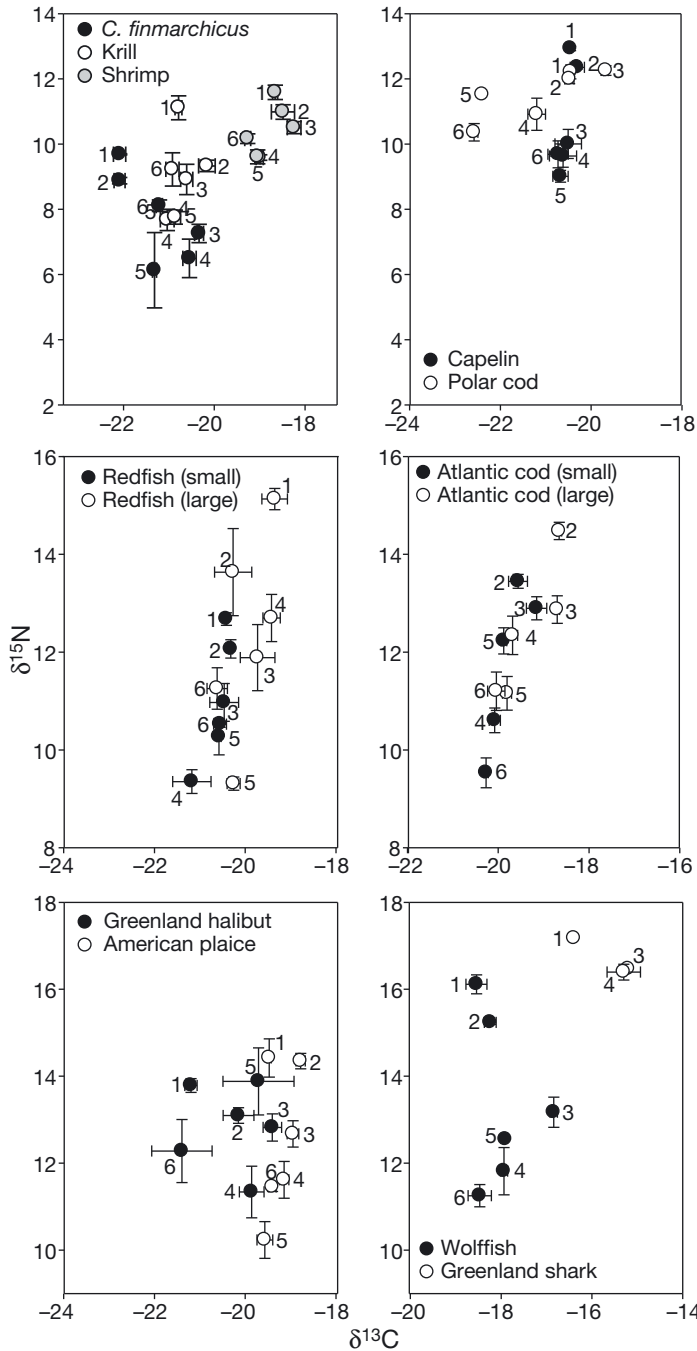


Fig. 2.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (‰) values (mean  $\pm$  SE) along the Greenlandic west and east coasts for the analyzed species. Numbers 1 through 6 indicate the different study areas

0.001) when comparing in- (Nuuk Fjord) and off-shore (Area 3) samples caught at approximately the same time (June and July 2010). In general, values were highest inshore; however, significant interaction terms ( $\delta^{13}\text{C}$ : ANOVA,  $F_{7,51} = 7.81$ ,  $p < 0.0001$ ;  $\delta^{15}\text{N}$ : ANOVA,  $F_{7,51} = 3.27$ ,  $p = 0.006$ ) show that the pattern was not similar for all species. Mean values of

