

Distributions and seasonal abundances of krill eggs and larvae in the sub-Arctic Godthåbsfjord, SW Greenland

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ABSTRACT: The larval krill community (*Thysanoessa* spp.) was investigated along the sub-Arctic Godthåbsfjord, SW Greenland, in June 2010. In addition, the progress of krill development from egg to furcilia was studied from March to August 2010 in a fjord branching off the Godthåbsfjord. Krill spawned from late April until early May, with a second spawning event in early July. Spawning took place in the warmer, innermost part of the fjord, correlated with phytoplankton blooms. Naupliar abundance peaked immediately after spawning, and naupliar stage duration was 3 d. Sequences of the calyptopis and furcilia stages lasted 22 and 63 d, respectively. The growth rate from metanauplius to calyptopis was 0.12 d⁻¹, while the growth rate across all developmental stages was 0.05 d⁻¹. Mortality rates were calculated as 25 % from eggs to nauplii, 48 % from eggs to calyptopes and 83 % from eggs to furcilia. During development, the larvae were dispersed from the shallow, warmer hatching area in the inner part of the fjord to the main fjord by tidal currents and runoff from land. The study showed that developmental stages of krill are a key group in Greenland coastal waters, one which should be considered in future studies of the pelagic food web.

KEY WORDS: *Thysanoessa* spp. · Larval development · Environmental factors

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INTRODUCTION

Krill (Euphausiacea) are a key component in western Greenland marine ecosystems (Einarsson 1945, Agersted et al. 2011). They have the same grazing potential as copepods (Tegllhus et al. 2015), thereby forming a major link between primary producers and marine vertebrate predators, including fish, birds and mammals (Mauchline & Fischer 1969, Astthorsson & Gislason 1997, Rosing-Asvid et al. 2013). It is crucial to understand the environmental drivers of krill population dynamics to predict how future changes in marine environments will affect plankton communities. Population processes have previously

been considered for adult krill (Agersted & Nielsen 2014). However, basic knowledge about reproduction and particularly development and succession of larval stages of Arctic krill is limited (Timofeyev 1993), providing inadequate background for evaluating how Arctic krill populations will be affected by expected environmental changes.

Krill pass through a number of larval stages before developing into mature adults. After the egg is fertilized and released, embryogenesis produces a free-swimming nauplius that hatches (Mauchline & Fischer 1969). In successive moults, this larva develops through a metanauplius stage, then 3 calyptopis stages and up to 14 furcilia stages. The calyptopis is

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the first feeding stage, and the larvae may begin to perform diel vertical migrations (Siegel 2000). After the last furcilia stage, the krill becomes a juvenile with most of the adult morphology and finally a sexually mature adult (Mauchline & Fischer 1969). Knowledge about the biology of krill larvae and the relationships among their spatial and seasonal distributions and experienced physical and biological parameters is essential to understanding krill population dynamics. This has been intensively investigated for the Antarctic species *Euphausia superba* (Huntley & Brinton 1991, Flores et al. 2012, Gao et al. 2013), but much less knowledge is available for the North Atlantic and sub-Arctic species (Astthorsson 1990, Astthorsson & Gislason 1997, Dalpadado et al. 2008, Agersted & Nielsen 2014).

In the Godthåbsfjord system, the krill population is dominated by *Thysanoessa raschii* but also includes species of *T. inermis*, *T. longicaudata* and *Meganyciphanes norvegica* (Agersted & Nielsen 2014). Sampling for adult krill usually ignores larvae due to the conflicting mesh size requirements and sampling techniques. Furthermore, krill larvae are rarely considered in micro- or mesozooplankton samples, leaving them mostly overlooked. Previous studies on the Godthåbsfjord zooplankton assemblages show linkages between hydrography and assemblage compo-

sitions (Calbet et al. 2011, Tang et al. 2011, Arendt et al. 2013), and a recent study by Agersted & Nielsen (2014) identified zonation of the 4 dominating krill species in relation to hydrography. Nevertheless, despite their obviously key role in this ecosystem, no investigations have been made so far on krill larvae in Greenland coastal waters.

Therefore, our aim in the present study was to investigate the spatial and seasonal successions and vital rates of the developmental stages of krill in relation to hydrography and food in the sub-Arctic Godthåbsfjord.

MATERIALS AND METHODS

Two complementary studies were carried out; one was a spatial study along the Godthåbsfjord in June, and the other considered the seasonal succession of krill larval stages from March to August in the Kapisigdlit fjord, a side branch to the Godthåbsfjord (Fig. 1).

The Godthåbsfjord is part of the largest fjord system on the western Greenland coast, receiving approximately 7.6 km³ of glacial meltwater annually (Mortensen et al. 2013). Along the 187 km main fjord branch, there is a temperature and salinity gradient

