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Krill diversity and population structure along the sub-Arctic Godthåbsfjord, SW Greenland

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Abstract:

In June 2010 four krill species were collected in Godthåbsfjord, SW Greenland, namely *Thysanoessa raschii, T. inermis, T. longicaudata* and *Meganyctiphanes norvegica.* A transect from offshore Fyllas Bank to the inner Godthåbsfjord revealed a zonation of the species in relation to hydrography. Offshore, in the Atlantic-influenced water, the Atlantic *T. longicaudata* dominated. All individuals of *T. longicaudata* found offshore were carrying spermatophores. Within the fjord *T. raschii* and *T. inermis* were present in high numbers but the former dominated. The boreal *M. norvegica* were only present in the inner part of the fjord. Presence of only 1-year-old individuals and no fertilized females suggests the population is sustained by advection of *M. norvegica* from offshore waters. Krill community abundance and biomass were lowest offshore and peaked in the innermost part of Godthåbsfjord. *Thysanoessa inermis* matured after 2 years, while *T. raschii* matured after 1 and 2 years, respectively, depending on temperature. The present study suggests that a warmer future will favour Atlantic species and result in a more diverse self-sustainable krill community in the Godthåbsfjord.

Keywords: *Thysanoessa* spp. ; *Meganyctiphanes norvegica* ; length–frequency distribution ; population structure ; length–weight relations

Introduction

Krill is a very important food chain component in the marine Arctic areas as a contributor to carbon sequestration and as a prey item for fish, marine birds and mammals (Mauchline & Fisher, 1969, Onsrud *et al.*, 2004, Rosing-Asvid *et al.*, 2013). However, limited knowledge is available concerning diversity and population dynamics of Arctic krill (e.g. Astthorsson & Gislason, 1997, Berkes, 1976, Dalpadado & Skjoldal, 1991, Einarsson, 1945).

Four species dominate the krill community in the North Atlantic, along western Greenland and north eastern Canada; *Thysanoessa raschii, T. inermis, T. longicaudata* and *Meganyctiphanes norvegica* (Berkes, 1976, Einarsson, 1945). *Thysanoessa raschii* and *T. inermis* both have a temperate to arctic distribution (Einarsson, 1945, Mauchline & Fisher, 1969, Siegel & Nicol, 2000). *Thysanoessa raschii* is mostly a coastal species (Einarsson, 1945, Mauchline & Fisher, 1969) , whereas *T. inermis* is regarded as a shelf species, inhabiting the coastal banks and therefore deeper waters than *T. raschii* (Einarsson, 1945, Mauchline & Fisher, 1969). *Thysanoessa longicaudata* is of Atlantic origin and occurs in offshore areas, whereas *M. norvegica* has a boreal distribution (Dalpadado & Skjoldal, 1991, Einarsson, 1945, Mauchline & Fisher, 1969) and occur in shelf-slope regions between coastal banks and deep basins (Melle *et al.*, 2004). *Meganyctiphanes norvegica* and *Thysanoessa* spp. occur along the West Greenland coast (Dunbar, 1940, Einarsson, 1945, Laidre *et al.*, 2010) but apart from these studies krill off West Greenland are understudied.

Thysanoessa inermis is one of the dominant species in Arctic regions (Dalpadado & Skjoldal, 1991, Dalpadado & Skjoldal, 1996) and has been found up to 70°N along West Greenland (Einarsson, 1945). Dalpadado and Skjoldal (Dalpadado & Skjoldal, 1991) found a positive and significant correlation between depth and the occurrence of adult *T. longicaudata* and *T. inermis* in the Barents Sea. Furthermore, a stronger positive correlation with salinity and temperature for *T. longicaudata* than for *T. inermis* was observed, indicating the former to be related to Atlantic water. In regions with low salinity and low temperatures both species were present but in small numbers . The boreal species *M. norvegica* has a preferred day depth of 100-500 m (Mauchline & Fisher, 1967, Melle *et al.*, 1993) and has been recorded as north as Disko Bay (69° N), West Greenland (Dunbar, 1942). *Thysanoessa raschii* has, on the contrary, been recorded further north (78°N) (Mauchline & Fisher, 1969) and in contrast to the other three species, *T. raschii* is the only species that spawns at temperatures below 0°C (Einarsson, 1945). In general, species distribution seem to depend on temperature and bathymetry (Einarsson, 1945, Mauchline & Fisher, 1969).

Godthåbsfjord, SW Greenland (64°N 51°W) is a sub-Arctic sill fjord with interannual variations in sea ice extent in the innermost part of the fjord (Mortensen *et al.*, 2013, Mortensen *et al.*, 2011). Along the 187 km main fjord branch, there is a temperature and salinity gradient from the warm salt offshore water to the colder and fresher water at the ice cape. Within this fjord system, different water masses and oceanographic regimes can be defined (Mortensen *et al.*, 2011, Tang *et al.*, 2011). Outside the fjord, off the coast of Greenland, the West Greenland Current brings relative warm and saline water of Atlantic and polar origin (Holland *et al.*, 2008, Myers *et al.*, 2009 and references herein). This area has been divided into two regions by Mortensen *et al.* (Mortensen *et al.*, 2011): the continental slope and the continental shelf. The main sill region is located at the entrance of the fjord and is influenced by strong tidal mixing, and thereby consists of mixed water masses from the fjord and from the outer regions (Mortensen *et al.*, 2011, Tang *et al.*, 2011). The main fjord basin is >400 m deep and characterized by strongly stratified water masses. The innermost part of the fjord is influenced by ice and freshwater run-off from glaciers and therefore also colder than the rest of the main fjord basin. Adjacent to the main fjord is a side branch named Kapisigdlit. This area is, in contrast to the main fjord branch, influenced by river run-off during the summer (Riisgaard *et al.*, *in press.*).

The plankton community is influenced by the oceanographic regimes (Agersted *et al.*, 2011, Arendt *et al.*, 2010, Calbet *et al.*, 2011, Tang *et al.*, 2011). Tang *et al.* (Tang *et al.*, 2011) and Arendt *et al.* (Arendt *et al.*, 2010) identified zonation of distinct zooplankton communities with regard to the different oceanographic regimes, while Agersted *et al.* (Agersted *et al.*, 2011) described the krill community in the area but without considering diversity and population structure.

The aim of the present study was to establish a baseline for the krill community in Godthåbsfjord using temperature- and salinity gradients, i.e. space-for-time, as a proxy for a future climate. A potential change in the krill community can have implications for higher trophic levels and consequently for the Greenland community who rely strongly on the fishery. Here, we investigate krill diversity, population composition and abundance. Distribution data will be analysed in relation to the oceanographic regimes of the Godthåbsfjord. Based on the pronounced oceanographic differences along the Godthåbsfjord and the different geographical origin for the four krill species, we hypothesize that different krill species are associated with specific oceanographic regimes.

Method

Field sampling

The present study was part of the BOFYGO project (Biological Oceanography of Fyllas Bank-Godthåbsfjord). Data was collected during a cruise from the June 6-24, 2010 with R/V Dana (National Institute of Aquatic Resources, Denmark). The stations were located along a transect from the offshore Fyllas Bank to the inner part of Godthåbsfjord, and along a transect through Kapisigdlit, a side branch to the main fjord (Fig. 1). Due to ice it was not possible to go all the way to the head of the Godthåbsfjord, but only to station GF12 (Fig. 1). Four hydrographic regimes along the transect were selected for more intensive sampling (following Mortensen ***et al.***, 2011); 1) Fyllas Bank located offshore and influenced by warm and saline Atlantic water, 2) The inner fjord, influenced by glacial melt-water, 3) The mouth of the fjord, where different water masses are mixed and 4) Kapisigdlit, a fjord branch, which is an area influenced by run-off from a river.

At each station temperature, salinity and fluorescence were measured by a CTD (SBE 911plus, SeaCat).

Krill was sampled with a MIK ring net (2 m in diameter, 1500-μm mesh size, black). The MIK net was towed in oblique hauls 0-140-0 m at a speed of 2.8 ± 0.9 knots. Sampling was generally done at night. However, intensified sampling with both day and night samples was conducted at stations GF1, GF12 and K4 (see e.g. Table 4) to investigate any differences due to diel vertical migration. After retrieval the krill were preserved in buffered formalin (4% final concentration). The 0-group was undersampled with the MIK net. Therefore, a Bongo net with finer mesh sizes (300 and 500-μm) was used to collect eggs and larvae (unpublished data).

Due to short summer nights at high latitudes only three hours (2230-0130 hr; local time) was defined as night, whereas the three hours before and after "night" were defined "dusk" (1930-2230 hr) and "dawn" (0130-0430 hr), respectively. The remaining hours were considered "day" (0430-1930 hr).

Laboratory analysis

Length-weight relationships

To determine length-carbon relationship, individual krill (not gender-differentiated) of all four species from the study area, together with specimens of *M. norvegica* from the Norwegian Sea (added to get a broader size range; see Fig. 2) were analysed. *Meganyctiphanes norvegica* from Greenland and the Norwegian Sea were not significantly different ($P > 0.05$; see result section). All were length-measured from tip of rostrum to end of telson (TL, mm) (Einarsson, 1945) and dried at 60°C for 24 h. Subsequently, dry weight (DW) was measured on a fine scale (Sartorius LE225D). To measure total carbon the krill were combusted at 900°C using a Solid Sample Modul (SSM 5000A TC, SHIMADZU). A standard curve was made using Acetanilide (97%). The carbon content in individual krill was calculated by the slope of the standard curve:

$$y = 0.0098x - 0.208, r^2 = 0.998 \quad \text{(Eq. 1)}$$

The combined length-weight regression (mm; mg C) from the four species was used to convert abundances into biomass.