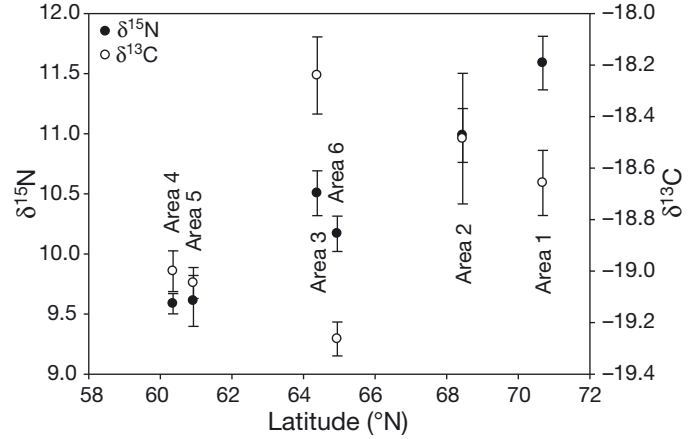


Fig. 3. General pattern of  $\delta^{15}\text{N}$  (‰) and  $\delta^{13}\text{C}$  (‰) values (mean  $\pm$  SE) with latitude, here represented by the shrimp *Pandalus borealis* at the 6 study areas along the Greenlandic west (Areas 1, 2, 3 and 4) and east coasts (Areas 5 and 6)

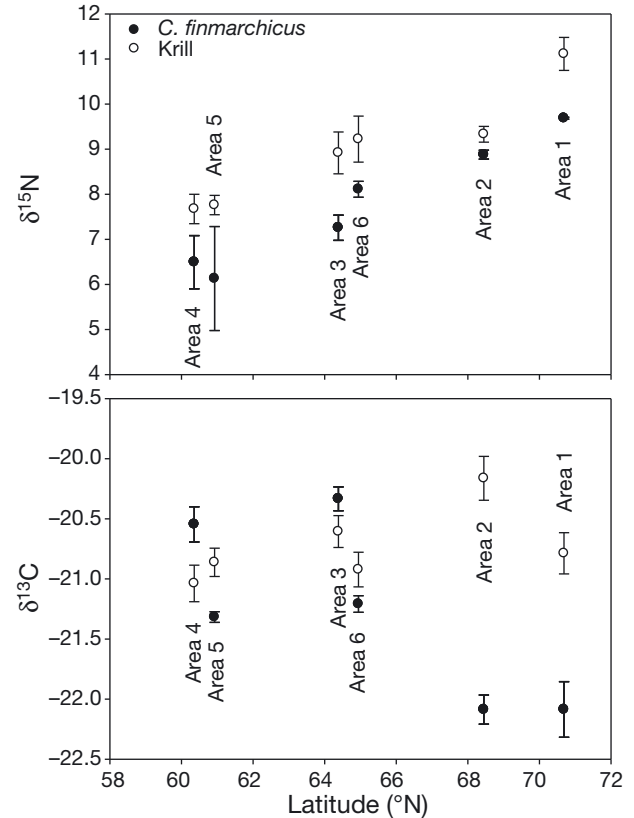


Fig. 4. Mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  ( $\pm$ SE) values of *Calanus finmarchicus* and the krill *Thysanoessa raschii*, varying with latitude at the 6 study areas along the Greenlandic west (Areas 1, 2, 3 and 4) and east coasts (Areas 5 and 6)

$\delta^{13}\text{C}$  for all species inshore were higher compared to offshore, and the difference was significant for 4 out of 8 species (Fig. 6). The isotopic signatures of *Calanus finmarchicus* from all areas overlapped. The

