Marine Ecology Progress Series
December 2014, Volume 516, Pages 139-151
http://dx.doi.org/10.3354/meps11055

Trophic position of coexisting krill species: a stable isotope approach

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Abstract:

Four krill species with overlapping functional biology coexist in Greenland waters. Here, we used stable isotopes to investigate and discuss their trophic role and mode of coexistence. Bulk carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope analyses of *Thysanoessa longicaudata*, *T. inermis*, *T. raschii* and *Meganyctiphanes norvegica* sampled in June 2010 in Godthåbsfjord, SW Greenland, revealed new insight into the species' trophic roles and positions. There was a general positive correlation between body length and trophic position. The largest species, *M. norvegica*, had the highest trophic position (TP [mean ± SE] = 2.8 ± 0.2) indicating carnivory, while *T. inermis* (TP = 2.4 ± 0.3) had a more omnivorous diet. In turn, *T. longicaudata* and *T. raschii* (TP = 2.2 ± 0.2) were herbivorous. Along the fjord, plankton composition affected trophic position. *T. longicaudata* was more omnivorous offshore than inshore, where it had the same trophic position as the baseline primary consumer *Calanus* spp. Similarly, *T. raschii* and *T. inermis* had higher trophic positions in the mouth of the fjord compared with the inner fjord. Regardless of spatial variations in potential food and the overlap in diet, typical of opportunistic species, body size appears as the key factor determining the role and position of krill in the food web.

Keywords: *Thysanoessa* spp. ; *Meganyctiphanes norvegica* ; Carbon stable isotope ; $\delta^{13}C$; Nitrogen stable isotope ; $\delta^{15}N$; Sub-Arctic ; Food web

INTRODUCTION

Krill are important vectors in the Arctic marine food web channelling primary production to upper trophic levels (Mauchline & Fisher 1969, Onsrud et al. 2004, Rosing-Asvid et al. 2013). Furthermore, krill contribute to the biological pump through production of fast sinking faecal pellets (Mauchline & Fisher 1969). In Greenland coastal waters four krill species coexist (Agersted & Nielsen 2014). However, knowledge on niche partitioning and the trophic position of the coexisting species is lacking.

Hutchinson (1961) discusses '*the paradox of the plankton'* and questions how phytoplankton species, competing for the same resources, are able to coexist. In accordance with *'the competitive exclusion principle'* (Hardin 1960) it would be expected that in a homogeneous environment one species would outcompete all others, and thereby lead to a population of a single species. However, this is in many cases not true, and factors as size-selective grazing (Wiggert et al. 2005) and spatio-temporal heterogeneity (Miyazaki et al. 2006) have been suggested to help resolve the paradox, and hereby determine the fate of a given population. An example of coexistence is the three copepod species *Calanus finmarchicus, C. glacialis* and *C. hyperboreus* in northern ecosystems (Conover 1988, Falk-Petersen et al. 2009). They all exploit the same size range of plankton (Levinsen et al. 2000) but have different phenology (Falk-Petersen et al. 2009), which could be the main factor making coexistence possible.

Krill have a broader prey size spectrum than copepods, and are capable of exploiting several trophic levels (Boyd et al. 1984, McClatchie 1985, Barange et al. 1991, Agersted et al. 2011). Being generalists could be a key trait that resolves *'the paradox'* for this group by reducing interspecific food competition. A prerequisite for interspecific competition to occur between sympatric congeners like krill is food scarcity, and therefore, if food is in excess competition for resources will be irrelevant.

A standard approach for investigating prey size spectrum and trophic position of zooplankton is bottle grazing experiments, where the experimental results furthermore can be extrapolated to grazing impacts *in situ*. However, the limitation of these experiments is that they only represent snap-shot-in-time. Thereby, they do not reflect the *in situ* prey variability in time and space because the migration behaviour of the experimental animals is prevented in a bottle.

Composition of gut content or faecal pellets is another approach to investigate krill feeding (e.g. Gonzalez 1992, Karlson & Båmstedt 1994, Schmidt et al. 2003). However, this method only provides snap-shot information of recently ingested prey and is biased towards prey with exoskeleton, such as larger zooplankton, and therefore soft bodied prey will be underestimated or ignored (Båmstedt et al. 2000).

Stable isotope analysis provides an alternative and complimentary method for determining the trophic position (Peterson & Fry 1987, Fry 1988, Hobson & Welch 1992). This method gives a time-integrated averaged trophic position of a given species, since the heavier isotopes accumulate from prey to predator over time (Fry & Sherr 1984, Fry 1988). Stable nitrogen isotope ($\delta^{15}N$) values provide an estimate of a trophic position in a consumer (Vander Zanden & Rasmussen 2001), whereas carbon isotope ($\delta^{13}C$) values can be used as proxy for the source of primary production, and inshore/benthic versus offshore/pelagic feeding preferences in a consumer (Hobson et al. 1994, France 1995). Previous studies have investigated stable isotopes in krill around Svalbard (Søreide et al. 2006, Søreide et al. 2013), Iceland (Petursdottir et al. 2008, Petursdottir et al. 2012) and Greenland (Hansen et al. 2012). . However, these studies only investigates a specific area and do not look at spatial differences in stable isotopes among species present. Because isotope signals at the base of the food web vary at spatial scales (e.g. Hansen et al. 2012), studies considering spatial differences in stable isotopes provide insights on the origin of nutrients as well as on the local variability of feeding preferences.

The Godthåbsfjord is a sub-Arctic sill fjord located in SW Greenland. The fjord is formed by several branches forming a complex system where the head of the main fjord drain three glaciers from the Greenland Ice Sheet (Mortensen et al. 2011). Outside the fjord, off the coast of Greenland, the West Greenland Current brings warm and saline water of Atlantic and polar origin (Sutherland & Pickart 2008, Mortensen et al. 2011), whereas the fjord is influenced by freshwater runoff from glaciers (Mortensen et al. 2011). The plankton composition in the fjord is affected by the oceanographic regimes, and varies along the fjord (Arendt et al. 2010, Calbet et al. 2011, Tang et al. 2011, Agersted & Nielsen 2014). The distribution of krill species in Godthåbsfjord during summer was studied in detail by Agersted and Nielsen (2014). In the offshore area, the Atlantic species *Thysanoessa longicaudata* dominated, whereas the fjord was dominated by the arcto-boreal *T. raschii* and *T. inermis*. By advection from offshore waters, the

boreal *Meganyctiphanes norvegica* was transported into the fjord and found in the inner part of Godthåbsfjord (Agersted & Nielsen 2014). These four species are all considered omnivorous and feed on different prey items depending on season and availability (Mauchline & Fisher 1969, Berkes 1976, Sargent & Falk-Petersen 1981, Falk-Petersen et al. 2000, Schmidt 2010).

The objectives of this study were 1) to analyse the spatial trend in stable isotopes in krill species along the Godthåbsfjord, from the offshore area to the glacier, in relation to nutrient sources, and 2) to determine the trophic position of the krill species in the different regions of the fjord.