To evaluate the relative importance of krill as grazers on the primary production, and as prey for higher trophic levels, krill biomasses were compared with that of the total copepod community (unpublished data).

Biomass samples

Krill samples were sorted with respect to species *(Thysanoessa raschii, T. inermis, T. longicaudata* and *Meganyctiphanes norvegica),* gender and stages (juvenile, adult, immature, mature). Individuals were length measured (TL). The whole sample or a subsample holding a minimum of 400 individuals was analysed.

Males and females were identified by their secondary sexual characters; petasma for males and thelycum for females, according to Einarsson (1945). Males were identified as mature when they had spermatophores visible in the abdomen and the petasma was fully developed. Otherwise they were identified as immature. Females were identified as mature when thelycum was fully developed (swollen), otherwise as immature. When thelycum or petasma were not present, the specimen was identified as juvenile. Few specimens that were larger than the usual mature size were observed to have immature appearance of, i.e. poorly developed, thelycum or petasma as observed by Einarsson (Einarsson, 1945) and Endo (Endo, 1989). These specimens were identified as immature females or males, respectively. If an individual larger than the usual mature size could not be sexed, the specimen was categorized as adult.

Statistical analysis

Bimodal distribution and mean length for different cohorts were estimated by fitting two Gaussian functions to the data using RStudio (ggplot2 package, R 3.0.1). If data was not bimodal a single Gaussian function was fitted. Distributions were bimodal if the two means from the two distinct cohorts were more than 2σ from each other. An ANOVA (R 3.0.1) was used to test if there were any significantly differences in power functions describing length-weight relationships for the four species. All deviations from means are reported as ± standard deviation (SD) unless other is stated.

Results

Bathymetry, hydrography and fluorescence

The fjord has three sills located between the mouth of the fjord (St. GF1) and the main fjord basin (St. GF6) (Fig. 3 and in Mortensen *et al.*, 2011). The depth in the sill region is between 330 and 400 m (366 ± 29 m), whereas the main fjord basin (GF8-12) has a mean depth of 592 ± 39 m (Table 3). The continental shelf (Fyllas Bank) has the shallowest depth of 47 m, whereas the stations on the outer part of the continental shelf, i.e. the continental slope, are >1000 m (Table 3). Average temperature and salinity for the upper 140-m did not differ much between regions. However, some distinct characteristics can be seen (Table 3, Fig. 3a, b). At the continental slope both temperature and salinity were high and there was some stratification of the water column. When entering the fjord, temperature and salinity decreased. In the outer sill region and in the middle fjord (GF1-6) vertical mixing of the water masses occurred, which was evident in the temperature, salinity and fluorescence data (Fig. 3). In the main fjord basin the upper water column was stratified with freshwater in a thin surface layer originated from glacial run-off (Mortensen *et al.*, 2011). Due to the run-off, the ice sheet region had low temperature (1.5°C ± 0.7 at GF12 in the upper 140 m) and salinity (>21 at GF12; >19 at GF10) in the upper water column (Table 3, Fig. 3). The average salinity was not much lower here than in the other regions but displayed a larger range (21.5-33.4) (Table 3). The same tendency was observed in Kapisigdlit where surface waters showed high temperatures (Fig. 3a, Table 3). Similar to the waters close to the ice sheet, the surface salinity in Kapisigdlit was low due to freshwater input (Mortensen *et al.*, 2013, Mortensen *et al.*, 2011, Riisgaard *et al., in press.*). In the whole branch of Kapisigdlit the water column was stratified. Subsurface blooms were observed in association with the pycnocline around 20-m depth in Godthåbsfjord and Kapisigdlit (Fig. 3c). Fluorescence was highest offshore in the continental slope region and in the innermost part of Godthåbsfjord, and lowest in the main fjord basin and in Kapisigdlit (Fig. 3c). In the main fjord basin near GF5-6, the fluorescence was similar throughout the whole water column indicating mixing.

Length-weight relationship

Power functions describing length-weight relationships for the four species are shown in Table 1. An ANOVA gave a significant difference between species (ANOVA, F=5.05, df=4, P < 0.05). Therefore, species were compared pairwise. *Meganyctiphanes norvegica* from Greenland and the Norwegian Sea were not significantly different ($P > 0.05$) and therefore pooled. Furthermore, *T. raschii* was not significantly different from *M. norvegica* ($P > 0.05$). *Thysanoessa inermis and T. longicaudata* were both significantly different from other species ($P < 0.05$). However, we chose a power function including all species for calculating community biomasses. This decision was based on 1) the different sizes of krill represented in the analysis (range: 9.5-50.5 mm, mean = 26.9 mm; median = 27.5 mm) 2) the possible difference in condition of the individuals 3) a strong linear relationship was found for all species when plotted on a log-log scale (Fig. 2; Table 1, $r^2 = 0.96$):

$$y = 7.25 \times 10^{-5} x^{3.792}, r^2 = 0.96 \qquad \text{(Eq. 2)}$$

where y=weight (mg C) and x=length (mm).

From krill used for length-weight analysis the percentage of carbon (C) from dry weight (DW) was calculated (Table 2). The highest percentage of C per DW was found in *M. norvegica* and *T. inermis* (53.1% ± 7.4 and 53.9% ± 5.8, respectively), whereas *T. raschii* and *T. longicaudata* had a lower carbon content (38.7% ± 10.0 and 40.0% ± 5.7, respectively).

Krill abundance, biomass and distribution

Abundance and biomass in the upper 140 m were highest at night compared to day, dawn and dusk samples (Table 4; Fig. 4). Abundance and biomass peaked in the innermost part of the fjord (GF12) with 709 ind m^{-2} and 67.3 mg C m^{-3}, respectively (Table 4; Fig. 4). Nevertheless, high biomasses were also found at GF8-GF11. The lowest abundance and biomass were found offshore (FB5-1) with 0.01-2.9 ind m^{-2} and 0.0002-0.01 mg C m^{-3}, respectively. However, no night samples were taken at these stations. No krill was found at station FB1.5 on the edge of Fyllas Bank.

In the offshore area the krill community was dominated by *T. longicaudata*, probably originated from the Atlantic water (Table 4). Conversely, *T. longicaudata* was found in very low numbers in the fjord area. *Thysanoessa raschii* had the highest abundance of all species in the fjord, and peaked in the inner part of the fjord at GF12 (642 ind m^{-2}), where it comprised 89.9% of the biomass (Table 4, Fig. 5). *Thysanoessa inermis* were found in second highest abundances and peaked at GF10, where the abundance (sample 518, Table 4) was almost similar to the one for *T. raschii*. At FB1 just outside the fjord, *T.inermis* and *T. raschii* displayed equal biomasses (2.6 ind m^{-2} and 1.8 ind m^{-2}, respectively). The relative biomass at FB1 was 67.1% for *T. inermis* in relation to 32.8% for *T. raschii*. *Meganyctiphanes norvegica* was only present in the inner part of the Godthåbsfjord and peaked at GF8, where the abundance was similar to the one for *T. raschii* (86.6 ind m^{-2} and 96.9 ind m^{-2} for *M. norvegica* and *T. raschii*, respectively). However, the biomass of *M. norvegica* contributed 88.3%, whereas *T. raschii* only contributed 8.8% of the total biomass (Table 4, Fig. 5). Only in the innermost part of Godthåbsfjord and in the mouth of Kapisigdlit (GF10-12, K1), all examined species were present concurrently (Table 4).

The importance of the krill community in relation to the other most important pelagic crustacean group, the copepods, changed along the fjord. Offshore, in the mouth of the fjord and in Kapisigdlit, the total zooplankton biomass was dominated by copepods (Fig. 6). This is in contrast to the main branch of the Godthåbsfjord, where krill were much more important. Compared to the biomass of the krill community, the copepod biomass was relatively stable.

Length-frequency distributions

Length-frequency distributions were analysed for all stations but only shown for stations representative for the different oceanographic regimes (Fig. 7). For *T. longicaudata* and *M. norvegica* only one year class (the I-group; Dalpadado & Skjoldal, 1991, Einarsson, 1945, Mauchline, 1960) was found, with most of the individuals being mature. For both *T. raschii* and *T. inermis* a bimodal distribution (two distinct cohorts) was present (however, not at all the stations for the latter; see Table 5). At FB1 the I-group and II-group (Einarsson, 1945) of *T. raschii* seem represented equal in numbers. For all other stations the I-group of *T. raschii* had higher numbers than the II-group and there was a tendency of the specimens being smaller in Kapisigdlit (K4) than in the main fjord (Godthåbsfjord, GF) (Table 5; Fig. 7). For *T. inermis* higher numbers were found for the I-group compared to the II-group, except on FB1.