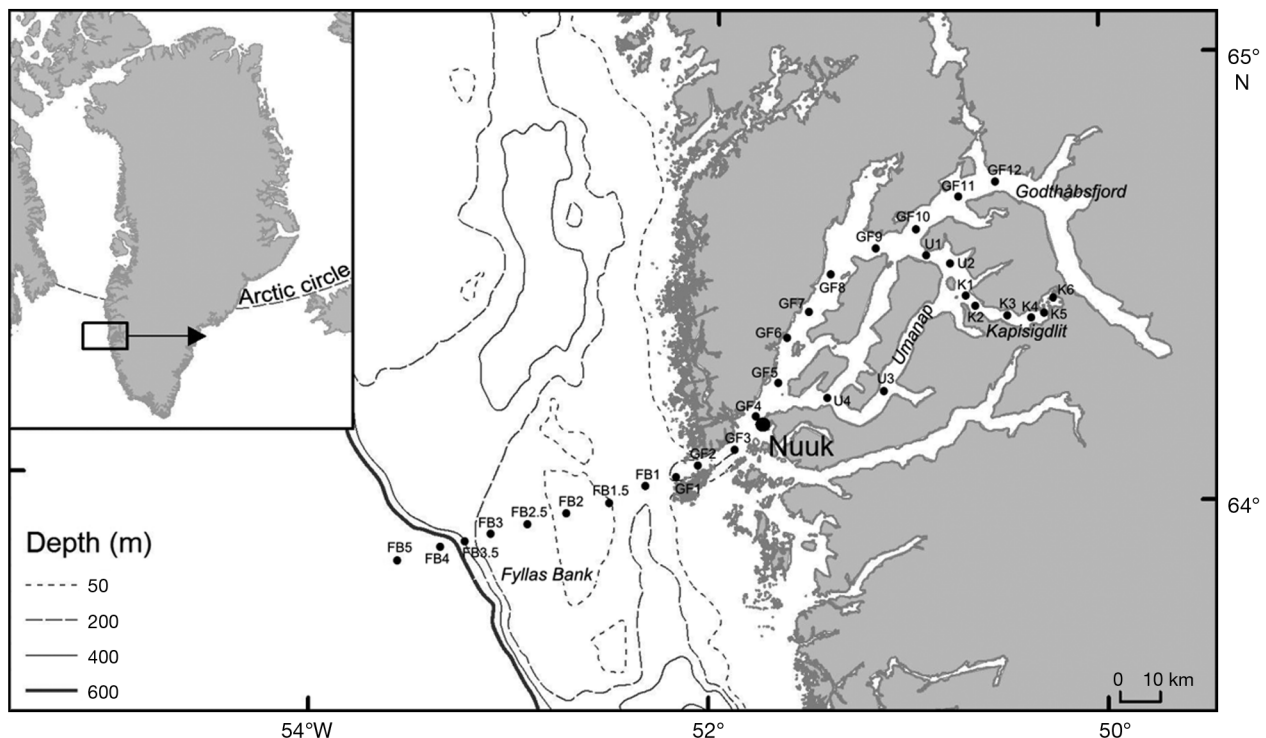


Fig. 1. Godthåbsfjord system showing the location of sampling stations within the study area. FB: Fyllas Bank; GF: Godthåbsfjord; K: Kapisigdlit; U: Umanap

from warmer water offshore to colder and fresher water at the ice edge. Within the fjord system, 4 different water masses and oceanographic regions can be defined (Mortensen et al. 2011, Tang et al. 2011): (1) the innermost part of the fjord that is most strongly influenced by ice and freshwater runoff from glaciers; (2) the deep regions of the main fjord basin, with strongly stratified water masses; (3) the main sill region at the entrance of the fjord that is influenced by strong tidal mixing; and (4) the offshore area of Fyllas Bank, where the West Greenland Current brings relatively warm and saline water of Atlantic and polar origin (Holland et al. 2008, Myers et al. 2009). Between the mouth of the fjord and the main fjord basin (Stns GF1 to GF6; Figs. 1 & 2) are 3 sills with depths between 330 and 400 m (366 ± 29 m mean depth). The main fjord basin (Stns GF8 to GF12) has an average depth of 592 ± 39 m, whereas Fyllas Bank on the continental shelf rises to 47 m. Stations on the outer part of the continental shelf (e.g. the continental slope) are >1000 m (Mortensen et al. 2011). Connected to the main fjord is a side branch, Kapisigdlit fjord, which is influenced by runoff during the summer from the Kapisigdlit River at its head (Riisgaard et al. 2014).

The Godthåbsfjord was sampled during a cruise of the RV 'Dana' (National Institute of Aquatic Resources, Denmark) from June 7 to 22, 2010. Stations were located along a 292 km transect from the offshore region of Fyllas Bank to the innermost part of Godthåbsfjord (Fig. 1). Along the fjord system, the cruise was split into 4 sections: (1) Umanap fjord branch in the southwestern part (Stns GF4, U3 and U4), (2) an eastern innermost part near the glacier in Godthåbsfjord proper (Stns GF1 to GF12), (3) an offshore region (Stns FB5 to FB1) and (4) an innermost section in Kapisigdlit fjord (Stns GF9, U1, U2 and K1 to K6, Fig. 1). The temporal study was conducted from March 24 to August 5, 2010, in Kapisigdlit fjord (Stns K1 to K6) using the vessel 'Lille Masik' on a total of 14 cruises every 7 to 10 d along a transect of 6 stations. Stn K1 was located at the mouth of the fjord branch, and Stn K6 was at the inner end (Fig. 1).

Hydrography and chl *a*

At each station, vertical profiles of water temperature, salinity and fluorescence were obtained using a CTD profiler (SBE 19plus or 911plus, SeaCat). In Kapisigdlit, water samples for chl *a* analyses were taken at Stn K4 from 8 depths (1, 10, 20, 50, 75, 100, 150 and 250 m) using a 5 l Niskin bottle. The seawater

samples for chl *a* concentration were filtered onto GF/F filters in triplicate subsamples of 100 to 500 ml. The filters were extracted for 12 to 24 h in 96% ethanol (Jespersen & Christoffersen 1987), and chl *a* concentrations were measured using a Turner TD-700 fluorometer calibrated against a chl *a* standard before and after acidification (Yentsch & Menzel 1963).

Krill sampling

In the Godthåbsfjord, krill eggs and larvae were collected using a 300 μ m mesh, 60 cm diameter Bongo net (eggs, nauplii, metanauplii and calyptopes) and a 500 μ m mesh Bongo net (furcilia). The nets were towed in oblique hauls from 110 m at 2.5 knots.

In Kapisigdlit, eggs and larvae were collected with a 300 μ m mesh, 60 cm Bongo net until July 5. Subsequently, sampling was carried out with a 600 μ m mesh Methot Isaacs-Kidd (MIK) ring net (2 m diameter, white). Oblique net tows were conducted from the surface to 35–50 m above the sea floor due to shallow depths and variable bathymetry at the 2 innermost stations, or to a maximum depth of 100 m, at 1.6 knots.