MATERIALS AND METHODS

Nutrients and Chlorophyll *a*

The sampling was carried out from R/V Dana (National Institute of Aquatic Resources, DTU Aqua) during a cruise from 6-24 June 2010. The sampling took place from the offshore waters (Fyllas Bank, FB) throughout the main branch of the Godthåbsfjord (GF) (Fig. 1). Furthermore, stations located in two side-branches were included in the sampling (Umanap, U; Kapisidglit, K; Fig. 1). Water for inorganic nutrients (phosphate, nitrate, ammonia and silicate) and Chlorophyll *a* (Chl *a*) were sampled in several depths. Water for Chl *a* was filtered onto GF/F filters and extracted in 96% ethanol for 12-24 h (Jespersen & Christoffersen 1987). Chl *a* was analysed using a fluorometer (TD-700, Turner Designs) calibrated against a pure Chl *a* standard (Turner Designs). Inorganic nutrient samples were immediately frozen (-20°C) for later analysis on a Skalar autoanalyser (Breda, Netherlands), following the procedures of Hansen and Koroleff (1999). Nutrient sample precisions were 0.06, 0.1, 0.3, and 0.2 µM for phosphate, nitrate, ammonia, and silicate, respectively.

Zooplankton sampling

Due to their diel vertical migration, krill were sampled at night in the upper 140 m with oblique hauls with a 2 m MIK ring net (black, mesh size 1500µm) at a speed of 2.8 ± 0.9 knots. Samples were preserved in buffered formalin (4% final concentration).

120

121 **Stable isotope analysis**

122 Four species of krill (not gender differentiated) and copepods of the genus *Calanus* (females of
123 *C. finmarchicus, C. glacialis* and *C. hyperboreus*) preserved in formalin (>1 year storage) were
124 collected for stable isotope analysis (see Fig. 1 for stations). Krill and *Calanus* spp. originated
125 from the same samples. For krill, three individuals of each species and year class (specimens of
126 similar size were assumed to represent the same year class) were sorted and length measured
127 from rostrum to end of telson to nearest mm. For *Calanus* spp. five individuals of similar size
128 were pooled (all prosome length measured to nearest µm), with three replicates per station. Both
129 krill and *Calanus* spp. were washed with filtered seawater and dried at 60°C for 48 h. Krill were
130 afterwards powdered for homogenizing muscle tissue. Trials of muscle aliquots were compared
131 with total body sample for at least 3 individuals of each species (except for *Thysanoessa*
132 *longicaudata* due to smaller size) to investigate whether there was a difference in isotope signal
133 (Schmidt et al. 2004). Stable isotope analyses (carbon and nitrogen) were performed on an
134 elemental analyser coupled to an Isotope Ratio Mass Spectrometer (EA-IRMS) and the variables
135 %N, %C (by dry mass), C:N (molar), ^{15}N and ^{13}C (‰) were determined as described in Bode
136 and Alvarez-Ossorio (2004). Precision of isotope determinations (standard error of 3 replicates)
137 was 0.06‰ and 0.12‰, for ^{15}N and ^{13}C, respectively. As they were used for internal
138 comparisons within the study, isotopic values were not corrected for the small effect caused by
139 formalin (Sarakinos et al. 2002, Bicknell et al. 2011). However, the resulting values are not
140 directly comparable with values for unpreserved samples reported in the literature. Similarly, no
141 corrections were applied for the small depletion in ^{13}C caused by lipids (Schmidt et al. 2003) as
142 C:N values of all species analysed were near the lower limits of the ranges reported in the
143 literature (Schmidt et al. 2003, Kiørboe 2013) and thus indicated low lipid content.

144

145 **Estimation of trophic position in krill**

146 We used *Calanus* spp. stable isotope values as isotopic reference baseline as in previous studies
147 (Søreide et al. 2006, Petursdottir et al. 2008, Hansen et al. 2012, Petursdottir et al. 2012),
148 assuming herbivorous diet during the spring bloom (Søreide et al. 2008). We did not distinguish

149 between the three species, *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* but analysed
150 individuals of a homogenous size through the study area (mean length = 2.95 mm, sd = 0.38, n =
151 188) to ensure that they were grazing on similar prey during the study period.

152 The trophic position of krill (TP_{krill}) was calculated from ^{15}N values (after Vander Zanden &
153 Rasmussen 2001) by using *Calanus* as primary consumer:

154 $$TP_{krill} = \frac{\delta^{15}N_{krill} - \delta^{15}N_{Calanus}}{\Delta\delta^{15}N} + TP_{Calanus} \quad \text{(Eq. 1)}$$

155 Where $^{15}N_{krill}$ is the measured ^{15}N value in the krill, $^{15}N_{Calanus}$ is the ^{15}N value measured in
156 *Calanus* in the same area as the one for the krill, $TP_{Calanus}$ is the trophic position of *Calanus*
157 assuming a herbivorous diet ($TP_{Calanus}$=2; Hobson & Welch 1992, Søreide et al. 2006, Søreide et
158 al. 2008) and Δ ^{15}N is the mean trophic enrichment factor of $\delta^{15}N$ (=3.4‰; Vander Zanden &
159 Rasmussen 2001, Post 2002, Søreide et al. 2006). Mean TP_{krill} values were computed using mean
160 $\delta^{15}N$ values measured at each station. Standard error of the estimates was computed by
161 propagation of errors of mean $\delta^{15}N$ values.

162 Computed trophic positions were classified as herbivores (TP ≤ 2.3), omnivores (TP = 2.4–2.7)
163 and carnivores (TP = ≥ 2.8) (after Søreide et al. 2013).

164 For estimating TP we did not correct for possible effects due to formalin on $\delta^{15}N$, as both
165 *Calanus* and krill samples were preserved in the same way. Other studies have shown that
166 formalin preservation may cause small losses of light isotopes on plankton but the effect is often
167 undetectable for nitrogen (Sarakinos et al. 2002, Bicknell et al. 2011) and did not prevent further
168 analysis of trophic structure (Rau et al. 2003, Chiba et al. 2012).

169

170 **Potential krill food**

171 As reference for the evaluation of trophic position of the krill in the different fjord regions, the
172 potential food available for the krill was compiled. The potential food was composed by
173 heterotrophic (copepod nauplii and small and large copepods) and autotrophic (phytoplankton
174 >10µm) prey, as cells <10µm is at the lower size limit that these krill species can exploit (Berkes
175 1973, Agersted et al. 2011, Agersted unpublished data). Small copepods included *Microsetella*

spp., *Pseudocalanus* spp., *Onchaea* spp. and *Oithona similis*, whereas large copepods were represented by *Calanus finmarchicus, C. glacialis, C. hyperboreus* and *Metridida longa.* Nauplii include all copepod nauplii stage I-VI. Copepods are copepodite stage I-VI. The data were sampled during the same cruise as for krill, and data on mesozooplankton originates from Swalethorp et al. (2014).

Data analysis

Differences in mean values of %N, %C, C:N, ^{15}N and ^{13}C between the four krill species across all stations were analysed using non-parametric ANOVA (Kruskall-Wallis). Multiple comparisons between the groups were done using Dunnett-C *post-hoc* tests. Additionally, both ANOVA and Dunnett-C *post-hoc* tests were used to test if there were any significant differences between stations with regard to the mean ^{15}N and ^{13}C values (‰) in *Calanus* spp. and in the four krill species, respectively.