Maturity

Females were generally larger than males (Fig. 8, 9). At K4 the highest percentage of *T. raschii* was comprised of juveniles. Only in the II-group, mature individuals were present and they all had spermatophores (Fig. 8). Conversely, not many juveniles were found at GF1, and mature individuals were present both in the I- and II-group. Here, a little less than half of the mature females carried spermatophores. GF11 and GF12 seemed like an intermediate zone, where half of the I-group consisted of juveniles and the other half of immature individuals. A few mature individuals (only females) were found here, where a little more than half had spermatophores. At GF11 and GF12 the population of *T. inermis* was dominated by the I-group, which consisted of juveniles and immature males and females. Only few mature males and females (all of the latter without spermatophores) were found and belonged to the II-group. Conversely, at GF1 the population was dominated by the II-group, which both consisted of mature males and females and immature males. Here, 25% of the mature females carried spermatophores. The I-group was mainly comprised of juveniles. At K4 only relatively few individuals (N = 10) were found and mainly juveniles in the I-group. Mature females were all without spermatophores. In the offshore samples only mature individuals of *T. longicaudata* were present (Fig. 9), all carrying spermatophores. None of the few mature females of *T. longicaudata* found in the innermost part of Godthåbsfjord and in Kapisigdlit had spermatophores. For *M. norvegica* both mature males and females were present at GF11, but only males had spermathophores. Also very few immature males were observed.

Sex-ratio

Sex-ratio (male/female) was calculated for stations where a minimum of 50 individuals were sexed (both mature and immature, excluding juveniles) (Fig. 8, 9). For *T. raschii* the sex-ratio was calculated at St. GF1, GF11, GF12 and K4, and for *T. inermis* at GF11. For *T. longicaudata* it was calculated at the two outermost stations offshore (FB5 and FB4), where *T. longicaudata* showed the highest abundance and furthermore was the only species present. The sex-ratio for *T. raschii* varied between stations (Fig. 8). In Kapisigdlit at K4 (sample 414 and 457) the average sex-ratio was the highest found for this species (2 ± 0.11). The sex-ratio in *T. inermis* at GF11 was lower than the one for *T. raschii* at the same station. For *T. longicaudata,* the sex-ratio was found to be similar at the two stations offshore (0.65 ± 0.13) (Fig. 9).

Discussion

Krill diversity in relation to hydrography

Along the Godthåbsfjord, a clear zonation of the plankton communities has been documented (Arendt *et al.*, 2010, Calbet *et al.*, 2011, Tang *et al.*, 2011). Calbet *et al.* (Calbet *et al.*, 2011) found the phytoplankton community to be dominated by diatom chains/cells >10µm in the innermost part of the fjord, whereas small cells (<10µm) dominated in the more stratified part of the fjord. At the well-mixed Fyllas Bank offshore, a high percentage of the phytoplankton consisted of cells >10µm. The zonation of water column properties and phytoplankton is also reflected in the mesozooplankton community composition; offshore the copepod *Calanus* spp. dominates, whereas the species *Metridia longa, Pseudocalanus* spp. and *Microsetella* sp. dominate within the fjord (Arendt *et al.*, 2010, Tang *et al.*, 2011).

Here we document significant differences in the diversity and stage compositions of the krill community, corresponding to the different oceanographic regimes. Offshore, in the continental shelf region, only *Thysanoessa longicaudata* was present, associated with Atlantic water masses as documented by others (Dalpadado & Skjoldal, 1991, Einarsson, 1945, Mauchline & Fisher, 1969). In the main fjord basin the more Arctic related species *T. inermis* and *T. raschii* took over. Krill biomass peaked closest to the ice sheet where *T. raschii* dominated. The presence of these two species is in accordance with observations in fjords around Iceland and Greenland (Astthorsson, 1990, Einarsson, 1945). Also in Balsfjorden, northern Norway, *T. inermis* and *T. raschii* have been found to dominate

(Falk-Petersen & Hopkins, 1981). Buchholz *et al.* (Buchholz *et al.*, 2010) compared two fjords with different hydrography in West Spitsbergen, Svalbard: Kongsfjorden (79° N), which is influenced by Atlantic warmer water, and Hornsund (77° N), which is influenced by Arctic colder water. Investigations revealed that the species composition differed between the two fjords, where *T. inermis* clearly dominated both in the area outside the sill and in the innermost part of the fjord in Hornsund. Contrary, more species with boreal Atlantic origin were present in Kongsfjorden, with *M. norvegica* dominating in the deeper area outside the sill and *T. inermis* dominating in inner part of the fjord.

Coastal populations of krill have the possibility of both being advected in and out of the fjord due to the prevailing circulation patterns (Mortensen *et al.*, 2013, Mortensen *et al.*, 2011). As *T. raschii, T. inermis* and *M. norvegica* are mainly found in the inner fjord basin it suggests that they can avoid the out-going water, and the retention may therefore be accomplished by the krill themselves (Kaartvedt, 1993). From a study in Jøsenfjord, south-western Norway, Kaartvedt and Svendsen (Kaartvedt & Svendsen, 1990) suggest that *T. raschii* adjust its vertical position to avoid being advected out of the fjord. Similar behaviour has been discussed for *M. norvegica* where lower salinity in the surface waters seems to control the vertical position of this species. As a consequence *M. norvegica* stayed in deeper more saline water layers (Kaartvedt & Svendsen, 1990). *Meganyctiphanes norvegica* has furthermore been found to alter its nocturnal vertical distribution to avoid unfavourable advection. In Masfjorden, western Norway, *M. norvegica* avoided the upper water layers that would lead to nocturnal inward transport into the shallow innermost shelf of the fjord, where susceptibility to visual predators would have been high during the day (Giske *et al.*, 1990). Moreover, by this behaviour *M. norvegica* hindered out-transport by staying below sill-depth (i.e. below the advective layer) (Giske *et al.*, 1990). In Kattegat, between Denmark and Sweden, *M. norvegica* was able to maintain its presence in one restricted area, the Læsø-Deep, which is situated in a region with strong currents (Boysen & Buchholz, 1984, Buchholz & Boysen-Ennen, 1988, Kaartvedt, 1993). Motility might be the reason for *M. norvegica* to be able to remain within the same area (Buchholz & Boysen-Ennen, 1988). Assuming an average swimming speed of 3.3 cm s^{-1} (Berkes, 1973) it would take 63 days to swim 180 km from the inner station GF12 to the offshore station FB5. The tidal currents in the middle fjord (around GF3-4) have been estimated to vary between 20 and 60 cm s^{-1} (Mortensen *et al.*, 2011), i.e. it takes 3.5 to 10.4 days to travel the same distance just by tidal transport. Therefore, *M. norvegica* and *Thysanoessa* spp. could be transported by the in- and outgoing currents just by adjusting their vertical position, and the horizontal migration could hereby be significantly accelerated.

Influence of bathymetry on krill distribution

Meganyctiphanes norvegica has been found to occur in areas deeper than 100 m (Hjort & Ruud, 1929, Melle *et al.*, 1993). This preference may explain why we only observe this species in the inner and deep part of the fjord (GF8-12). The abundance of *M. norvegica* was highest at GF8, close to the slope of the sill (~600 m depth; see e.g. Fig. 3). This is supported by observations in the Norwegian Sea by Melle *et al.* (Melle *et al.*, 2004), who report *M. norvegica* to occur on slopes, and to prefer the areas between coastal banks and deep basins. Aggregations of krill at bathymetric slopes have previously been observed (e.g. Kaartvedt & Svendsen, 1990, Simard *et al.*, 1986, Simard & Mackas, 1989) and could be caused by passive accumulation (e.g. Simard *et al.*, 1986, Simard & Mackas, 1989). However, the high abundance of *M. norvegica* at GF8 compared to GF10-12, indicate an active selection of a favorable location, as suggested by Kaartvedt and Svendsen (Kaartvedt & Svendsen, 1990).

In the Barents Sea, Dalpadado and Skjoldal (Dalpadado & Skjoldal, 1991, Dalpadado & Skjoldal, 1996) found the highest abundance of *T. inermis* at slopes and in deep waters (>300 m), and suggest that the association with the bottom and bottom topography is not particularly strong for this species (Dalpadado & Skjoldal, 1991). Conversely, *T. raschii* has been found to be associated with shallower bottom depths and is considered a more neritic species than *T. inermis* (Dalpadado & Skjoldal, 1991, Dalpadado & Skjoldal, 1996, Einarsson, 1945, Kaartvedt & Svendsen, 1990, Mauchline & Fisher, 1969, Sameoto, 1976). In the present study both *T. inermis* and *T. raschii* were present in the deep part of the fjord (GF8-GF12; ~600 m depth), illustrating that the abundance of these species are not particularly associated with bottom topography. *Thysanoessa longicaudata* was the only species found on the continental slope (FB5-4), where the depth is >1000 m, as found by Einarsson (Einarsson, 1945).

Population structure

The boreal *M. norvegica* was only present in the inner part of the Godthåbsfjord and only the I-group were found, with all individuals being >20 mm. In the North Atlantic *M. norvegica* spawn from March to July (Einarsson, 1945). In the present study absence of smaller individuals and non-fertilized females suggest that *M. norvegica* do not reproduce this far north. This is supported by the lower temperature limit for spawning being 5°C (Einarsson, 1945). Hence, the fjord population must be seeded from the offshore population. Similar distribution patterns were found by Astthorsson (Astthorsson, 1990). He did not find any sign of spawning by *M. norvegica* in Ísafjord-deep, north-west Iceland, whereas *M. norvegica* larvae were found in the warmer water outside the fjord (in Astthorsson, 1990, Kristmannsson, 1989, Stefánsson, 1969). Nor did Falk-Petersen and Hopkins (Falk-Petersen & Hopkins, 1981) find eggs or larvae of *M. norvegica* in Balsfjorden and they suggest, like Astthorsson (Astthorsson, 1990) and the present study, that the fjord population colonised from the outside area. Only day samples were taken offshore outside Godthåbsfjord and since preferred day depth for *M. norvegica* is >100 m (Mauchline & Fisher, 1967, Melle *et al.*, 1993) there is a possibility that this species was present here but not collected. In addition to this, *M. norvegica* has been found off the coast of West Greenland in a previous study (Einarsson, 1945).