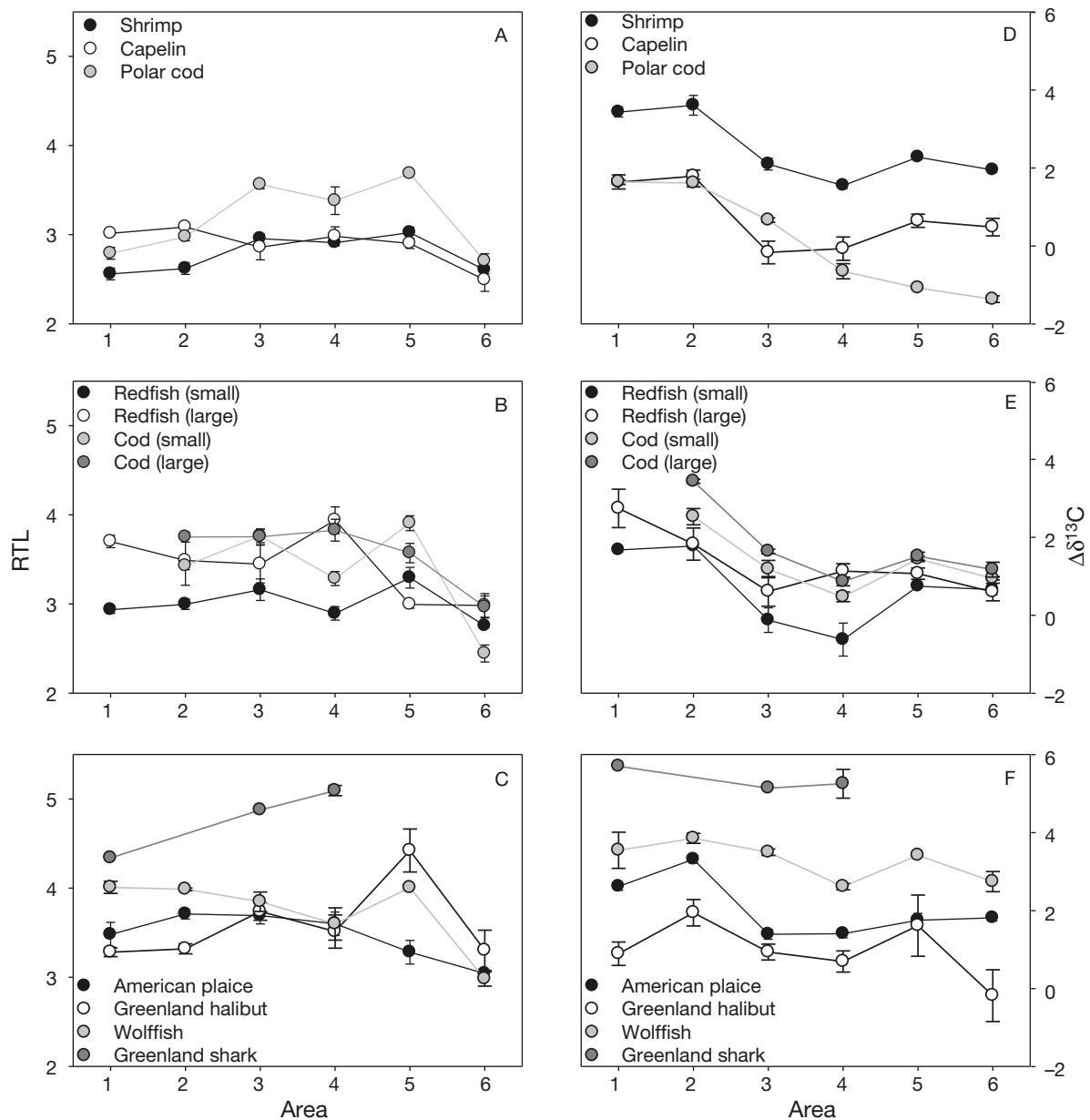


Fig. 5. Variation in (A–C) relative trophic level (RTL; mean  $\pm$  SE) and (D–F)  $\delta^{13}C$  relative to the baseline ( $\Delta\delta^{13}C$ ,  $\pm$  SE) along the Greenlandic west (Areas 1, 2, 3 and 4) and east coasts (Areas 5 and 6)

largest difference was seen in American plaice ( $-16.2 \pm 0.5\text{‰}$  and  $-19.0 \pm 0.1\text{‰}$  in- and offshore, respectively).  $\delta^{15}N$  values were also significantly higher inshore compared to offshore for 5 out of 8 species, including *C. finmarchicus* (Fig. 6). It is notable that  $\delta^{15}N$  values (mean  $\pm$  SE) for *C. finmarchicus* ( $10.0 \pm 0.2\text{‰}$ ) and krill ( $10.2 \pm 0.2\text{‰}$ ) inshore were approximately the same, while there was a difference of 1.7‰ in  $\delta^{15}N$  values between *C. finmarchicus* ( $7.3 \pm 0.3\text{‰}$ ) and krill ( $8.9 \pm 0.5\text{‰}$ ) offshore.

Mean RTLs were generally higher offshore compared to inshore, but there was a significant area–species interaction (ANOVA,  $F_{7,51} = 3.3$ ,  $p < 0.005$ ). The difference was significant in 4 species (ANOVA, krill  $F_{1,8} = 8.00$ ,  $p = 0.022$ ; American plaice,  $F_{1,6} = 34.05$ ,  $p = 0.001$ ; small cod,  $F_{1,8} = 38.51$ ,  $p = 0.0003$ ; large cod,  $F_{1,8} = 6.59$ ,  $p = 0.033$ ; Fig. 7). The largest difference in RTL between in- and offshore was seen in American plaice and small cod, both approximately 1 RTL lower inshore compared to offshore. In krill and large cod the difference was  $<0.5$  RTL.