All nets were fitted with a flow meter and a CTD (MicroCat SBE 25 SM) to record flow of water into the net and haul profiles, respectively. After retrieval, eggs and larvae were preserved in buffered formalin (4% final concentration). A minimum of 400 individuals from each sample were later sorted by stages (egg, nauplius, metanauplius, calyptopis, furcilia 1 to 9) and counted; carapace length was measured to the nearest 10 μ m. Krill larval stages were identified to genus (*Thysanoessa* spp.) according to Einarsson (1945). For the seasonal study in Kapisigdlit, additional sampling was conducted with a Multinet (50 μ m mesh, Hydrobios mini) hauled vertically at 0.2 to 0.3 m s^{-1} . All Multinet samples were preserved in buffered formalin (4% final concentration) and individuals later identified to stage in the Plankton Sorting and Identification Centre, Poland. As eggs were not identified to particular taxa, a size distinction was made. Eggs between 350 and 625 μ m in diameter were considered as krill eggs following Einarsson (1945).

Gear correction factor

Oblique hauls with the Bongo and MIK nets were conducted to collect adult krill. The finer-mesh Multinet was used concurrently for younger stages and

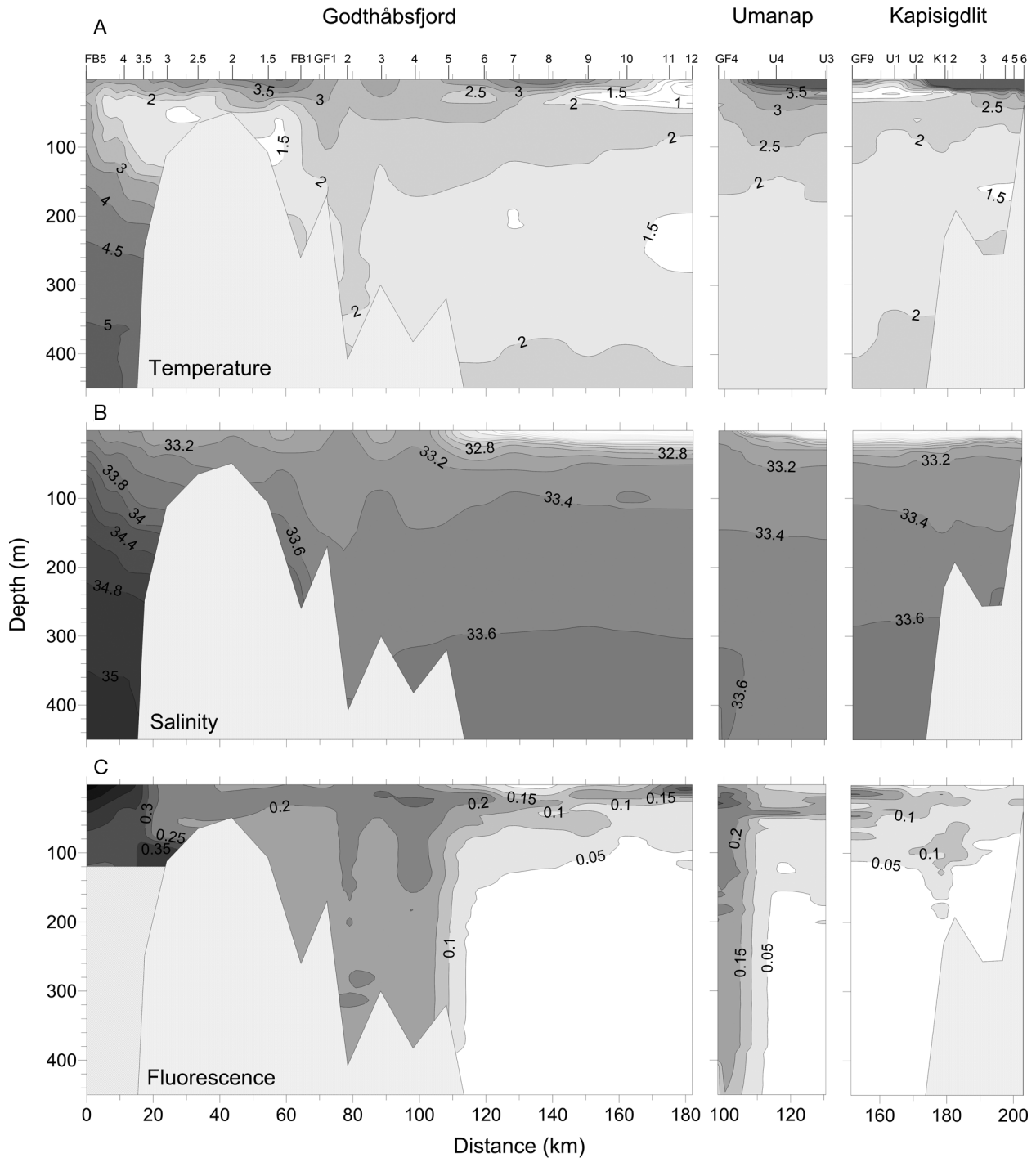


Fig. 2. Hydrography along the Godthåbsfjord, Umanap and Kapisigdlit during June 2010 (see Fig. 1 for stations). (A) Temperature (°C), (B) salinity and (C) fluorescence (arbitrary units). Stations are above and distances between stations are below the graph. Umanap was plotted in conjunction with Godthåbsfjord (Stns GF4, U3 and U4) and Godthåbsfjord and Kapisigdlit (Stns GF9, U1 and U2, K1 to K6)

eggs. During the end of the seasonal study in Kapisigdlit, a coarser-mesh MIK net was applied instead of the Bongo net. A correction factor was calculated to harmonize egg and larval abundance estimates from

the different equipment. The correction factor was calculated from a regression between (1) the abundance of a specific stage caught by each net type and (2) the abundance of the stage in consideration esti-

mated from the gear giving the highest number, assuming this to represent the true abundance (Table 1).

Cumulative development time, growth rates and mortality estimates

Stage-specific development times for krill larvae from the Kapisigdlit fjord branch were determined using the method of median development time (MDT) as described by Landry (1983). The MDT is defined as the time when 50% of the population had moulted to a specific stage. This was calculated from least-squares regressions of time versus the proportion of the population which had completed a given moult stage. The initial time was taken as the midpoint between the beginning and end of egg production (Landry 1983).