For *T. longicaudata* only the I-group was present and all individuals were mature. Offshore where *T. longicaudata* dominated, all females had spermatophores attached. According to Einarsson (1945) and Dalpadado and Skjoldal (1991) the spawning period for this species is spring or early summer in the Atlantic and sub-Arctic part of the Barents Sea (Dalpadado & Skjoldal, 1991, Dalpadado & Skjoldal, 1996) and south of Iceland (Einarsson, 1945)Therefore, spawning had probably already occurred for this species found in the present study. From Multinet samples (45 µm mesh size; unpublished data) it was revealed that nauplii, calyptopis and furcilia were present in the offshore area, which could indicate that *T. longicaudata* had spawned since this was the only species found offshore. However, these larvae were not identified to species. In the North Atlantic region, Williams and Lindley (Williams & Lindley, 1982) observed that the major spawning by *T. longicaudata* occurred at 9-10°C. Since the temperature in the offshore region is lower in the present study, it is highly probable that this species does not spawn. Instead, adults, eggs and larvae could have been transported northwards by the West Greenland Current as shown by model simulations for larval shrimp drift along West Greenland (Ribergaard *et al.*, 2004). *Thysanoessa longicaudata* was found in the fjord though in low numbers, and furthermore, none of the females here had spermatophores attached (data not shown). Similar to *M. norvegica*, we therefore suggest that *T. longicaudata* must be seeded from the offshore population and therefore does not have a self-sustaining population in the fjord.

Here we document that *T. inermis* mature after 2 years since only the II-group have been identified as mature (Fig. 8, >22 mm in length). Similar conclusions have been made in other studies (Astthorsson, 1990, Dalpadado & Skjoldal, 1991, Einarsson, 1945). It is not possible to make any concluding remarks regarding the III-group since data is too scarce. However, the length-frequency distributions indicate a third group comprised by larger individuals, as mentioned by Einarsson (1945). *Thysanoessa raschii* matured after 1 year in the mouth of the fjord as found by Einarsson (Einarsson, 1945) and Astthorsson (Astthorsson, 1990). However, in the innermost part of Godthåbsfjord only few individuals from the I-group were mature (only females), and in Kapisigdlit none individuals from the I-group were mature. At all stations almost all from the II-group were mature and few large specimens were found to show immature external sexual characteristics, which suggests that these individuals are older than 2 years. Einarsson (Einarsson, 1945) found similar results for *T. raschii* at the north and east coast of Iceland, which is a region influenced by cold water from the East Icelandic Current (Astthorsson & Gislason, 1997). Here, only the II-group consisted of mature individuals (Einarsson, 1945). Contrarily, he found individuals of *T. raschii* to reach maturity at an age of 1 year in the south-west coast of Iceland, which is an area highly influenced by warmer Atlantic water. In addition, Macdonald (Macdonald, 1928) found *T. raschii* in the Firth of Clyde to be mature after 1 year. Mauchline and Fisher (Mauchline & Fisher, 1969) also stated that *Thysanoessa* spp. living closer to Arctic regions, in relation to the same species occurring in warmer regions, require 2 years as opposed to 1 year to become mature. In the present study it is evident that the temperature difference in the various regions of the fjord is large enough to cause the differences in age of maturity we see for *T. raschii*.

It appears that *T. raschii* already spawned in the innermost part of the fjord and in Kapisigdlit, given that females were fertilized. Conversely, *T. inermis* females with spermatophores were only found in the mouth of the fjord. This indicates a higher spawning temperature limit for *T. inermis* in the inner fjord. In a previous study, *T. inermis* have been recorded to spawn North of Iceland where temperatures were just over 3°C (late April to late May) (Astthorsson & Gislason, 1997). Additionally, Einarsson (Einarsson, 1945) observed spawning by *T. inermis* in West Greenland at temperatures about 0°C, while at the south coast of Iceland they spawned at temperatures above 6-7°C. Therefore, spawning by *T. inermis* should not be temperature limited in our study. In relation to his findings, Einarsson (Einarsson, 1945) suggests that the main trigger for spawning is the phytoplankton spring bloom rather than temperature. This is supported by other studies on *Thysanoessa* spp. and *M. norvegica* (Astthorsson, 1990, Astthorsson & Gislason, 1997, Dalpadado, 2006, Dalpadado & Skjoldal, 1991). However, since our data is not sampled in time but only is a “snapshot-in-time” we cannot conclude anything regarding timing of spawning in relation to the bloom. Berkes (Berkes, 1976) and Falk-Petersen and Hopkins (Falk-Petersen & Hopkins, 1981) both documented a later spawning in *T. raschii* compared to *T. inermis* in the Gulf of St. Lawrence and in Balsfjorden, respectively. Furthermore, Drobysheva (Drobysheva, 1987) reported a prolonged spawning season for *T. raschii* in the Barents Sea, which may lead to less interspecific competition. Therefore, another more realistic explanation for the lack of *T. inermis* females with spermatophores is that *T. inermis* already spawned. Bongo net samples revealed that only furcilia larvae stages I-II were present in the Godthåbsfjord and all identified only to genus level, i.e. *Thysanoessa* spp.. Few later furcilia stages were found and all identified as *T. raschii* (unpublished data). It is therefore a possibility that the juveniles of *T. inermis* we found in the fjord samples originate from advection of larvae from offshore populations.

Future perspectives

In the Godthåbsfjord system, krill is the dominating zooplankton group. Therefore, climate mediated changes in the composition and biomass of the krill community have to be taken into account, when we want to understand the dynamics of this ecosystem in a warmer future. Studies in the Barents Sea have illustrated such potential changes in community composition and biomass between “warm” and “cold” years (Eriksen & Dalpadado, 2011, Zhukova *et al.*, 2009). In warmer years more Atlantic species were observed, whereas in colder years the arcto-boreal *Thysanoessa raschii* was dominating the biomass (Zhukova *et al.*, 2009). Eriksen and Dalpadado (Eriksen & Dalpadado, 2011) furthermore observed higher biomasses of krill in warmer years in relation to colder years.

Here we document a distinct zonation of the different krill populations in relation to the oceanographic regimes along the fjord. These regimes will probably change in the future since a warmer climate will increase melt water runoff (ACIA, 2005), and hereby change current patterns in fjords . This will cause stronger inflow of offshore water, and increase the abundance of the Atlantic krill species *Meganyctiphanes norvegica* and *T. longicaudata*. Additionally, increasing temperatures could lead to spawning in these two species. We suggest that a future warmer climate will result in a more diverse, self-sustaining krill community in the Godthåbsfjord area.

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Tables

Table 1. Power functions describing length-weight relationships in the different species ($y = ax^b$; y = weight (mg C), x = length (mm)). N describes the number of animals analysed.

Species	**a**	**b**	**r^2**	**N**
Thysanoessa longicaudata	3.60×10^{-11}	9.445	0.46	26
T. raschii	1.31×10^{-4}	3.549	0.92	52
T. inermis	1.59×10^{-5}	4.306	0.73	82
Meganyctiphanes norvegica	3.89×10^{-5}	3.930	0.94	89
T. raschii* and *M. norvegica	7.33×10^{-5}	3.751	0.97	141
All species	7.25×10^{-5}	3.792	0.96	249

Table 2. Size range (mm) and % carbon (C) of dry weight (DW) for the four krill species found in the Godthåbsfjord area. Also included is data from *Meganyctiphanes norvegica* from the Norwegian Sea.

Species	Size range (mm) Mean ± SD	% C of DW
***Thysanoessa raschii* (Greenland)**	9.5-29.5 mm (n=52) Mean 18.4 ± 5.5 Median 17.5	38.7 ± 10.0 Median 40.1
***T. inermis* (Greenland)**	16.5-34.5 mm (n=79) Mean 27.4 ± 3.7 Median 27.5	53.9 ± 5.8 Median 55.0
***T. longicaudata* (Greenland)**	12-14 mm (n=26) Mean 13.3 ± 0.6 Median 13.5	40.0 ± 5.7 Median 38.4
***Meganyctiphanes norvegica* (Greenland)**	25.5-50.5 mm (n=77) Mean 37.3 ± 4.7 Median 36.5	54.8 ± 5.8 Median 54.8
***M. norvegica* (Norwegian Sea)**	19.5-34.5 mm (n=12) Mean 23.6 ± 3.8 Median 22.5	42.3 ± 8.0 Median 41.3
***M. norvegica* (Greenland + Norwegian Sea)**	19.5-50.5 mm (n=89) Mean 35.4 ± 6.6 Median 35.5	53.1 ± 7.4 Median 53.9
All species	9.5-50.5 mm (n=246) Mean 26.9 ± 9.3 Median 27.5	48.9 ± 10.0 Median 51.5

Table 3. Average temperature (°C) and salinity ± SD in the depth strata where krill were caught (see Table 4). Temperature and salinity range displayed in brackets. Bottom depth (m) ± SD in the different regions is stated. Fyllas Bank (F), Godthåbsfjord (G) and Kapisigdlit (K). Main fjord basin has been further subdivided into GF6-10 and GF12. No data from GF5 and GF11. Regions (except for Kapisigdlit) after Mortensen et al. (2011).