Differences in the analysed variables between muscle or whole-body samples were investigated using the median test on both individual and pooled krill species. To test whether body size had any effect on ^{13}C and ^{15}N values of *Calanus* and krill, we used mean square regressions.

All results are presented as mean±se, unless otherwise stated. All tests were run using SPSS statistical software (v. 11.5).

RESULTS

Nutrients and chlorophyll *a*

The surface concentration of nitrate (µM) and chlorophyll *a* (Chl *a*; µg l^{-1}) varied along the fjord (Fig. 2). In general, nitrate was depleted in the surface layers and the Chl *a* values were low with two major exceptions; the inner part of Godthåbsfjord where upwelling made nutrients available, and in the well mixed stations in the mouth of the fjord. The inner fjord displayed nitrate concentrations up to 8 µM and high Chl *a* (up to 14 µg l^{-1}) in the upper 10 m of the water column. In contrast, most of the main fjord basin and shelf waters displayed lower nutrient

concentrations in the upper 20 m of the water column with correspondingly low Chl *a* values. Close to the entrance of the fjord there was a noticeable increase in Chl *a* in the upper 60 m associated to a relative decrease in nitrate. The surface layers in the fjord branch Kapisigdlit were nitrate depleted. A subsurface bloom (up to 4 µg Chl *a* l^{-1}) was however observed associated with the deepening of the nutricline. Ammonium concentrations (not shown) were generally low through the study area (up to 2 µM) while silicate and phosphate (not shown) closely followed the distribution of nitrate. Temperature and salinity data for this cruise have already been described by Agersted and Nielsen (2014).

Differences in body composition between species

Among the four species of krill found (*Meganyctiphanes norvegica, Thysanoessa inermis, T. longicaudata* and *T. raschii*) there were no significant differences in carbon (^{13}C) and nitrogen (^{15}N) between muscle or whole-body samples for the main species (*T. longicaudata* were too small for a reliable separation of muscle from other body parts) (Table 1). These differences were also non-significant within species (median test, $P>0.05$, results not shown). Therefore, either muscle or whole body samples were considered representative for the analysis of the variability among species or stations (median test, $P>0.05$, Table 1).

Significant differences ($P<0.05$) were measured in the relative C and N content (lowest for *Calanus*), and C:N ratios (highest for *Calanus*) (Table 2). Furthermore, a marked ranking in ^{13}C and ^{15}N values among species were found (ANOVA, $P<0.05$, Table 2). Only *T. longicaudata* had mean ^{15}N and ^{13}C values equivalent to that of *Calanus*, while all other krill species had significantly higher values for both isotopes (Table 2). *Meganyctiphanes norvegica* had the highest ^{15}N values, and was clearly separated from the other species. No effect of size was found for ^{13}C and ^{15}N when considering individual species. However, both ^{15}N and ^{13}C increased linearly with body length when considering all krill species (Fig. 3A, B), although body length explained a larger fraction of ^{15}N compared to ^{13}C.

Spatial differences in stable isotopes

Calanus spp. showed significant differences for ^{13}C and ^{15}N among stations (Fig. 4). Station GF12 was not significantly different from GF8 and GF11 nor from K1-4 and U3. However, GF8 and GF11 were significantly different from K1-4 and U3. When considering the main branch of Godthåbsfjord, there was a significant linear increase of both ^{15}N ($r=0.97$, $P<0.001$, $n=7$) and ^{13}C values ($r=0.85$, $P<0.05$, $n=7$) with distance from the offshore shelf to the inner part of the fjord. Inside the fjord, however, ^{15}N values were comparatively less variable while there was a large variability in ^{13}C. Inside the fjord area, the highest ^{15}N (and the lowest ^{13}C) values occurred in the eastern branches of the fjord (stations K1-4 and U3). This spatial pattern was less evident for krill species as some were only found at certain locations (e.g. ***M. norvegica***), but in general ^{15}N was higher and ^{13}C lower at inner fjord stations than at shelf stations (Fig. 5). When considering all krill species found in the main branch of the fjord, there was a significant linear increase in ^{15}N ($r=0.66$, $P<0.05$, $n=20$), but not in ^{13}C, with distance from the shelf break.

Krill trophic position and potential food

When averaging across stations, ***M. norvegica*** had the highest trophic position (TP) (2.8 ± 0.2) followed by ***T. inermis*** (2.4 ± 0.1) and subsequently by ***T. longicaudata*** and ***T. raschii***, the two latter with the same trophic position (2.2 ± 0.2 and 2.2 ± 0.1, respectively) (Fig. 6). Consequently, the trophic position of the krill species was in general above the position of *Calanus* spp. (TP = 2). These differences, however, were not statistically significant because of the variability of the estimates. For instance, the trophic position for ***T. longicaudata*** and ***T. raschii*** was higher in the offshore area, compared to the inner part of Godthåbsfjord and in the fjord branches Kapisigdlit and Umanap (Fig. 6). The same trend was observed for ***T. inermis*** at station GF1 where it had a similar trophic position as ***M. norvegica*** had in the inner fjord. Trophic positions for *Thysanoessa* species in Kapisigdlit and Umanap were very similar between species and stations, and furthermore similar to trophic positions in the inner Godthåbsfjord (GF8-12). Additionally, there was a significant linear decrease in the mean trophic position of *Thysanoessa* species with the distance from the shelf break for the main branch of the fjord

(r=0.56, P<0.05, n=17). When *M. norvegica* was included there was also a linear increase in fjord-averaged trophic position with size of the krill, irrespective of species, (r=0.52, P<0.01, n=30). This result supports the fact that regardless of where the samples came from, trophic position increased with size of the krill.

The potential food for krill was divided into different groups (Fig. 7) and was characterized as autotrophs (>10µm in cell size) and heterotrophs (e.g. Berkes 1973, Agersted et al. 2011). Small autotrophic cells (<10µm) dominated the plankton biomass in Godthåbsfjord (Fig.7). Potential prey biomass (autotrophs >10µm and heterotrophs) was highest in the inner part of Godthåbsfjord at station GF11and lowest offshore at station FB2. Offshore, at station FB3-1, autotrophic prey >10µm made up a large part of the available prey (73±11%) (Fig.7). This was also true for the fjord stations GF2-5 and the inner part of Godthåbsfjord (GF11-12) with 80±1% and 73±7%, respectively, being autotrophic prey >10µm. At the outermost stations (FB5-3.5), potential prey was dominated by heterotrophs making up 69±15% of the total potential prey biomass. In Kapisigdlit, the highest potential prey biomass was found at the entrance of the fjord branch (station K1), with similar prey availability as in the inner part of Godthåbsfjord (Fig. 7). The potential prey biomass decreased towards the inner part of Kapisigdlit and with exception of the entrance station K1, the potential prey biomass was dominated by heterotrophic prey.