Development times were converted to rates (the reciprocal of development time) and normalized to a temperature of 5°C for comparison with other studies, based on Q_{10} as calculated from data in Pinchuk & Hopcroft (2006) using the formula:

$$Q_{10} = \left(\frac{R_2}{R_1} \right)^{10/(T_2 - T_1)} \quad (1)$$

where R_1 and R_2 = development rate (d^{-1}) at temperature T_1 and T_2 (°C), respectively.

Growth and mortality rates were calculated from the peak average egg and larvae abundances (ind. m^{-3}) in the Kapisigdlit fjord.

Daily growth rates (GR, d^{-1}) were calculated by the equation:

$$\text{GR} = \frac{1}{t_2 - t_1} \times \ln \left(\frac{W_2}{W_1} \right) \quad (2)$$

where $t_2 - t_1$ is the estimated time in days between peak abundances of a given stage and the succeed-

ing stage, and W_1 and W_2 are weights of those stages in μgC at times t_1 and t_2 , respectively. Length data for each development stage (nauplius, metanauplius, calyptopis and furcilia) were converted from total length (TL) to wet body weight (WW) and then dry body weight (DW) following the regressions from Dalpadado & Skjoldal (1996):

$$\log \text{WW} = 3.33 \log \text{TL} - 2.58 \quad (3)$$

$$\text{DW} = 0.34 \text{WW} - 1.26 \quad (4)$$

Carbon content was then calculated as 48.9% of total DW (Agersted & Nielsen 2014).

Mortality rates (M , %) were calculated by determining the percentages of the individuals surviving from the egg stock to a given stage (Lindley & Williams 1980):

$$M = 100\% - \left(\frac{N_2}{N_1} \times 100 \right) \quad (5)$$

where N_1 is maximum average egg abundance (ind. m^{-3}) and N_2 is maximum larval abundance for each successive stage (nauplius, metanauplius, calyptopis and furcilia).

RESULTS

Hydrography and fluorescence, Godthåbsfjord

During the RV 'Dana' cruise in June, temperature and salinity were high in the offshore region with a stratified water column (Fig. 2). Moving up the fjord, temperature and salinity decreased along the transect. At the mouth of the fjord, strong mixing was apparent (Stns FB1 and GF1 to GF5, Fig. 2). In the main and inner fjord basin, the upper water column was stratified, with freshwater in a thin surface layer

Table 1. Differences in catch efficiency of the 3 net types (Multinet, Bongo net and Methot Isaacs-Kidd [MIK] net) calculated for each stage. Values give the relative catch efficiency compared to the one with highest catch. Equations for regression between net types and r^2 from each regression are also presented. For metanauplii, no data were available from the Multinet. Instead, the mean correction factor from eggs and nauplii was applied, since all of these stages are similarly sized and do not swim. –: this net not used to sample the given stage

Larval stage	Length (mean \pm SD, μm)	Multinet (y)	Gear correction factor Bongo (x) MIK (x)		Equation	n	r^2
Egg	413 \pm 58	1	5	–	$y = 5.4x + 45.5$	18	0.85
Nauplius	454 \pm 84	1	213	–	$y = 213x + 2$	19	0.63
Metanauplius	474 \pm 52	1	109	–	Mean of egg and nauplius	–	–
Calyptopis	1262 \pm 540	1	20	–	$y = 20x - 11$	14	0.56
Furcilia	3624 \pm 889	1	–	2	$y = 2.2x + 3.4$	6	0.95

emanating from the inland ice sheet and Kapisigdlit River (see Fig. 2). Because of the runoff, the inner region had lower temperature ($\leq 1^\circ\text{C}$) and salinity (≤ 32.8) in the upper water column. In Kapisigdlit, surface waters showed higher temperatures (Fig. 2A). Fronts were established on either side of Fyllas Bank, in the central sector of Godthåbsfjord, at the mouth of the Kapisigdlit fjord and in southwestern Umanap.

Subsurface blooms were observed in association with the pycnocline around 20 m depth in the Godthåbsfjord and Kapisigdlit (Fig. 2C). Fluorescence was highest offshore and close to the glacier and lowest in the central parts of Godthåbsfjord and Kapisigdlit (Fig. 2C).

Seasonal hydrography and fluorescence, Kapisigdlit

In March and early April, the water column of Kapisigdlit was well mixed in the upper 100 m and was cold, saline and nutrient rich (Fig. 3). In mid-April, warming of the upper 30 m began in the inner half of the fjord, and a thermocline was established. During the end of April and beginning of May, a subsurface bloom was identified (at Stn K4), and the temperature increased from the mouth of the fjord branch toward the inner fjord. During May, meltwater from land formed a weak halocline at 20 m depth. This strengthened after the breakup of ice in the Kapisigdlit River around June 20. At Stns K4, K5 and K6, the upper water column (0 to 25 m) became stratified by June, leading to a subsurface bloom in mid-June with the highest chl *a* levels ($>10 \mu\text{g l}^{-1}$) (dark areas, Fig. 3). This stratification was most likely caused by the release of freshwater from the river. The inner part of the fjord (Stn K6) experiences higher surface temperatures earlier than stations farther out (Stns K4 and K5). Chl *a* levels seemed generally stable in March to April and again in June to August.

Abundance, spatial distribution and composition of krill larvae in Godthåbsfjord

Total abundance (mean \pm SD) of eggs, nauplii, metanauplii, calyptopes and furcilia 1 to 4 averaged $470 \pm 700 \text{ ind. m}^{-3}$, with the highest abundance of 3224 ind. m^{-3} in the central part of the fjord (Stn GF8) (Table 2, Fig. 4). On the continental slope and shelf (Stns FB2 to FB5) and in the outer sill region (Stns GF1 and GF2), abundance was lower (Table 2,

Fig. 4). Low abundances were also found in Kapisigdlit (Stns K1 to K5) and Umanap (Stn U4) (Table 2).

Egg abundances were highest at Stns GF5 to GF8 and peaked at Stn GF8 with a maximum abundance of 244 eggs m^{-3} . In Kapisigdlit and Umanap, egg abundance was highest at the entrance, with 29 and 33 eggs m^{-3} at Stns K1 and U2, respectively.