Station	Region	Temperature (°C)	Salinity	Depth (m)
FB5-4	Continental slope	2.6 ± 0.7 (1.5-3.4)	33.8 ± 0.3 (33.1-34.4)	1008 ± 74 (956-1060)
FB3.5-1	Continental shelf	2.2 ± 0.9 (1.4-4.7)	33.4 ± 0.2 (32.9-33.4)	130 ± 94 (47-273)
GF1-4	Outer sill	2.5 ± 0.3 (2.0-3.5)	33.3 ± 0.1 (32.8-33.5)	366 ± 29 (330-400)
GF6-12	Main fjord basin	2.1 ± 0.6 (-0.6-4.8)	33.0 ± 0.9 (21.5-33.5)	592 ± 39 (531-630)
GF6-10	Main fjord basin	2.3 ± 0.5 (0.7-4.8)	33.0 ± 0.8 (24.2-33.5)	612 ± 22 (579-630)
GF12	Ice sheet	1.5 ± 0.7 (-0.6-2.2)	32.8 ± 1.5 (21.5-33.4)	531
K1-5	Kapisigdlit	2.6 ± 1.8 (0.8-9.3)	33.1 ± 0.7 (29.7-33.4)	217 ± 46 (149-257)

Table 4. Abundance data (ind m^{-2}) of the four krill species found along the transect. Also included is time, station and sample number.

Time	**Station**	**Sample no.**	**Net haul depth (m)**	**Abundance (ind. m^{-2})**				
				T. longicaudata	*T. raschii*	*T. inermis*	*M. norvegica*	Total
Day	FB5	46	110	2.85				2.85
Dusk	FB4	57	110	1.53				1.53
Day	FB3.5	96	110	0.32				0.32
Dawn	FB3.5	108	110	0.17	0.01	0.11		0.29
Dawn	FB3.5	109	110	0.06				0.06
Day	FB3	127	80	0.12				0.12
Day	FB2.5	134	80	0.23				0.23
Day	FB2	148	40	0.03				0.03
Day	FB2	149	48	0.01				0.01
Day	FB1.5	156	35					
Day	FB1.5	157	35					
Night	FB1	168	110	0.09	1.80	2.58		4.46
Day	GF1	215	110	0.02	0.08	0.06		0.17
Day	GF1	218	140		6.43	1.56		7.99
Dusk	GF1	241	110		0.02			0.02
Night	GF1	243	140	0.01	1.00	0.46		1.47
Day	GF1	251	110	0.03	1.32	0.54		1.89
Dusk	GF2	266	110		0.03			0.03
Night	GF2	276	140		26.70	3.47		30.17
Day	GF3	200	110	0.01				0.01
Dusk	GF4	291	140		0.05	0.04		0.09
Dawn	GF5	302	140		34.09	1.28		35.37
Day	GF6	316	140		9.16	0.99		10.16
Night	GF8	332	140		96.90	15.18	86.56	198.64
Day	GF10	349	110		179.92	5.39		185.31
Day	GF10	518	140	0.80	243.71	151.52	2.76	398.79
Day	GF11	494	140	0.88	137.77	130.03	3.16	271.84
Day	GF11	495	60		110.10	23.80	1.41	135.30
Day	GF12	473	140	0.60	140.63	70.31	2.94	214.48
Night	GF12	480	80	2.41	641.61	63.80	1.16	708.98
Dawn	GF12	481	140	1.43	298.35	71.72	6.10	377.60
Dawn	K1	372	140	0.06	258.52	7.21	0.06	265.86
Day	K2	385	140	0.29	123.37	0.57		124.22
Night	K4	414	140	0.21	79.50	1.06		80.77
Dawn	K4	418	140		23.17	0.62		23.79
Day	K4	434	140	0.14	19.02	0.64		19.80
Night	K4	457	140	0.26	110.94	3.13		114.33
Dusk	K5	399	140	0.10	1.84	0.03		1.97
Dusk	U2	362	140	1.06	130.39	0.80		132.25
Dawn	U3	549	140	1.03	157.76	4.66		163.45
Day	U4	557	140		3.30	0.12		3.42

Table 5. Mean length ± SD (mm) of the different species. In brackets is the size range (mm). If length-frequency was bimodal, two mean lengths are shown. All data (day, night, dusk, dawn, see e.g. Table 3) at the respective stations; GF1, GF12 and K4; were not significantly different from each other, and therefore data were merged.

Station	**Species**			
	T. longicaudata	*T. raschii*	*T. inermis*	*M. norvegica*

FB5	12.5 ± 0.9 (9.5-15.5 mm)			
FB1	12.6 ± 0.6 mm (11.5-15.5 mm)	18.4 ± 2.1 28.7 ± 2.1 (14.5-34.5 mm)	19.5 ± 1.1 27.8 ± 1.9 (15.5-34.5 mm)	
GF1	13.0 ± 1.7 (11.5-14.5 mm)	17.2 ± 1.5 25.3 ± 1.7 (12.51-31.5 mm)	23.5 ± 4.4 (14.5-31.5 mm)	
GF2		17.7 ± 1.4 27.1 ± 2.5 (13.5-30.5 mm)	22.0 ± 4.0 (17.5-34.5 mm)	
GF8		17.0 ± 1.4 27.4 ± 2.0 (13.5-33.5 mm)	18.9 ± 1.5 27.9 ± 1.2 (13.5-33.5 mm)	36.3 ± 2.1 (22.5-50.5 mm)
GF11	13.0 ± 1.8 (10.5-14.5 mm)	16.9 ± 1.6 27.3 ± 2.1 (13.5-31.5 mm)	18.4 ± 1.8 28.3 ± 1.2 (13.5-32.5 mm)	37.0 ± 8.1 (27.5-43.5 mm)
GF12	14.5 mm (four individuals of same size)	17.5 ± 1.7 27.6 ± 2.2 (11.5-34.5 mm)	18.5 ± 2.0 28.7 ± 1.5(12.5-32.5 mm)	39.1 ± 3.2 (20.5-46.5 mm)
K4	13.5 ± 0.8 (10.5-14.5 mm)	13.4 ± 1.9 24.9 ± 2.3 (8.5-31.5 mm)	17.3 ± 1.3 (12.5-33.5 mm)	

Figures

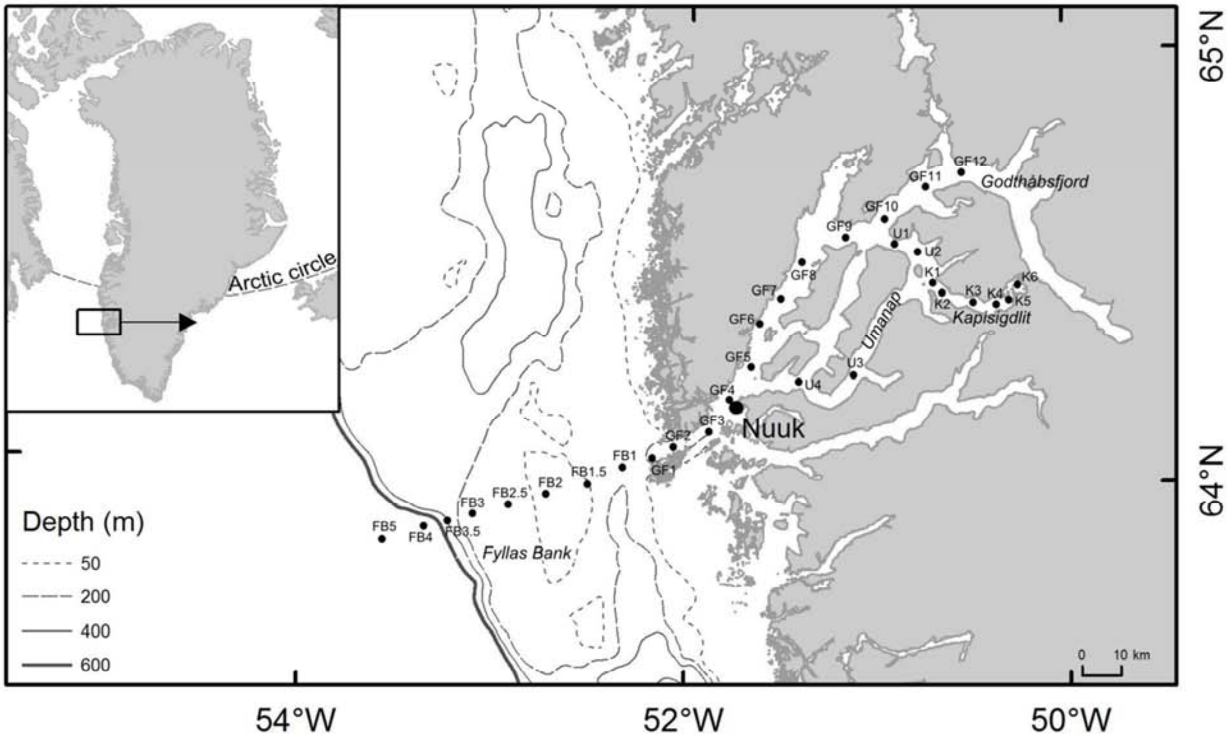


Fig. 1. The Godthåbsfjord system. FB=Fyllas Bank; GF=Godthåbsfjord; K=Kapisigdlit; U= Umanap. GF1, GF12 and K4 were intensive stations.