DISCUSSION

Differences between species

Here we present new insight regarding spatial differences in trophic position in coexisting krill species. We found differences between the four coexisting krill species, with the largest *M. norvegica* occupying the highest trophic position followed by *T. inermis*, while *T. longicaudata* and *T. raschii* displayed similar lower trophic position. These results agree with the classification of *M. norvegica* as carnivorous-omnivorous and *T. inermis* as omnivorous-carnivorous (terms defined by Søreide et al. 2013). In turn, *T. longicaudata* and *T. raschiii* were to a lesser extent omnivore and could be described as herbivorous-omnivorous (Søreide et al. 2006, Søreide et al. 2013). However, there were spatial differences in trophic positions within species. *Thysanoessa longicaudata* and *T. raschii* were both primarily herbivore in the inner part of Godthåbsfjord,

having the same trophic position as *Calanus* spp. (TP=2; Hobson & Welch 1992, Søreide et al. 2006). However, both species reached trophic levels of ~2.5 in the offshore area, which indicates a shift to a more mixed diet offshore. Here, the potential food was dominated by heterotrophic plankton. In contrast, the inner Godthåbsfjord was dominated by autotrophs >10µm. It is likely that krill grazed on the autotrophic rather than heterotrophic prey in the inner fjord, illustrated by the lower trophic positions here. Additionally, the offshore mesozooplankton community consisted of a higher fraction of copepod nauplii and copepods compared to inshore, which can be exploited by *T. raschii* (Agersted et al. 2011) and *T. inermis* (Agersted unpublished data) Also, predation on smaller stages of the larger copepod species is likely to take place. In Kapisigdlit, autotrophic organisms dominated the plankton community although with the smaller cells dominating (Fig.7). However, very high biomasses of protozooplankton has been reported here (Riisgaard et al. 2014), and *Thysanoessa* spp. might feed on these rather than the mesozooplankton, explaining the lower trophic position in the krill found here.

Petursdottir et al. (2008) found $\delta^{15}N$ values in *M. norvegica* and *C. finmarchicus* from the Reykjanes Ridge in June, to be almost one trophic level apart (Vander Zanden & Rasmussen 2001, Post 2002, Søreide et al. 2006, Petursdottir et al. 2008), with *M. norvegica* having a trophic position of 2.9 and *C. finmarchicus* of 2, which is similar to what we found in our study. Petursdottir et al. (2008) also measured fatty acids in *M. norvegica* and found low levels of *Calanus* fatty acid trophic markers (FATMs), but high amounts of 18:1(n-9), the latter indicating carnivorous feeding (Falk-Petersen et al. 2000, Dalsgaard et al. 2003). This suggests that *C. finmarchicus* is not the primarily food item for *M. norvegica*, and other non-*Calanus* species might be a preferable prey item for *M. norvegica* in this area . This result, however, does not affect the estimations of TP in our study as *Calanus* was used as a reference primary consumer for the entire food web (Vander Zanden & Rasmussen 2001). Petursdottir et al. (2012) studied trophic positions in pelagic species in the Subarctic Iceland Sea in August. Here *M. norvegica* had the lowest trophic position among the krill (TP=2.4), and a diet mainly consisting of phytoplankton and to a lesser extent on *Calanus* spp., investigated by phytoplankton FATMs. The other two species, *T. longicaudata* and *T. inermis,* occupied trophic positions of 2.5-2.7 and were concluded to predate rather on smaller copepods than on *Calanus* spp. (Petursdottir et al. 2012). Similar trophic positions for *T. longicaudata* and *T. inermis* have been found in other studies around Svalbard in the Barents Sea and the Arctic Ocean shelf-break region (Søreide et

al. 2006, Tamelander et al. 2006), and furthermore agree with our results for the two species in the mouth of Godthåbsfjord and in the offshore region. Based on results from our and previous studies, we therefore conclude that the trophic position of the species might to a large extent depend on available prey, since krill can consume a wide range of prey types (Boyd et al. 1984, McClatchie 1985, Barange et al. 1991, Agersted et al. 2011).

Differences in nutrient and food sources along the fjord

We document significant trends in the baseline isotope signals of *Calanus* spp. along the fjord, with an increase of both ^{13}C and ^{15}N with distance from the shelf to the inner part of the fjord. Similar results were found by Hansen et al. (2012) in the Godthåbsfjord area, where the inshore population of *C. finmarchicus* had higher ^{15}N values than the offshore population. The differences observed in the stable isotope signals along the fjord could be due to different hydrography and nutrient availability in the different areas, thus affecting isotope fractionation (Vander Zanden & Rasmussen 2001). The fjord area has been divided into four different regions by Mortensen et al. (2011) based on differences in hydrography: 1) the continental slope, 2) the continental shelf, 3) the outer sill region, and 4) the main fjord basin. The plankton communities have been found to be influenced by the oceanographic regions (Arendt et al. 2010, Calbet et al. 2011, Tang et al. 2011, Agersted & Nielsen 2014), and these regions were applied in Agersted and Nielsen (2014) to identify different krill assemblages.

Different circulation modes in Godthåbsfjord contribute to glacial ice melt (Mortensen et al. 2011), and an increased freshwater addition to surface waters will lead to an enhanced estuarine circulation (Kaartvedt & Svendsen 1990, Rysgaard et al. 2003) and increase nutrient availability in the innermost part of the fjord. In addition, sub-glacial freshwater discharge (30-60 m depth) will enhance upwelling in the bottom of the fjord (Mortensen et al. 2013), but reversely lead to stratification of the main fjord basin preventing new supply of nutrients from deeper waters (Dziallas et al. 2013). These factors would explain the high nitrate concentration we found in the innermost part of the fjord and the low values within the fjord basin, whereas nutrient depletion offshore indicates post-bloom conditions. Besides, nitrate resulting from nitrification-denitrification inside semi-enclosed systems, like estuaries, has been reported to have higher

349 ^{15}N values than nitrate from marine waters (Alkhatib et al. 2012). Increased nitrate supply and
350 local nitrogen transformations would thus lead to changes in the ^{15}N baseline signal in *Calanus*
351 spp. where we document the highest ^{15}N inshore and the lowest offshore. From data derived
352 from the same cruise as the present study, Calbet et al. (2011) additionally showed that nitrogen
353 availability reflect the composition and distribution of the phytoplankton communities. In the
354 inner fjord, high concentrations of fast-growing large diatom cells were found, whereas small,
355 less-abundant cells were found in the mouth of the main fjord and in Kapisgdlit (Calbet et al.
356 2011). Similar to Calbet et al. (2011), Arendt et al. (2010) also found a dominance of large
357 diatoms in the innermost part of Godthåbsfjord in May 2006, whereas other centric diatoms and
358 the colonial haptophyte *Phaeocystis* spp. dominated in the rest of the fjord and in the offshore
359 waters.

360 Differences in ^{13}C in the baseline signal indicate different food sources in the different areas
361 (Perry et al. 1999, Søreide et al. 2006). Diatoms have been found to be rich in ^{13}C compared to
362 nanoplankton (Gearing et al. 1984). Also Fry and Wainright (1991) found fast growing diatoms
363 at Georges Bank to have high values of ^{13}C compared to other phytoplankton. This is in
364 correspondence with the phytoplankton community (Calbet et al. 2011) and the high values of
365 ^{13}C in *Calanus* spp. found in inner Godthåbsfjord in the present study.