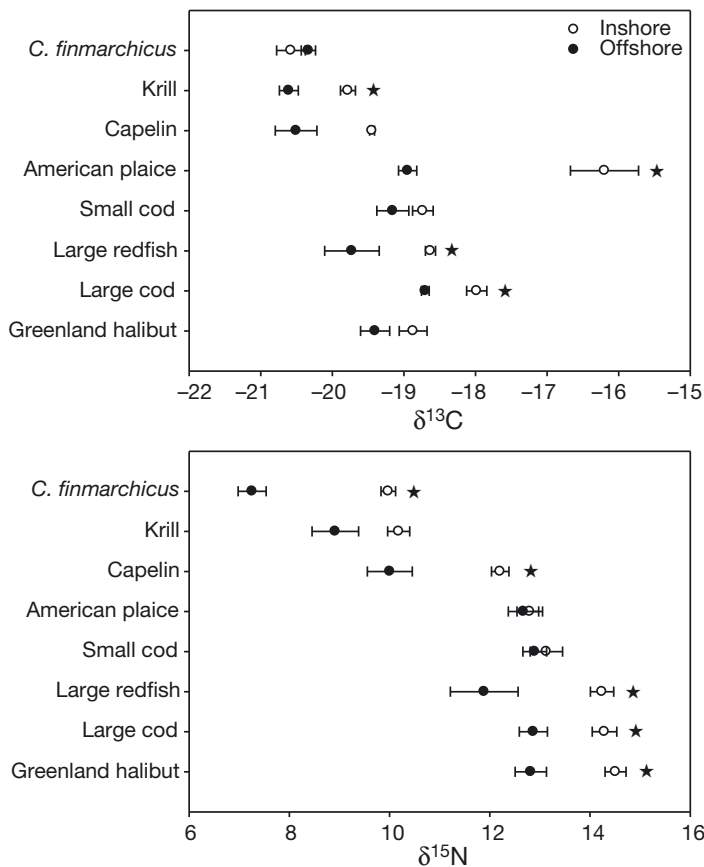


Fig. 6. Inshore and offshore comparisons of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  (‰) values (mean  $\pm$  SE). (★) significantly different values between inshore and offshore samples ( $p \leq 0.05$ )

## DISCUSSION

### Large-scale variation in baseline and food web structure

The  $\delta^{15}\text{N}$  values of the studied species differed significantly among 6 predetermined areas along the west and east coasts of Greenland and were positively correlated with latitude. For all species,  $\delta^{15}\text{N}$  values increased between 2 and 5‰ (Fig. 2) from the most southern areas (4 and 5) to the northernmost study area (1); a shift equivalent to a full trophic level (Post 2002). *Calanus finmarchicus* (and the krill *Thysanoessa raschii*) displayed the same pattern (Fig. 4), with the same order of magnitude. Thus, latitudinal differences reflected  $\delta^{15}\text{N}$  baseline shifts to a large extent (Fig. 5).

The behavior of the species likely contributes to the inter-species differences seen in the spatial variability of  $\delta^{15}\text{N}$ . For instance, wolffish are

somewhat stationary (Rigét & Messtorff 1988) and exhibited a large latitudinal gradient of 4.3‰, whereas the more migratory behavior seen in Greenland shark (Skomal & Benz 2004) could be the reason for a relatively small effect of latitude on its  $\delta^{15}\text{N}$  values (0.8‰).

No clear latitudinal gradient in baseline  $\delta^{13}\text{C}$  values was found. Large differences in  $\delta^{13}\text{C}$  were found between the ecologically similar *Calanus finmarchicus* and krill.  $\delta^{13}\text{C}$  of *C. finmarchicus* was more variable among areas, while values for krill were relatively stable (Fig. 4), a pattern that could be influenced by the fact that only *C. finmarchicus* were lipid extracted. Unlike the RTL values, the baseline-corrected  $\delta^{13}\text{C}$  values showed a latitudinal trend, suggesting predictable spatial variation in the carbon source fueling the higher trophic levels. However, this trend disappears if krill is used as the baseline species (data not shown). This suggests that there is latitudinal variation in the food web structure beginning with krill and propagating further up the food web that is unrelated to the variation found in *C. finmarchicus*. Alternatively, *C. finmarchicus*, especially in the northern areas (1 and 2), could be poor representatives of the food web base, i.e. krill, but not *C. finmarchicus*, transfer carbon from primary producers to higher trophic levels (Hedeholm et al. 2012).