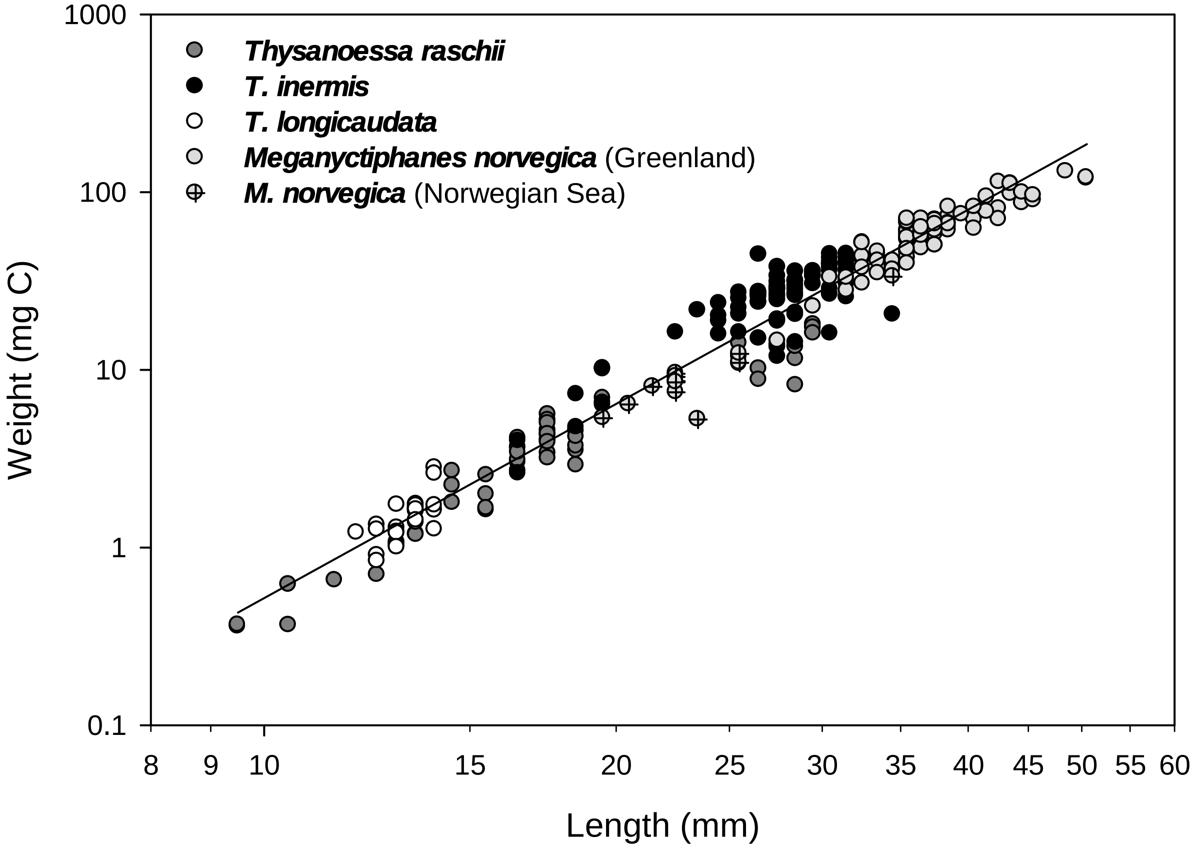


Fig. 2. Length-weight relationship for all species on a log-log scale. R^2=0.96. See Table 1 for power functions describing the relationship.

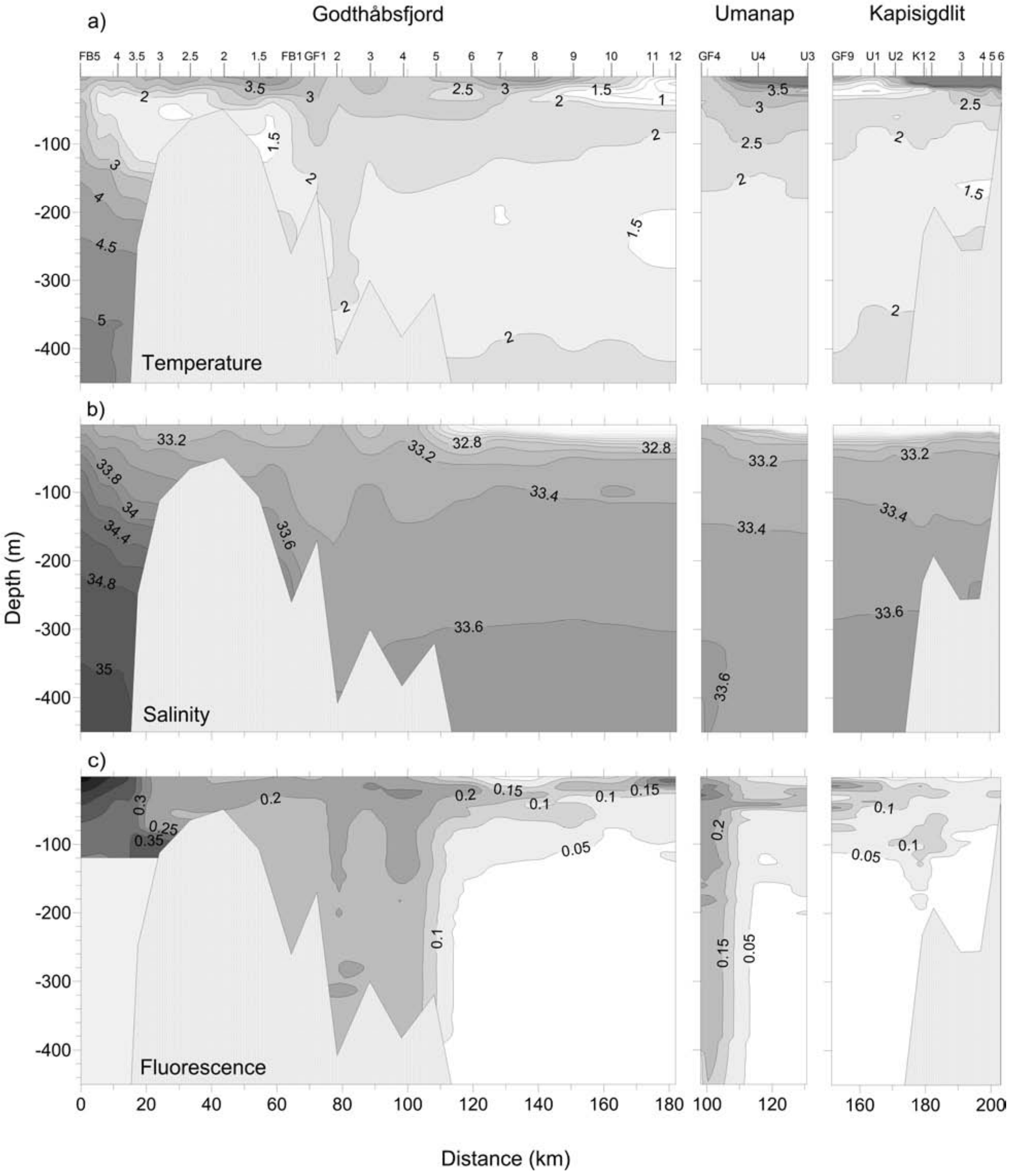


Fig. 3. Hydrography a) Temperature (°C) b) salinity and c) fluorescence (arbitrary units) in Godthåbsfjord, Umanap and Kapisigdlit, June 2010. Stations are inserted above, and distances between stations below graphs. Umanap was plotted in conjunction with Godthåbsfjord (GF4, U4-3), and Godthåbsfjord and Kapisigdlit (GF9, U1-2, K1-5). See Fig. 1 for location of the different stations and fjord branches.

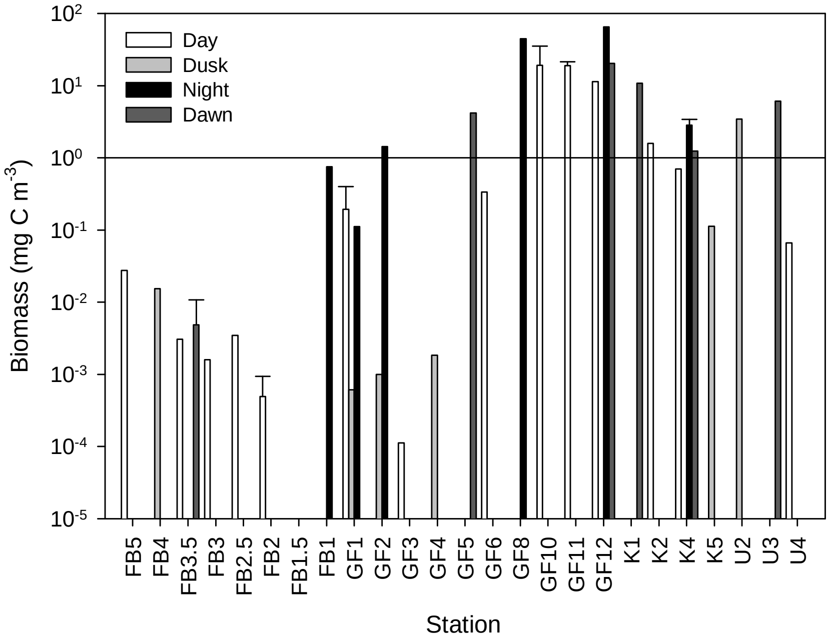


Fig. 4. Biomass (mg C m^{-3}) for all krill species combined (log scale). The different time of sampling are shown (Day: 0430-1930; Dusk: 1930-2230; Night: 2230-0130 and Dawn: 0130-0430). FB=Fyllas Bank; GF=Godthåbsfjord; K=Kapisigdlit; U= Umanap.