366 Hansen et al. (2012) did not find any difference in ^{13}C between inshore and offshore
367 populations of *Calanus finmarchicus* from the Godthåbsfjord area in June/July 2010. Differences
368 between our study and the study by Hansen et al. (2012) in ^{13}C inshore vs. offshore could be
369 due to different time of sampling (June 2010 in our study and June/July 2010 in the latter). Rapid
370 changes in stable isotope signatures of plankton, along with changes in the sources of nutrients
371 and prey, were reported in other studies (Goering et al. 1990, Rolff 2000, Bode & Alvarez-
372 Ossorio 2004). Therefore, any differences observed between the two studies could be due to a
373 change in the phytoplankton community (Gearing et al. 1984, Fry & Wainright 1991) or to an
374 increase in the relative contribution of other prey items, i.e. protozoans, as documented in the
375 Kapisigdlit fjord branch (Riisgaard et al. 2014). In contrast to *Calanus*, krill species did not show
376 clear spatial patterns in ^{13}C, a feature that can be attributed to their greater mobility and feeding
377 plasticity allowing them to integrate different food items.

Trophic position in relation to size

In general, the trophic position of krill species increased with length. Our results confirm the overall increase of TP with body size as found for marine communities of fish and benthic invertebrates (Jennings et al. 2001, Jennings et al. 2002). However, this increase of TP was only significant when the largest species ***M. norvegica*** was included. Yet, an ontogenetic shift in diet in krill has been found in other studies. In spring and autumn medium sized specimens (10-19 mm) of ***T. inermis*** were predominantly herbivorous or herbivorous-omnivorous, whereas larger ***T. inermis*** (> 22 mm) were carnivorous (Søreide et al. 2006). Also, Polito et al. (2013) found an ontogenetic change in trophic level of the Antarctic krill species ***Euphausia superba.*** Adults had higher and more variable $\delta^{15}N$ values but consistent $\delta^{13}C$ compared to juveniles, indicating that both adults and juveniles were feeding on phytoplankton, but the adults furthermore fed on prey of higher trophic levels (Polito et al. 2013). Stowasser et al. (2012) also report a positive and significant correlation between $\delta^{15}N$ values and body mass of ***E. superba.*** In contrast, Park et al. (2011) found significantly lower $\delta^{15}N$ values in adults of the krill ***Euphausia pacifica*** compared to juveniles. This was explained by the adults shifting to a more detritivorous diet containing carcasses of the copepod *Neocalanus cristatus*. Krill larvae are found to be herbivorous and to some extent omnivorous depending on season and species (Daly 1990, Frazer 1996, Meyer et al. 2002, Schmidt et al. 2003), supporting the general observation of a ontogenetic increase in trophic position.

The paradox of the krill

Krill have a prey size spectrum that spans several trophic levels, supported by the trophic overlap in stable isotopes documented here. A wide prey size spectrum can be an advantage when species feeding on the same prey coexist, since this will lower interspecific competition. Another adaptation for coexistence is differences in behavior such as diel vertical migration patterns and vertical spatial partitioning (Barange 1990, Barange et al. 1991). The ability of krill to utilize prey that occurs in different depth strata might also be a mechanism that reduces interspecific competition and thereby makes coexistence possible. In addition, Falk-Petersen et al. (2000)

found that lipid dynamics are closely related to the different life cycle strategies of krill species, and makes it possible for the different species to utilise different ecological niches.

Agersted and Nielsen (2014) found four krill species in the Godthåbsfjord. There was spatial overlap between species but different species dominated inshore and offshore. According to *'the competitive exclusion principle', 'complete competitors cannot coexist'* (Hardin 1960). In other words, two species competing for the same resources will not be able to coexist if other ecological factors are constant, and interspecific competition will lead to either extinction of one species or that the species must come to occupy different ecological niches (Hardin 1960). As the krill species in the Godthåbsfjord have spatial overlap and different species dominate in different areas, it results in coexistence only in some areas of the fjord and therefore coexistence of several krill species in the fjord is possible. We therefore suggest that limited interaction among species, differences in behaviour and life cycle strategies, a wide prey size spectrum and high productivity in the fjord resolve the paradox of the krill, and explain how these closely related species can coexist.

Acknowledgements

We would like to thank the captain and crew on board R/V Dana for good cooperation and our colleagues on board for their help and support. We also acknowledge the Greenland Institute of Natural Resources for good support and logistics, and A.F. Lamas (IEO) for sample preparation for isotopic analysis. Isotopic determinations were made by the Servicio de Apoyo a la Investigación (SAI) of the University of A Coruña (Spain). This project (BOFYGO) was funded by the Danish Centre for Marine Research, DCH. The research leading to these results has received funding from the European Union Seventh Framework Programme project EURO-BASIN (ENV.2010.2.2.1-1) under grant agreement n° 264933 and the Greenland Climate Research Centre (project 6505).

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589 **Tables**

590 Table 1. Mean and se (n = number of samples) differences between muscle and whole-body
591 samples in relative carbon (%C) and nitrogen content (%N) and in natural abundance of stable
592 carbon (^{13}C) and nitrogen (^{15}N) for all krill species analyzed (except for ***T. longicaudata***). At
593 least 9 individuals of each species were analyzed. None of the differences was significant
594 (Median test, P>0.05).

Difference	Mean	se	n
%N	1.25	0.61	41
%C	3.32	2.22	40
C:N	-0.31	0.17	40
^{15}N	0.11	0.09	41
^{13}C	0.13	0.11	40

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596

597 Table 2. Mean and se (n = number of samples) values of relative carbon (%C) and nitrogen
598 content (%N) and natural abundance of stable carbon (^{13}C) and nitrogen (^{15}N) for *Calanus*
599 spp. and krill. Different letters indicate significant differences between groups tested by
600 ANOVA, followed by multiple comparisons using Dunnett-C *post-hoc* tests, $P<0.05$.

601

Species	Variable	Mean	se	n	Group
	%N				
Calanus spp.		7.35	0.12	38	c
M. norvegica		11.25	0.59	21	a
T. inermis		10.59	0.28	46	a
T. longicaudata		8.72	0.34	21	b
T. raschii		10.33	0.34	51	a
	%C				
Calanus spp.		38.73	0.78	38	c
M. norvegica		46.66	2.09	19	a
T. inermis		45.30	1.14	46	a
T. longicaudata		40.90	2.03	21	b
T. raschii		42.05	1.38	51	a
	C:N				
Calanus spp.		6.23	0.18	38	a
M. norvegica		5.16	0.19	19	a, b
T. inermis		5.12	0.21	46	a, b
T. longicaudata		5.53	0.25	21	a, b
T. raschii		4.77	0.07	51	b
	^{15}N (‰)				
Calanus spp.		8.40	0.21	38	d
M. norvegica		11.36	0.26	21	a
T. inermis		9.89	0.15	46	b
T. longicaudata		8.64	0.28	21	d
T. raschii		9.19	0.08	51	c
	^{13}C (‰)				
Calanus spp.		-22.89	0.12	38	d
M. norvegica		-21.99	0.10	19	b
T. inermis		-21.75	0.10	46	a, b
T. longicaudata		-22.60	0.15	21	c
T. raschii		-21.59	0.07	51	a