In short, the baseline shifts appeared to explain most of the spatial variation in  $\delta^{15}\text{N}$  values, whereas it remains unclear to what extent the differences in  $\delta^{13}\text{C}$  are due to baseline shifts. The question now becomes, what processes generate the latitudinal differences in the baseline?

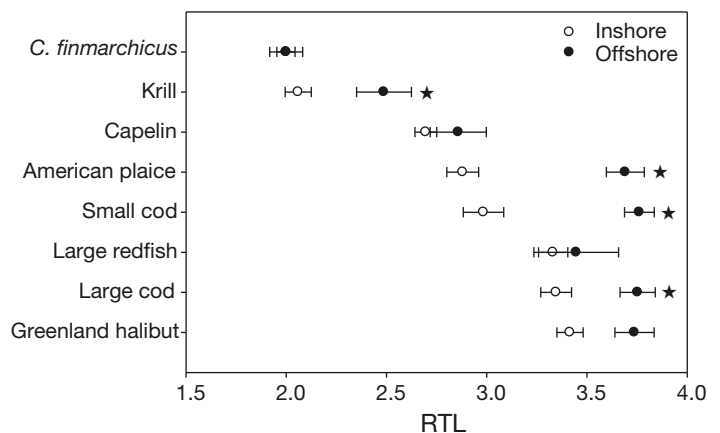


Fig. 7. Relative trophic levels (RTL) (mean  $\pm$  SE) for inshore and offshore samples. (★) significantly different values between inshore and offshore samples ( $p \leq 0.05$ )

Baseline isotope values are influenced by the physical and biological properties of local currents (Pantoja et al. 2002), terrestrial input (Carlier et al. 2007) and species composition and bloom progression (Tamelander et al. 2009). The combined effect of these direct and indirect factors on primary producers will propagate up the food web, influencing the isotopic signatures of all trophic levels, though with diminishing strength towards higher trophic levels.

The currents along the Greenlandic west coast are a mixture of the cold, low-saline East Greenland Current coming from the Arctic Ocean and the temperate, saline Irminger Current branching off from the North Atlantic Current (Ribergaard 2011). The 2 currents meet at the southern Greenland east coast and then merge gradually, homogenizing as the water masses move north along the west coast. If the water masses differ in the isotopic signal of biologically available nutrients this will be reflected in phytoplankton and, consequently, in higher trophic levels. Thus, the trend in food web changes with latitude may be related to shifts in the relative contributions of the 2 dominant water masses around Greenland (Ribergaard 2011). These differences were also reflected in the isotopic signature of the same species sampled in the different water masses. For instance, large differences in  $\delta^{15}\text{N}$  values were found when comparing copepod, capelin and redfish caught in 4 areas influenced by different water masses (Areas 1 and 6, present study; Reykjanes Ridge south of Iceland, Petursdottir et al. 2008, Sarà et al. 2009; Fram Strait [75° 06' N to 80° 29' N, 09° 38' W to 07° 40' E], Søreide et al. 2006a, Falk-Petersen et al. 2009; Table 2). The highest values were seen in Area 1, and values from Fram Strait were all higher than values from Reykjanes Ridge. All  $\delta^{15}\text{N}$  values in the most northern area on the west coast (Area 1) were higher than values in the northern area on the east coast

(Area 6), which is unexpected if mixing of the 2 different water masses was the main driver of the different baseline signals.