Nauplii and metanauplii were dispersed throughout the fjord (Fig. 4). However, the average relative contribution ($\% \pm \text{SD}$) of nauplii was lower than that of metanauplii (21 ± 14 and $33 \pm 16\%$, respectively). Highest abundances of nauplii and metanauplii were found at Stn GF8, with $1332 \text{ nauplii m}^{-3}$ and $1084 \text{ metanauplii m}^{-3}$ (Table 2).

The relative contribution of calyptopes to the total larvae abundance was generally high throughout the fjord (average of $45 \pm 24\%$), with the highest number of $583 \text{ calyptopis larvae m}^{-3}$ at Stn GF8. In Umanap and Kapisigdlit, abundance of calyptopes peaked in the central regions, with 206 and 210 ind. m^{-3} (at Stns U2 and U3, respectively) and 248 and 258 ind. m^{-3} (at Stns K3 and K4, respectively) (Table 2).

Abundances of furcilia were generally low throughout the fjord. Furcilia stages were mostly found in the offshore region (Stns FB5 and FB3). But higher abundances of furcilia were also found at the mouth of the Kapisigdlit (Stn K2) and Umanap (Stn U2), with 7 and $2 \text{ furcilia m}^{-3}$, respectively (Table 2). Furcilia 1 and 2 (FI and FII) stages dominated. Later stages (FIII and FIV) were only observed at Stns FB3.5 and FB5, K1 to K2 and U1 to U2. Furcilia abundance was lowest over the outer sill and in the main fjord basin (Stns GF2 to GF8), with 0.02 to 1.3 ind. m^{-3} , with the highest abundance at Stn GF8.

Seasonal distribution and succession of eggs and larvae in Kapisigdlit

The seasonal succession of krill egg and larval stages was observed from March to August 2010. Krill initiated spawning between April 3 and 22 (Fig. 5A), when the average temperature in the upper 30 m was between 0.8 and 2.1°C . Egg abundance peaked in late April (380 eggs m^{-3} on April 30) to early May (1130 eggs m^{-3} on May 10) in the inner creek (Fig. 5A). Egg abundance was lower in the outer region of the fjord than close to the tributary creek (Fig. 5A). Egg abundance was low during late May and June, but concentration peaked again with 426 eggs m^{-3} estimated at the beginning of July (Stn K5, Fig. 5A). The majority of eggs were restricted

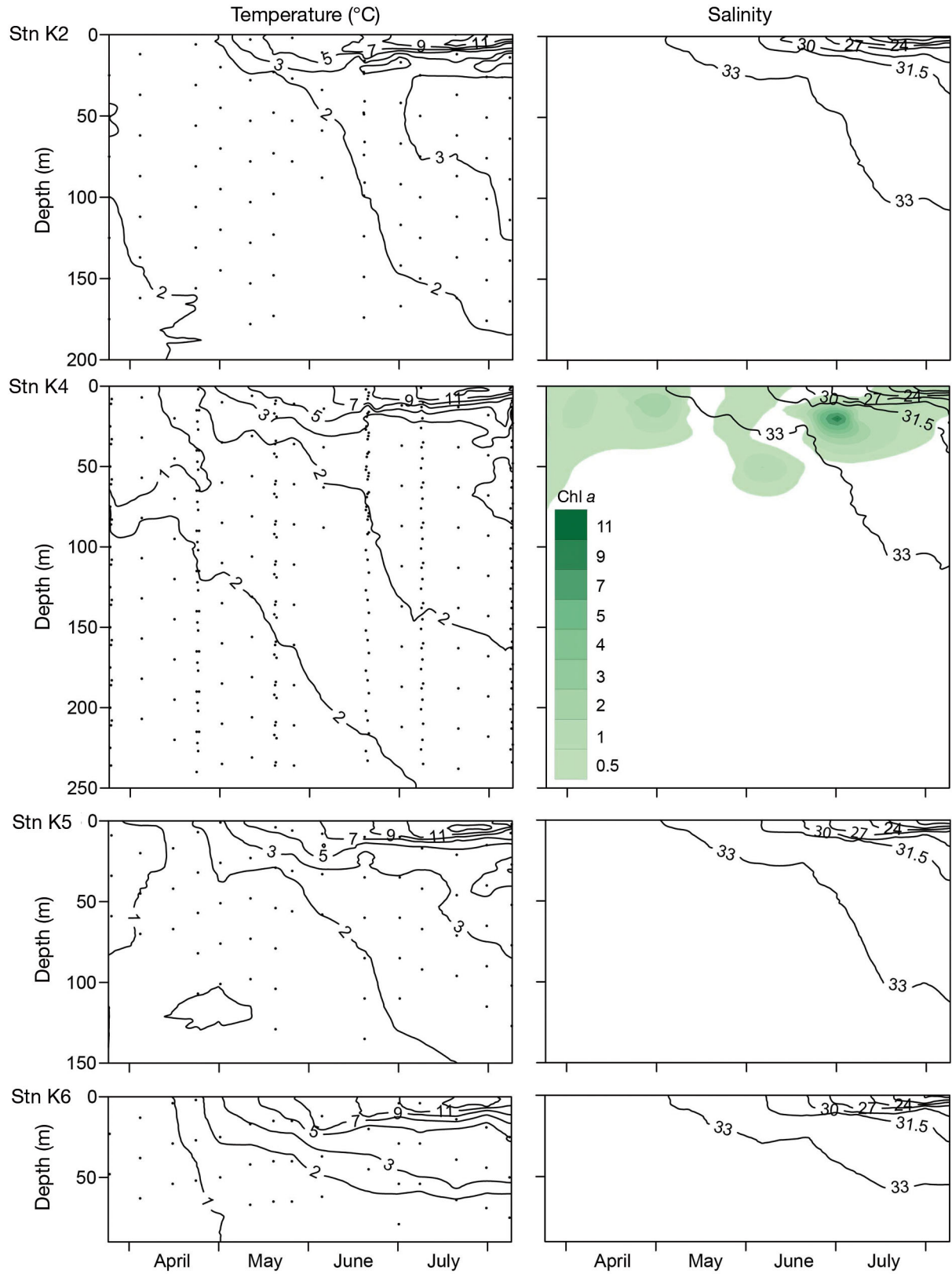


Fig. 3. Temporal variation of temperature and salinity of stations along the Kapisigdlit fjord between March 24 and August 5, 2010. Seasonal development in chl *a* ($\mu\text{g l}^{-1}$) only available for Stn K4 (right panel). Note different scales on y-axis