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Figures

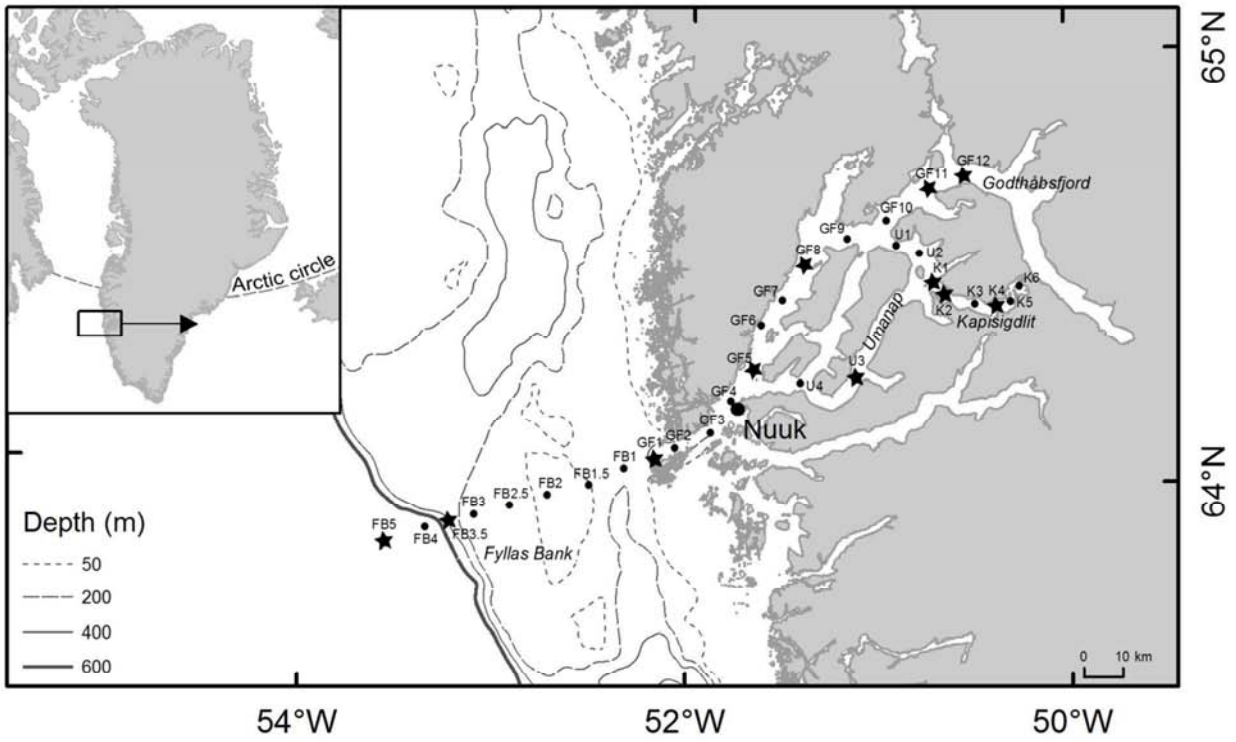


Figure 1. Location of krill sampling stations in Godthåbsfjord. Station abbreviations: FB=Fyllas Bank; GF=Godthåbsfjord; K=Kapisigdlit; U= Umanap. Stars indicate stations where specimens have been analyzed for stable isotopes.

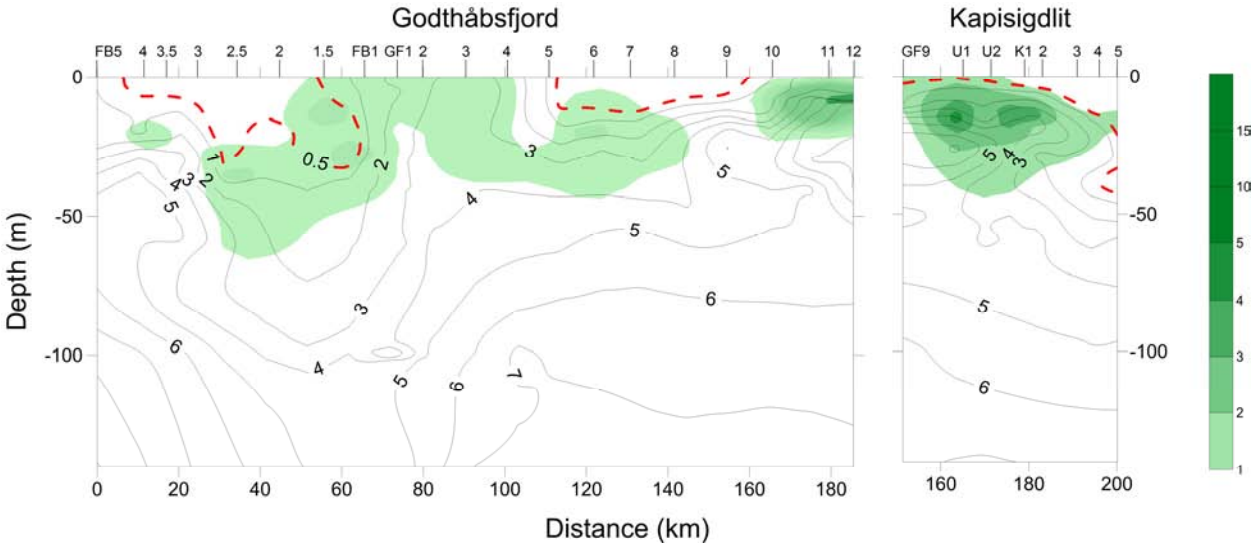
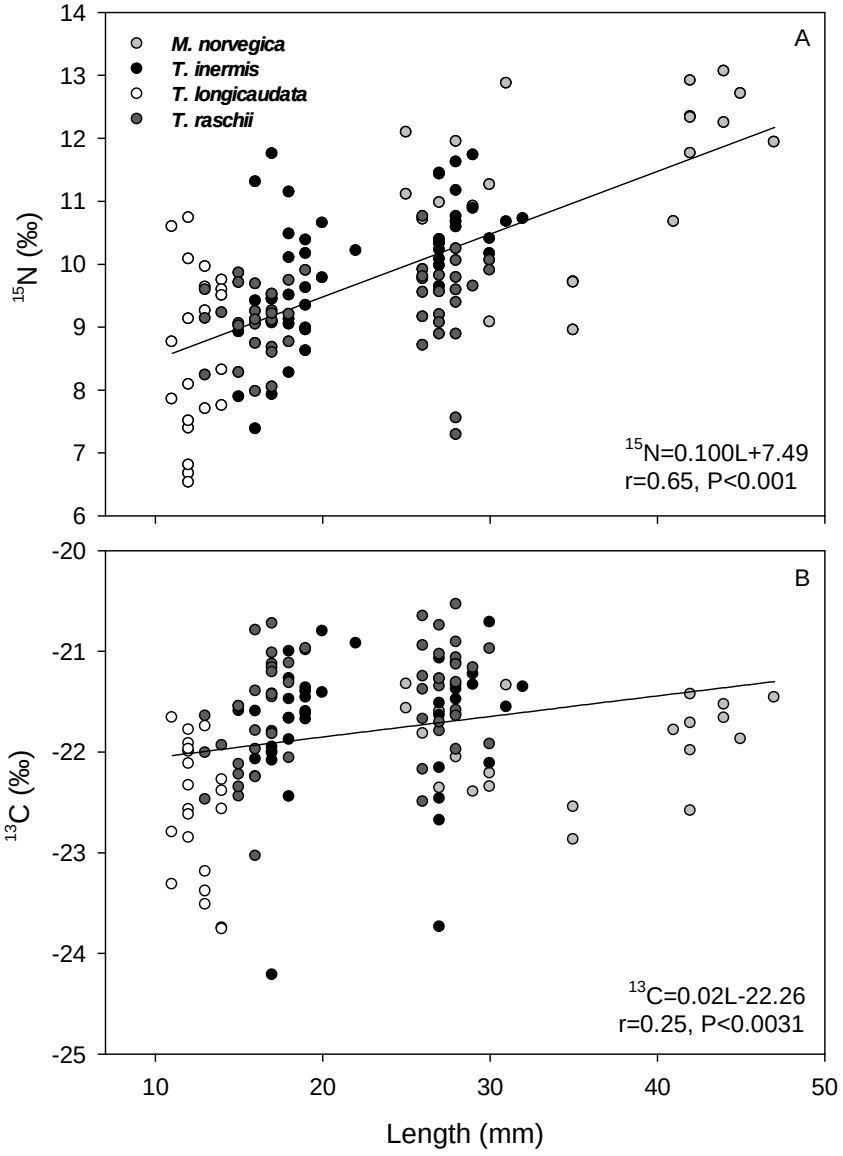