The parallel shift in  $\delta^{15}\text{N}$  values with latitude across groups could also be related to the length of the productive open-water period (Blicher et al. 2007). There is a significant negative relationship between the productive open-water period and the baseline  $\delta^{15}\text{N}$  values among areas (*Calanus finmarchicus*: Pearson's correlation,  $t_{[25]} = -3.82$ ,  $p = 0.0008$ ; krill: Pearson's correlation,  $t_{[38]} = -6.46$ ,  $p < 0.0001$ ; Fig. 8). In high-Arctic areas, this period is identical with the ice-free period, while diminishing day-lengths have a pronounced effect further south where ice-free periods are longer. The productive open-water period is defined here as the annual number of days with open water and a minimum day length of 6 h (Blicher et al. 2007). A possible explanation for the negative correlation between productive open-water period and baseline  $\delta^{15}\text{N}$  could be that a longer ice-cover period reduces mixing and stabilizes the water column resulting in partial depletion, and high  $\delta^{15}\text{N}$ , of the nitrate pool (Tremblay et al. 2006, Tamelander et al. 2009). Thus, high arctic blooms of autotrophs following ice melt will be characterized by higher  $\delta^{15}\text{N}$ , and this signal is passed on in the food web. Further south the nitrate pool is more frequently renewed by deep nitrate resulting in lower  $\delta^{15}\text{N}$  of secondary producers. This scenario is also consistent with data from Iceland and the Fram Strait where higher values were found in the more northern Fram Strait (Søreide et al. 2006a, Petursdottir et al. 2008, Falk-Petersen et al. 2009, Sarà et al. 2009).

Lastly, the latitudinal gradient in the present study is associated with a temperature gradient. Barnes et al. (2007) showed that rising temperature can have a negative effect on  $\delta^{15}\text{N}$  values, but the scale of the effect (e.g.  $-0.1\%$  per  $1^\circ\text{C}$  assuming linearity; Barnes

Table 2. Comparison of 3 species sampled in different water masses, based on literature review and the current study. Data from Iceland are from Petursdottir et al. (2008) and Sarà et al. (2009), data from Fram Strait are from Søreide et al. (2006a) and Falk-Petersen et al. (2009), while Greenland Areas 1 and 6 are from the current study (Fig. 1). <sup>SD</sup>: standard deviation instead of standard error

Species	Iceland, Irminger Current		Fram Strait, East Greenland Current		Greenland, Area 1, West Greenland Current		Greenland, Area 6, East Greenland Current	
	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
<i>Calanus</i> sp. (copepod)	$3.5 \pm 0.1$	$-20.4 \pm -$	$6.4 \pm 0.2$	$-21.6 \pm 0.1$	$9.7 \pm 0.0$	$-22.1 \pm 0.4$	$8.1 \pm 0.4$	$-21.2 \pm 0.2$
<i>Mallotus villosus</i> (capelin)	$10.8 \pm 0.1$	$-22.5 \pm 0.3$	$11.6 \pm 0.1^{\text{SD}}$	–	$12.9 \pm 0.1$	$-20.5 \pm 0.1$	$9.7 \pm 0.9$	$-20.7 \pm 0.5$
<i>Sebastes mentella</i> (redfish)	$11.6 \pm 0.1$	$-18.6 \pm 0.1$	$12.2 \pm 0.8^{\text{SD}}$	–	$12.7 \pm 0.3$	$-20.4 \pm 0.1$	$10.5 \pm 0.1$	$-20.6 \pm 0.3$