Table 2. Abundance data of adult krill (*Thysanoessa raschii*, *T. inermis*, *T. longicaudata* and *Meganyctiphanes norvegica*, all combined) and different life stages (egg, nauplius [N], metanauplius [MN], calyptopis [C] and furcilia 1 to 4 [FI to FIV]) of *Thysanoessa* spp. along the transect in the Godthåbsfjord. –: no data

Stn	Date (2010)	Depth (m)	Adults ^a (ind. m ⁻³)	Total	Euphausiid larvae								
					Abundance (ind. m ⁻³)								
					Egg	N	MN	C	FI	FII	FIII	FIV	Furcilia total
FB5	Jun 7	0–110	0.03	229	6	–	–	202	10	10	0.5	–	21
FB4	Jun 7	0–110	0.01	37	3	18	2	13	1	1	–	–	2
FB3.5	Jun 9	0–125	0.002 ± 0.001 ^b	276	5	90	111	64	4	1	0.5	0.5	6
FB3	Jun 10	0–80	0.002	15	–	–	–	–	8	7	–	–	15
FB2.5	Jun 10	0–60	0.004	188	0	49	86	53	0.2	0.1	–	–	0.3
FB2	Jun 10	0–40	0.0005 ± 0.0004 ^b	138	1	34	17	83	3	1	–	–	4
FB1.5	Jun 10	0–95	–	889	10	142	145	591	1	0.5	–	–	1.5
FB1	Jun 10	0–110	0.04	366	3	158	168	34	2	2	–	–	4
GF1	Jun 12	0–110	0.01	139	1	7	22	106	1	1	–	–	2
GF2	Jun 13	0–110	0.27	238	0	28	91	118	0.2	0.1	–	–	0.3
GF4	Jun 14	0–110	0.001	333	8	63	158	104	0.1	0.1	–	–	0.2
GF5	Jun 15	0–110	0.32	1140	46	411	444	239	0.1	0.04	–	–	0.14
GF6	Jun 15	0–110	0.09	1340	19	359	676	286	0.01	0.01	–	–	0.02
GF8	Jun 15	0–110	1.02	3224	224	1332	1084	583	1	0.3	–	–	1.3
GF10	Jun 16	0–110	2.25 ± 0.8 ^b	61	9	3	19	31	–	–	–	–	0
K1	Jun 17	0–110	2.42	85	29	10	24	20	2	1	1	0.1	3.1
K2	Jun 17	0–110	1.13	7	–	–	–	–	4	3	0.3	0.2	7.5
K3	Jun 17	0–110	–	480	2	55	174	248	0.3	0.1	0.03	–	0.43
K4	Jun 17	0–110	0.7 ± 0.2 ^b	299	–	–	36	258	3	2	–	–	5
K5	Jun 17	0–110	0.02	30	–	–	4	24	0.4	1	0.1	–	1.5
U2	Jun 16	0–110	1.20	588	33	30	318	206	1	1	0.1	–	2.1
U3	Jun 22	0–110	1.49	615	1	52	351	210	1	0.2	0.2	0.1	2.5
U4	Jun 22	0–110	0.03	93	1	11	29	52	0.2	0.1	–	–	0.3

^aFrom Agersted & Nielsen (2014); ^bAverage of day/dawn/dusk (mean ± SD)

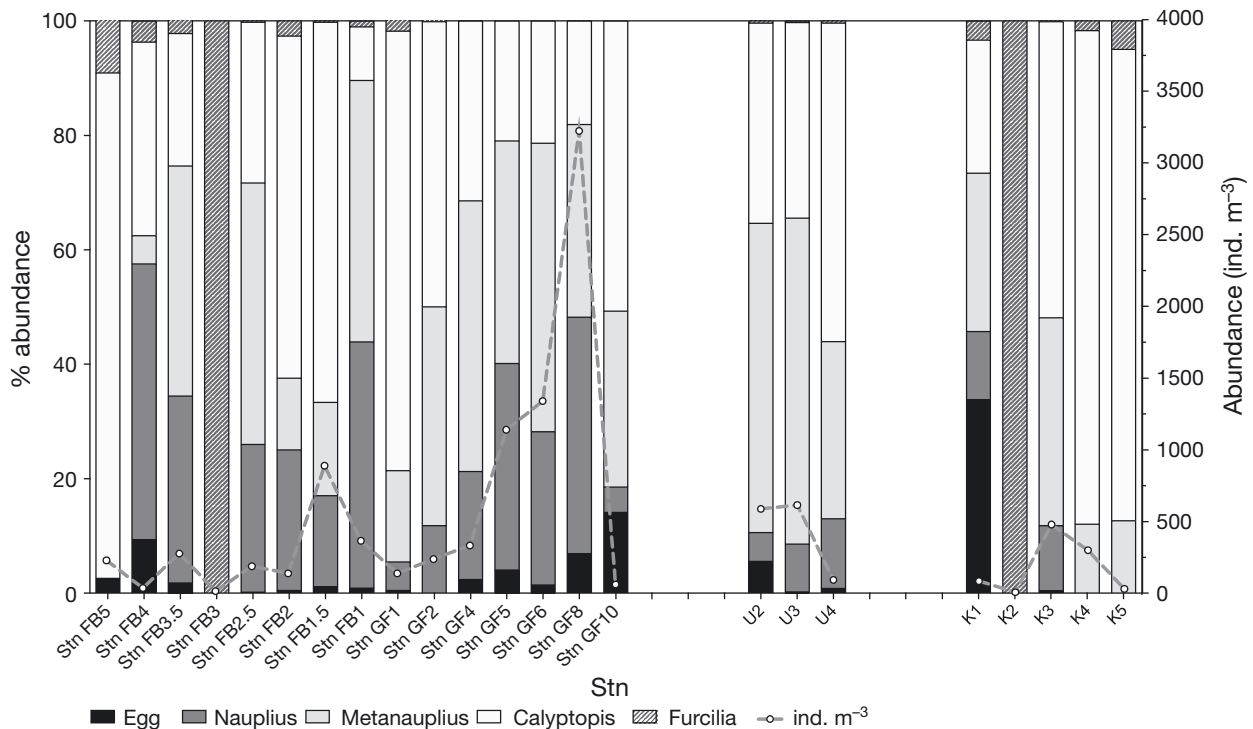


Fig. 4. Total larval abundances and relative contribution of the different life stages of krill throughout the Godthåbsfjord system, June 2010