Figure 2. Depth distribution of nitrate (µM) and chlorophyll *a* (µg Chl *a* l^{-1}) from the offshore Fyllas Bank (FB) to the inner part of Godthåbsfjord (GF) and for Kapisigdlit (K) and Umanap (U) in the upper 140 m of the water column where krill have been collected. Station numbers are inserted above graph. Nitrate is displayed as contour line with the lower detection limit (<0.5 µM) indicated by the red dotted line. Chlorophyll *a* is displayed as shaded green areas. See Fig. 1 for the location of the different stations and fjord branches.



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630 Figure 3. Relationship between ^{15}N (A) or ^{13}C (B) values (‰) and body length (L, mm) for
631 krill specimens. The lines indicate the significant relationship using data for all species.

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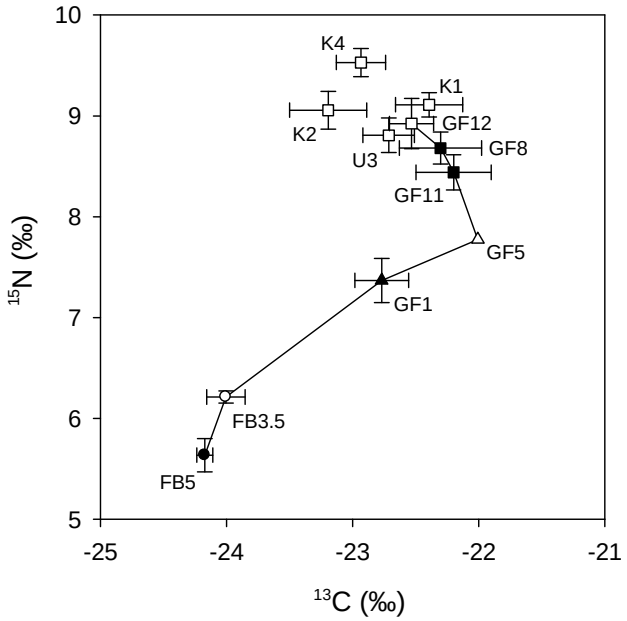

Figure 3. Mean (±se) ^{15}N and ^{13}C values (‰) for *Calanus* spp. The line links the values for stations in the main branch of the fjord (see Fig. 1). Different symbols (in different colours to facilitate separation) indicate significant differences for ^{15}N among stations (ANOVA and Dunnett-C *post hoc* test, $P<0.05$). Only for stations FB5 and FB3.5 the mean ^{13}C values were significantly lower than values for other stations.