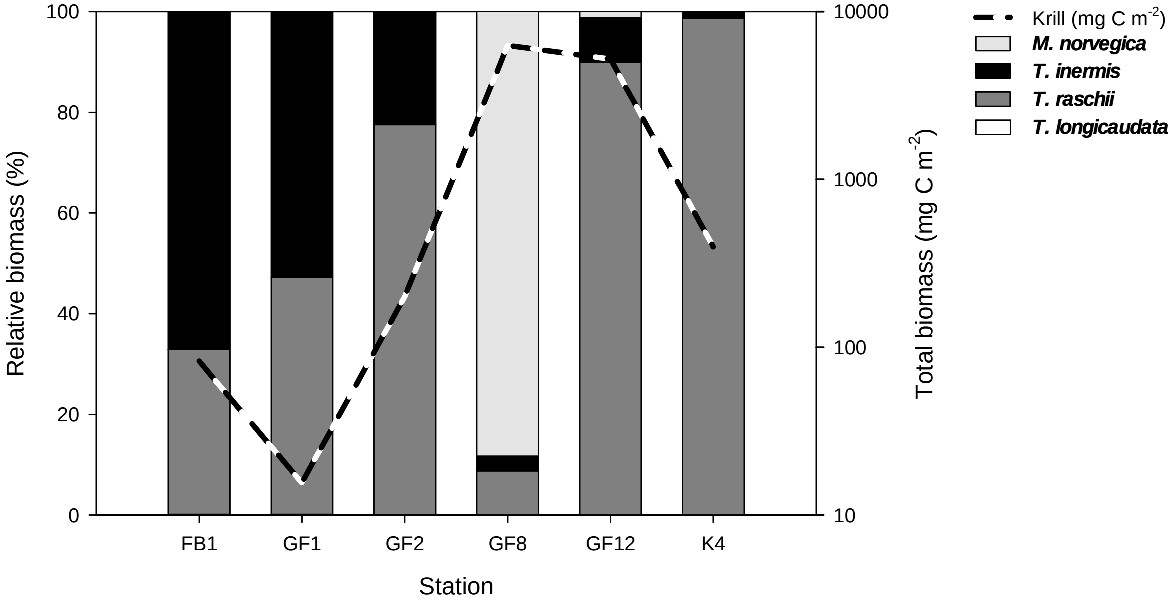


Fig. 5. Integrated biomass of krill (line; note log scale) (see Table 4 for depths) and relative species biomass (bars, %) at night stations. For station abbreviations see Fig. 4.

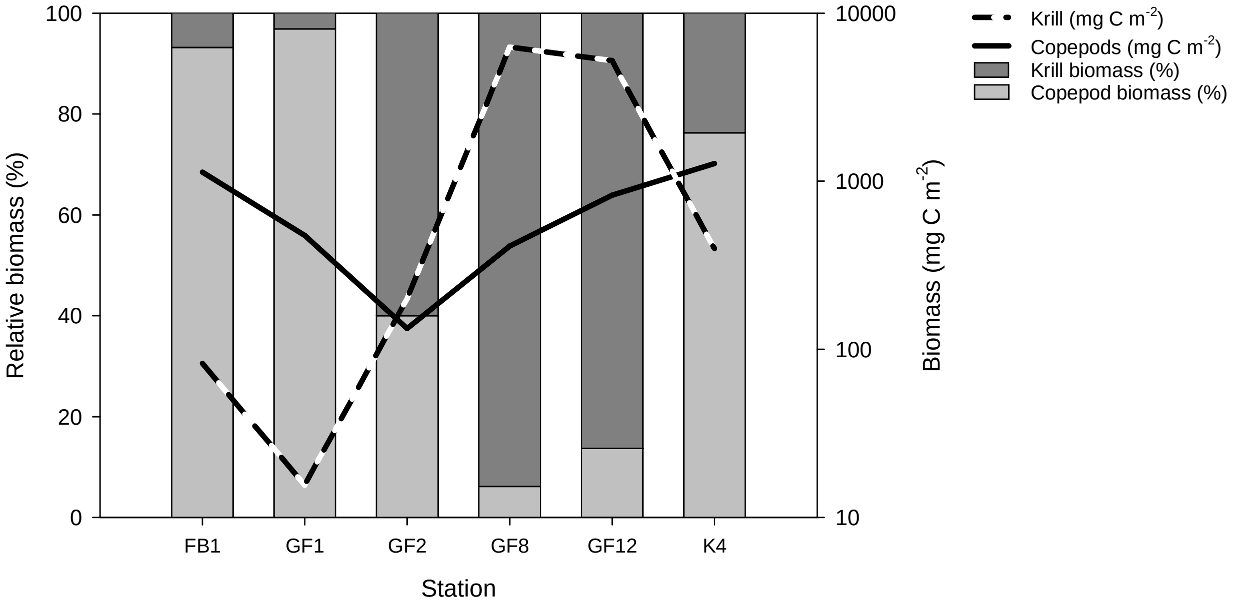


Fig. 6. Integrated biomass of krill (see Table 4 for depths) and copepods (0-100 m) (lines; note log scale), and the relative contribution of the two groups (bars; %) at night stations. For station abbreviations see Fig. 4.

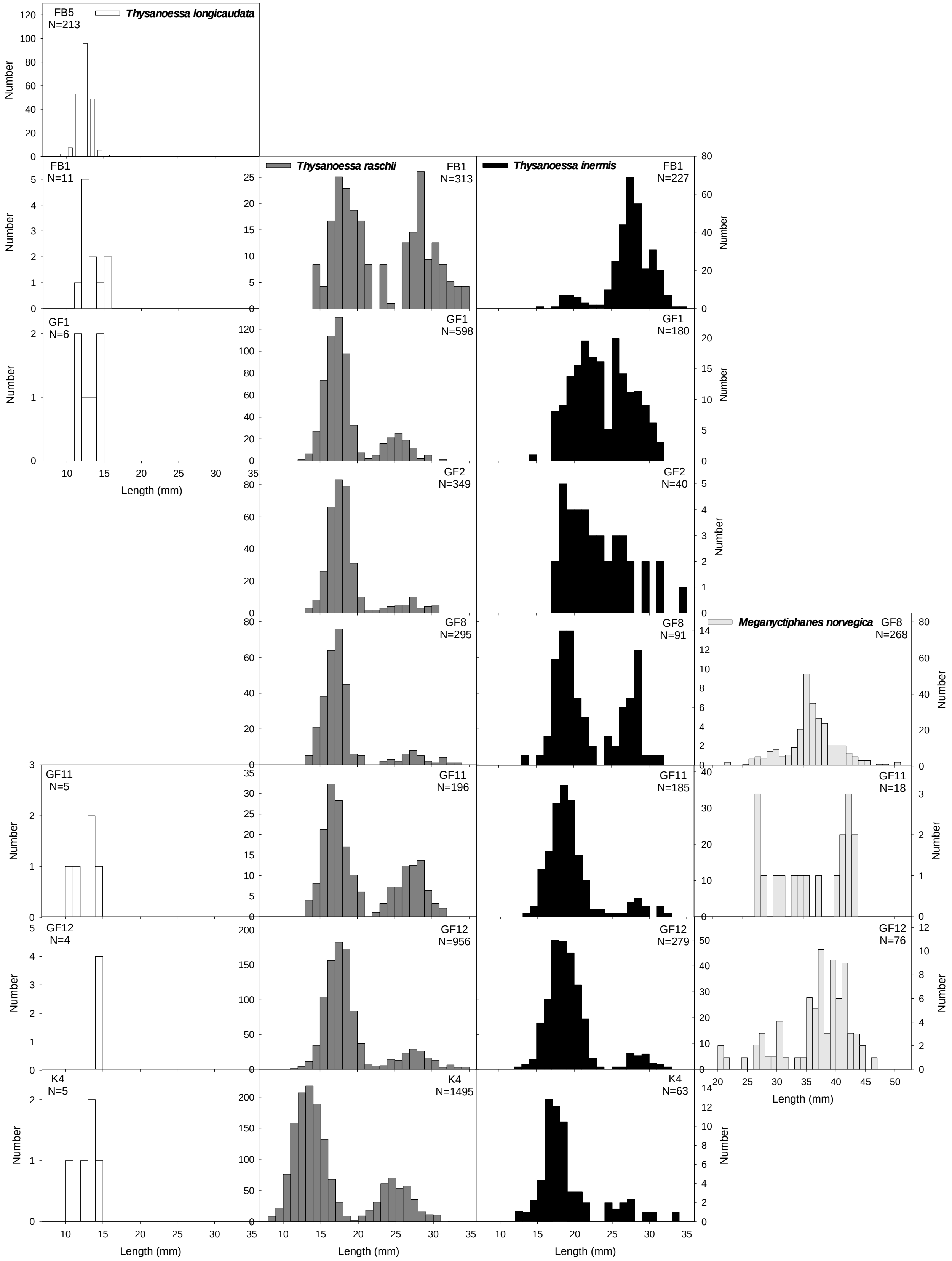
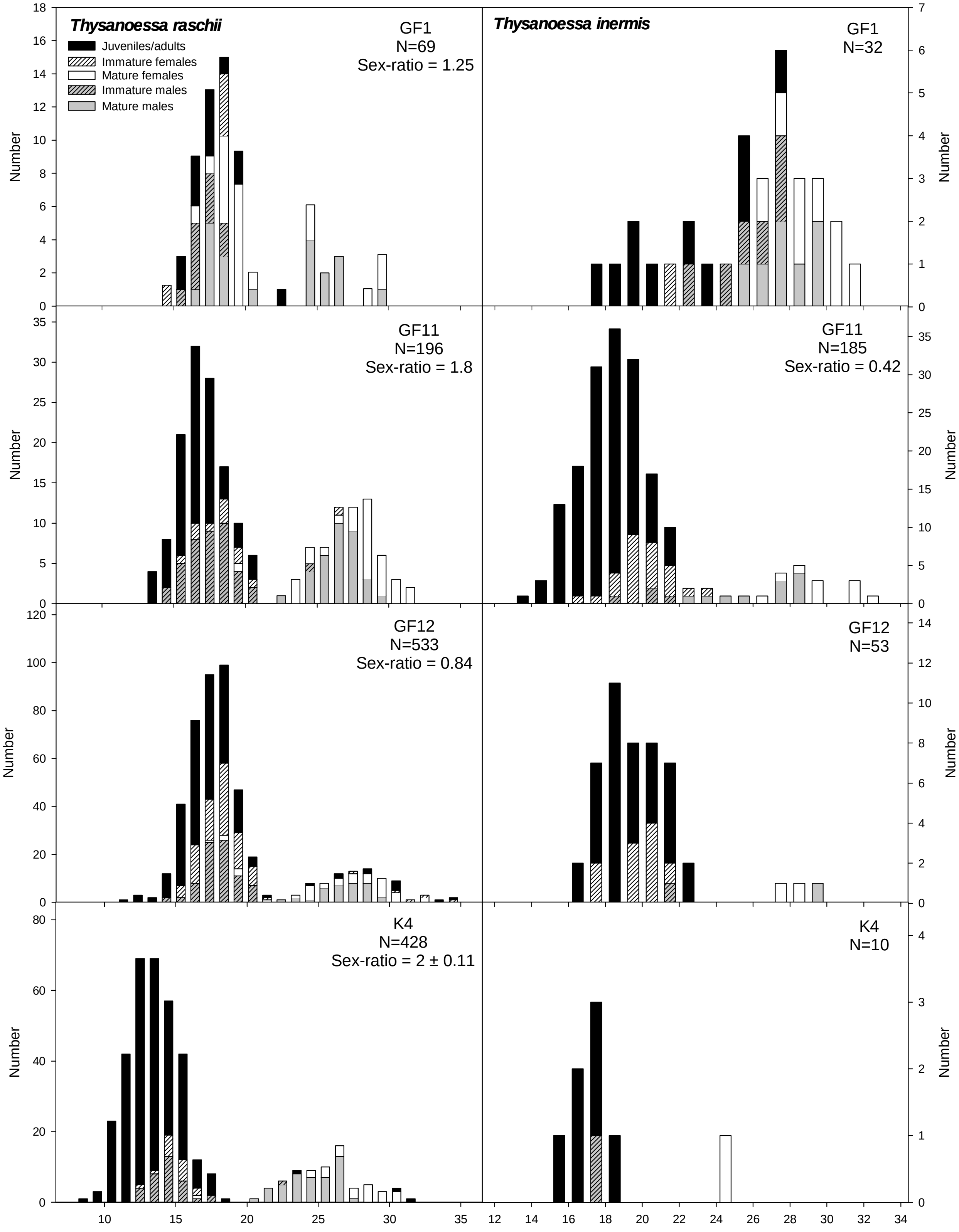