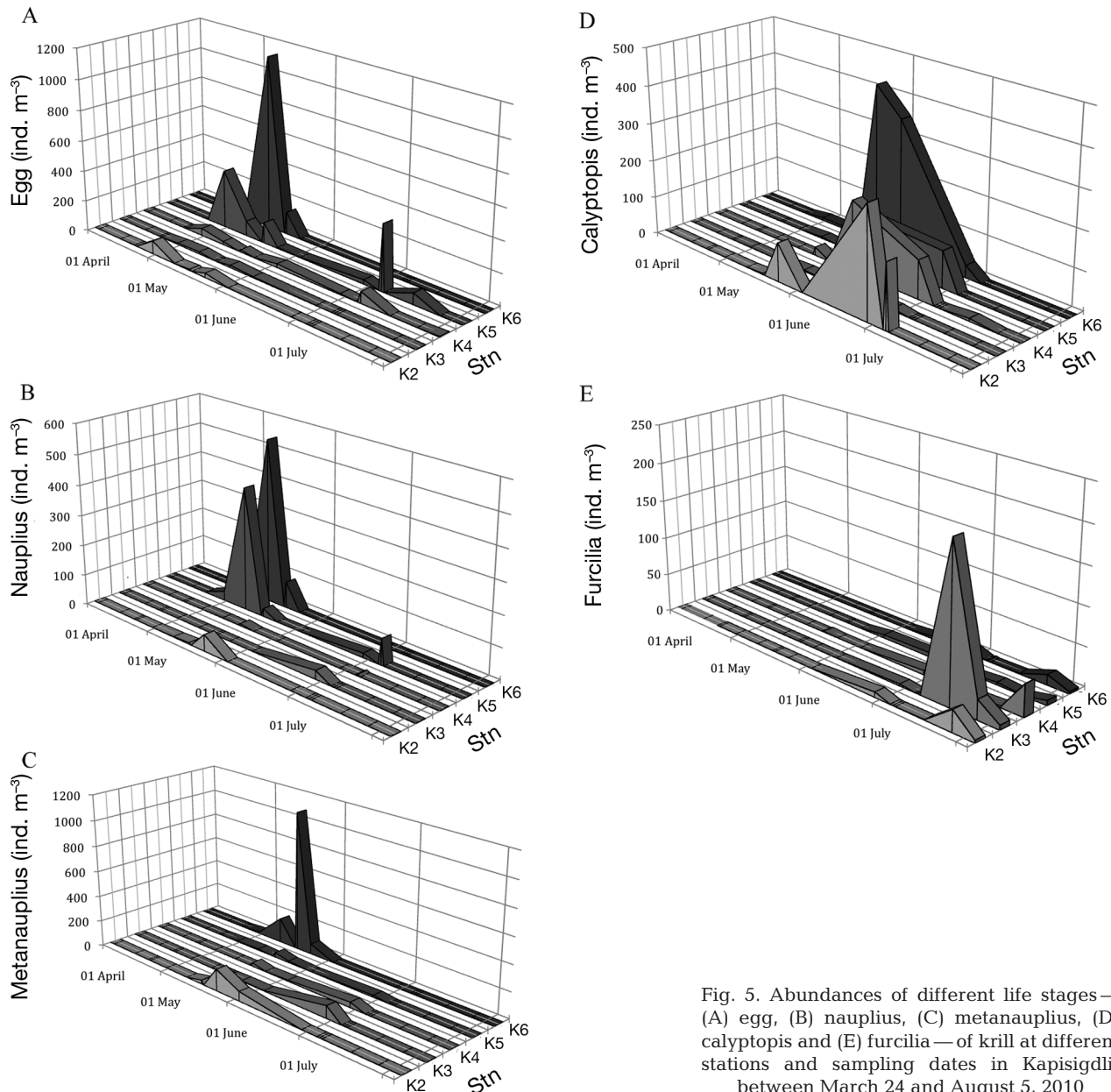


Fig. 5. Abundances of different life stages — (A) egg, (B) nauplius, (C) metanauplius, (D) calyptopis and (E) furcilia — of krill at different stations and sampling dates in Kapisigdlit between March 24 and August 5, 2010

to the upper 50 m during the main spawning period (Fig. 6A).

Nauplii first appeared in samples on April 22, approximately 19 d after first observation of eggs. The number of nauplii was lower at the mouth of the fjord than in the inner part, where it peaked around May 10 (540 ind. m⁻³, Stn K6) or May 17 (407 ind. m⁻³, Stn K5) (Fig. 5B). As for eggs, nauplii were primarily caught in the upper water column during their main abundance peak (Fig. 6B).

Metanauplii were first recorded on April 30 (Stns K5 and K6), and their abundance peaked on May 18 (1085 ind. m⁻³) at Stn K6 (Fig. 5C). Calyptopis stages

were first found on April 30. Their abundance peaked on May 24 (423 ind. m⁻³) in the inner region of the fjord branch (Stn K6), on June 3 (188 ind. m⁻³) at Stn K4 and on June 29 (294 ind. m⁻³) at Stn K2 (Fig. 5D).