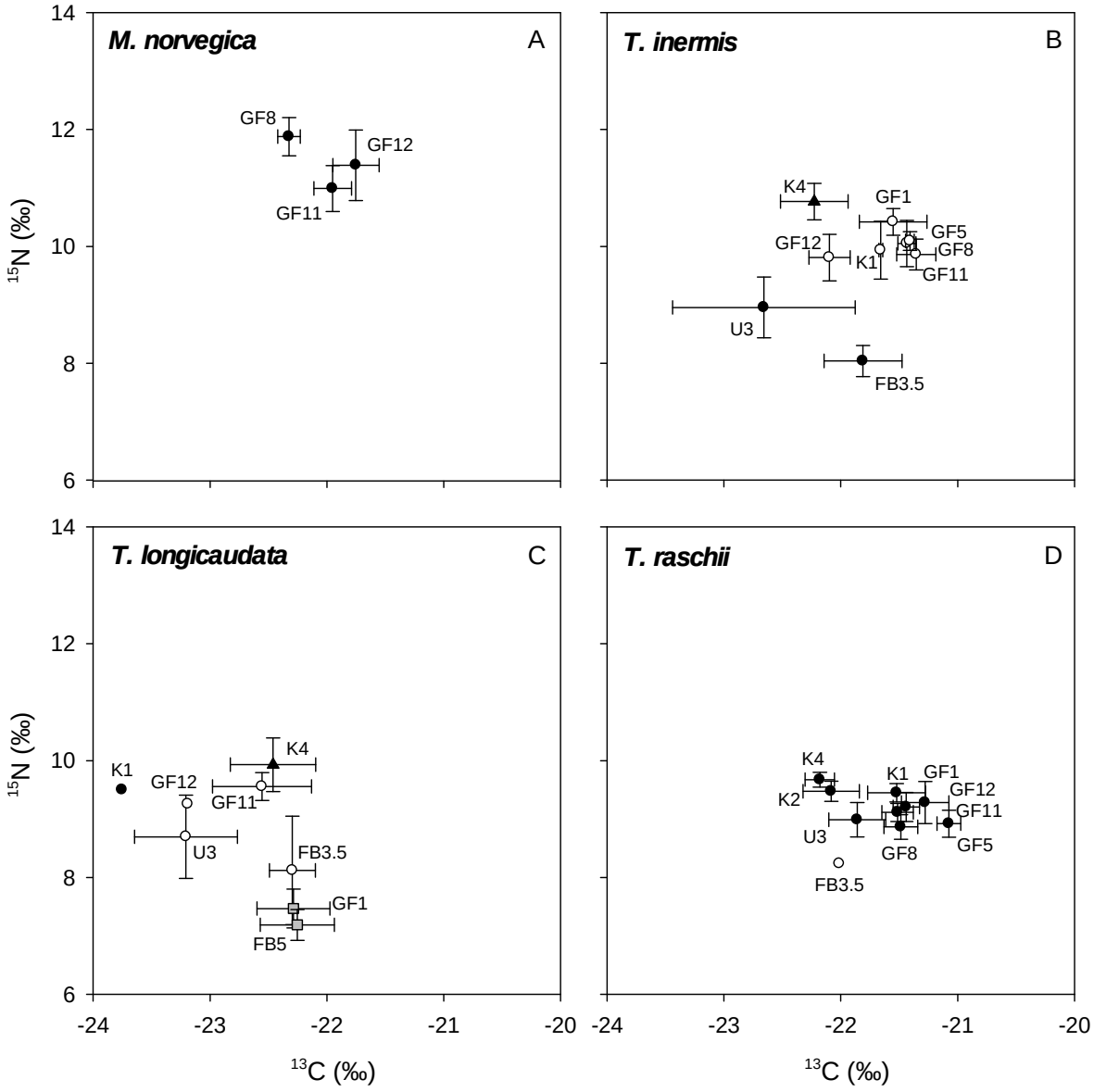

Figure 5. Mean (±se) ^{15}N and ^{13}C values (‰) for the four krill species in relation to stations (see Fig. 1). Different symbols (in different colours to facilitate separation) indicate significant differences for either ^{15}N or ^{13}C among stations (ANOVA and Dunnett-C *post hoc* test, $P<0.05$).

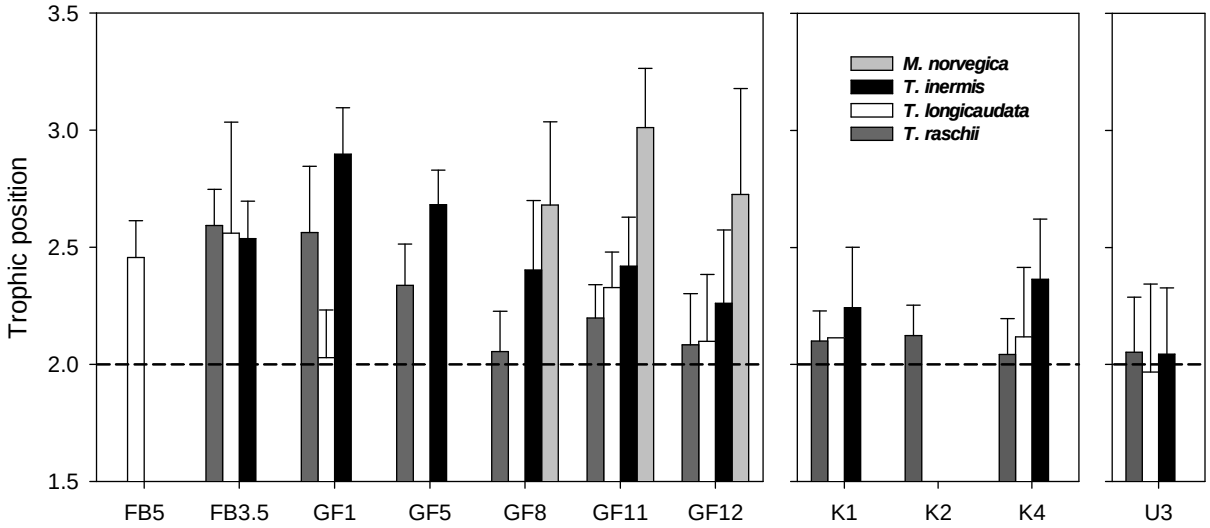

Figure 6. Mean (+sd) trophic position of the four krill species found at the different stations (see Fig. 1). The dotted line indicates the trophic position of *Calanus* spp. used as the reference baseline.

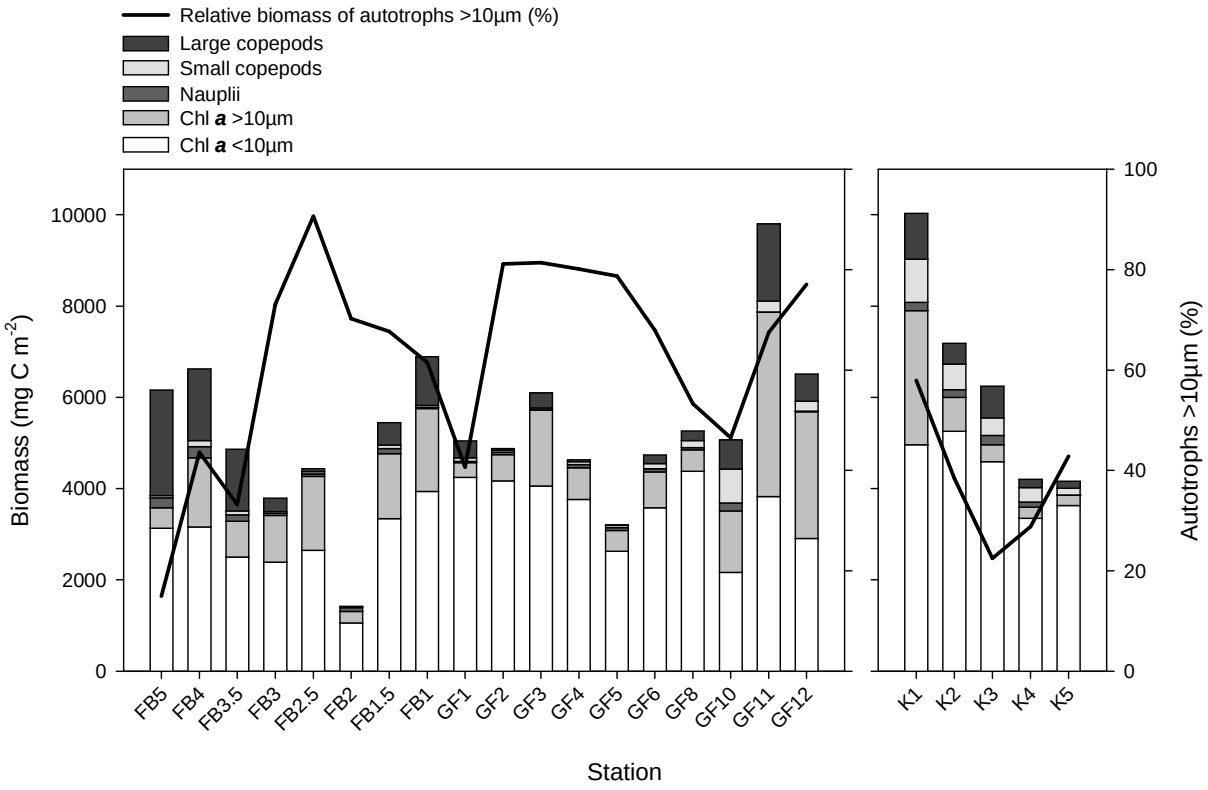

Figure 7. Integrated biomass (mg C m^{-2}) of different plankton groups from Fyllas Bank (FB), Godthåbsfjord (GF) and Kapisigdlit (K). Chlorophyll *a* (Chl *a*) is presented as size fractions > and <10µm. Note that protozooplankton is not included in the graph due to no data available. The line represents the relative contribution of autotrophic prey >10µm compared to heterotrophic prey.