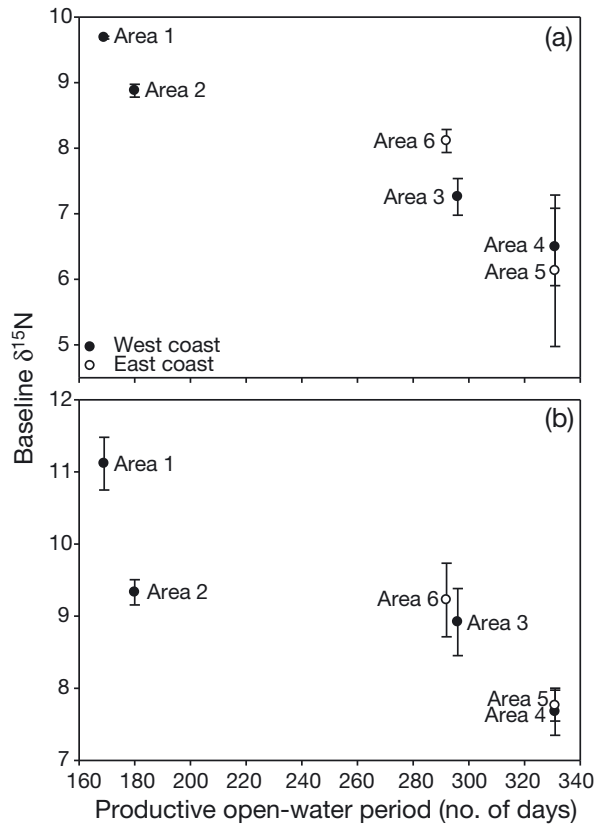


Fig. 8. Baseline  $\delta^{15}\text{N}$  ( $\pm$ SE) values of (a) *Calanus finmarchicus* and (b) *Thysanoessa raschii* against the productive open-water period at the 6 study areas along the Greenlandic coast

et al. 2007) is not sufficient to explain the latitudinal variation in the present study.

Whether these factors cause the differences in  $\delta^{15}\text{N}$  values remains unknown, as other undocumented factors such as changes in the composition of primary production or seasonal progression could result in similar variation (Tamelander et al. 2009).

The calculation of RTL extricated the influence of changes in the isotopic baseline to identify possible variability in food web structure. Generally, the RTL variation was small which suggests little difference in food web structure among areas. The variability was most pronounced in smaller demersal fish species, such as small cod and polar cod. The spatial differences in RTL in these omnivorous species may indeed be indicative of diet changes, as might be expected considering the large distances between sampling sites (Yano et al. 2007, Walkusz et al. 2011) and potential shifts in prey species composition. In the case of the Greenland shark, the RTL differences may also be explained by the fact that the higher RTL

values in Areas 3 and 4 compared to 2 were based on sharks that on average were 4.5 m long compared to 2.7 m in Area 2. Moreover, the catch area baseline value may not reflect the baseline for a migratory species such as the Greenland shark.

The turnover rate in the baseline species is high (Mayor et al. 2011), and, consequently, there may be short time-scale variation at these lower trophic levels that are not identified. However, the use of muscle tissue, which has a lower turnover rate (Hesslein et al. 1993) means these short-term fluctuations do not influence our estimates at higher trophic levels.

In addition to some irregular variation in RTL among west coast areas, the only general pattern appeared to be a decline in RTL at the most northern area on the east coast. It is important here to point out that RTL estimation based on fixed trophic enrichment factors results in highly generalized food web structures that may only loosely reflect the true structure. Among other things, trophic enrichment depends on composition of the diet (e.g. amino acid composition; Vanderklift & Ponsard 2003). Thus, while significant differences in RTL may not necessarily represent true RTL differences, they may indicate differences in diet composition.

### Inshore–offshore comparison

When comparing stable isotope data measured offshore (Area 3) and inshore (Nuuk Fjord) all species except *Calanus finmarchicus* had higher  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values inshore (Fig. 6). The enriched values of  $\delta^{13}\text{C}$  inshore are consistent with the general observation that species inshore were enriched in  $\delta^{13}\text{C}$  compared to offshore species (Hobson et al. 1994, Sherwood & Rose 2005, but see France 1995b). One explanation for the enriched  $\delta^{15}\text{N}$  values inshore could be a high degree of vertical mixing caused by physical processes involving ocean currents, wind and tides, leading to high levels of nutrient availability and productivity in the inshore waters (Sherwood & Rose 2005, Mortensen et al. 2011). Offshore *C. finmarchicus* and krill demonstrated a difference in mean  $\delta^{15}\text{N}$  values of 1.7‰, while no significant difference was observed inshore. A possible explanation for this might be that both species feed on phytoplankton inshore, while the krill offshore also feed on copepods and, therefore, have a  $\delta^{15}\text{N}$  value corresponding to a half trophic level higher than the copepods (Agersted et al. 2011). Because of the relatively large difference at the base of the food web (i.e. copepods) between inshore and offshore areas,

the RTL for all species offshore is shifted upwards, but maintains the same relative pattern (Fig. 7).

In conclusion, there are clear spatial effects on the stable isotope signatures at both large and small scales around Greenland. Whatever the ultimate cause of the latitudinal patterns in isotopic baseline values, and inshore–offshore differences, these must be taken into account when addressing hypotheses by means of stable isotope analysis covering a notable geographical range (Møller 2006, Rig  t et al. 2007). While the differences in baseline signals among areas are considerable, there are only weak indications of differences in food web structure along the coast of Greenland.

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