Thysanoessa longicaudata
FB5 N=213
FB1 N=11
GF1 N=6
GF11 N=5
GF12 N=4
K4 N=5
Thysanoessa raschii
FB1 N=313
GF1 N=598
GF2 N=349
GF8 N=295
GF11 N=196
GF12 N=956
K4 N=1495
Thysanoessa inermis
FB1 N=227
GF1 N=180
GF2 N=40
GF8 N=91
GF11 N=185
GF12 N=279
K4 N=63
Meganyctiphanes norvegica
GF8 N=268
GF11 N=18
GF12 N=76
Number
Length (mm)
10 15 20 25 30 35
20 25 30 35 40 45 50

Fig. 7. Length-frequency distributions of *Thysanoessa longicaudata, T. raschii, T. inermis* and *Meganyctiphanes norvegica* at eight stations (FB5, FB1, GF1, GF2, GF8, GF11, GF12 and K4) from Fyllas Bank (FB) off-shore to the bottom of the Godthåbsfjord (GF), and for the side-branch Kapisigdlit (K). For GF1, GF12 and K4 separately, data from different samples (i.e. night, day, dawn and dusk) were not significantly different (P>0.05) and therefore data from the respective stations were merged. In graphs number (=N) of krill measured is stated.



Thysanoessa raschii
Juveniles/adults
Immature females
Mature females
Immature males
Mature males
GF1
N=69
Sex-ratio = 1.25
Thysanoessa inermis
GF1
N=32
GF11
N=196
Sex-ratio = 1.8
GF11
N=185
Sex-ratio = 0.42
GF12
N=533
Sex-ratio = 0.84
GF12
N=53
K4
N=428
Sex-ratio = 2 ± 0.11
K4
N=10
Number
Number
0
2
4
6
8
10
12
14
16
18
0
1
2
3
4
5
6
7
0
5
10
15
20
25
30
35
0
20
40
60
80
100
120
0
2
4
6
8
10
12
14
0
20
40
60
80
0
1
2
3
4
10
15
20
25
30
35
12
14
16
18
20
22
24
26
28
30
32
34

Fig. 8. *Thysanoessa raschii* and *T. inermis* divided into different stages. Data only from focus areas (although not a focus station GF11 is also displayed due to a higher sampling number for *T. inermis,* compared to GF12). N = numbers of krill analysed. Sex-ratio (number of males per female) was calculated at stations where N>50 for males and females (excluding juveniles). Sex-ratio for St. K4 has been calculated as a mean from sample 414 and 457 and GF1, GF11 and GF12 from sample 243, 494 and 480, respectively. Note different scales.

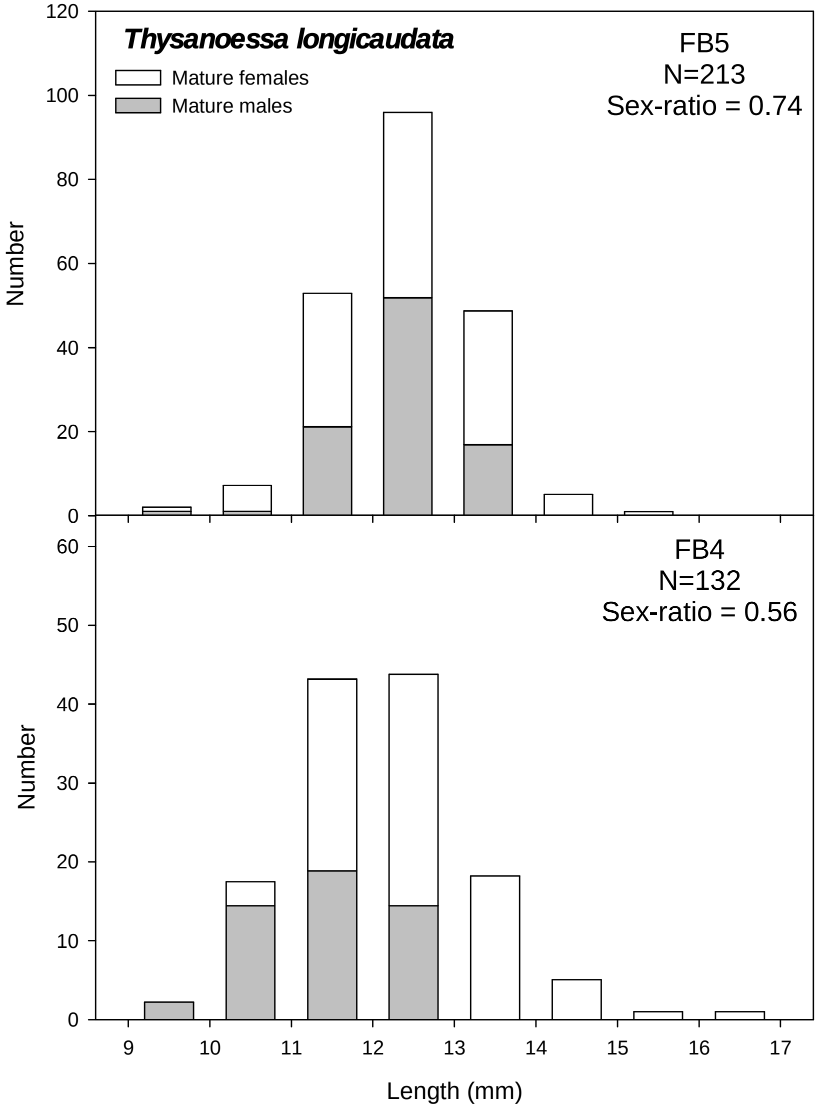


Fig. 9. *Thysanoessa longicaudata* divided into different stages (only mature males and females were found). Data from two off-shore stations; FB5 (sample 46) and FB4 (sample 57) where *T. longicaudata* was the only species present. N = numbers of krill analysed. Sex-ratio (number of males per female) is stated. Note different scales.