Calyptopes were concentrated in the upper 50 m of the water column (93%) (Fig. 6C). Calyptopes appeared in succession after the egg, nauplius and metanauplius peaks, but they were generally more evenly distributed throughout the fjord branch (Fig. 5D). Furcilia were present from early June and peaked in abundance on July 18 (206 ind. m⁻³) at Stn K3, on July 28 (28 ind. m⁻³) at Stn K2 and on

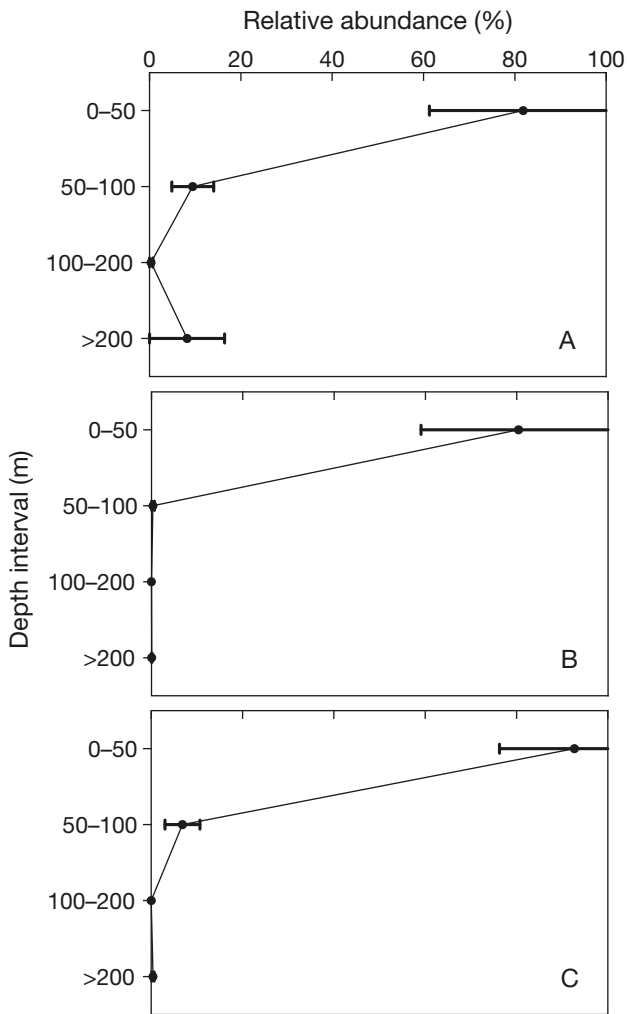


Fig. 6. Depth distributions of (A) eggs, (B) nauplii and (C) calyptopes caught with the Multinet (% of total abundance \pm SE) during periods with maximum abundance ($n = 4$ d) (see Fig. 5). Distribution is presented at 4 depth intervals: 0 to 50, 50 to 100, 100 to 200 and >200 m

August 5 (42 ind. m^{-3}) at Stn K4 (Fig. 5E). This was approximately 3 mo after the very first krill eggs were observed and 60 to 65 d after the peak abundance of krill eggs.

The average abundance ($\text{ind. m}^{-3} \pm \text{SE}$) sequence of larval stages followed the progression of ontogenetic development at all stations in Kapisigdlit (Fig. 7). Immediately after spawning (Fig. 7A), there was an increase in nauplii and metanauplii (190 and 287 ind. m^{-3} , respectively) (Fig. 7B,C), followed by

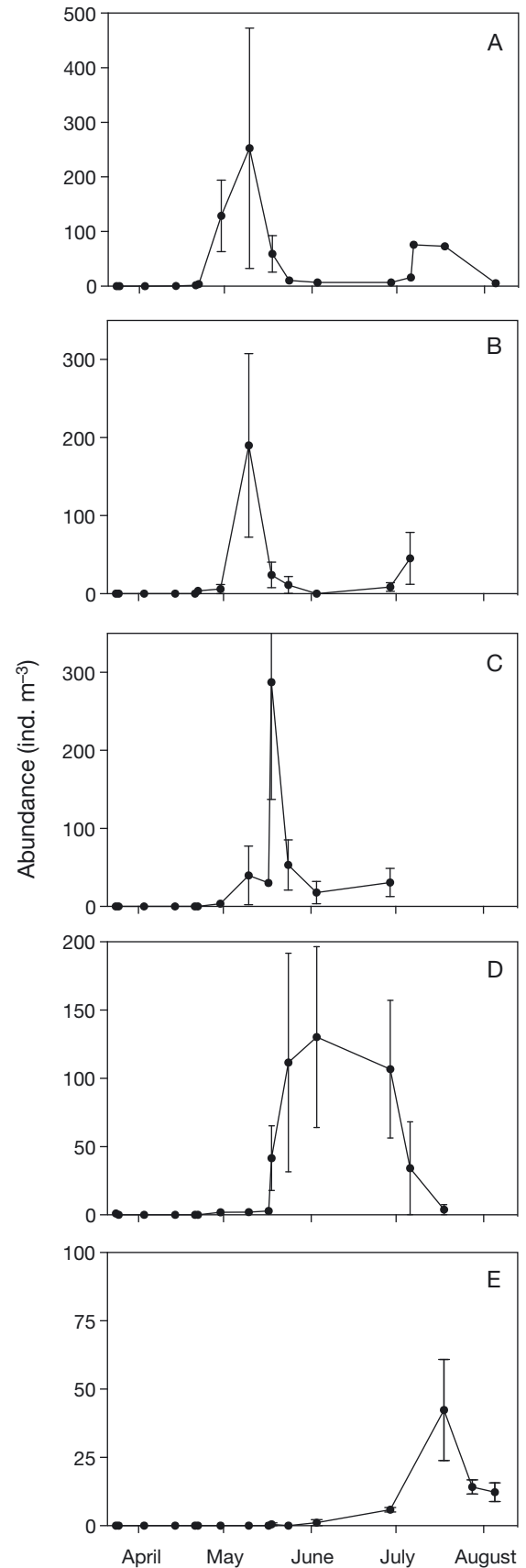


Fig. 7. Seasonal abundances of eggs and larvae of krill, mean of all stations \pm SE) in Kapisigdlit from March 24 to August 5, 2010. (A) Eggs, (B) nauplii, (C) metanauplii, (D) calyptopes and (E) furcilia. Note different scales on y-axes

Table 3. Cumulative development times (d) for different life stages of krill larvae, standardized to 5°C with a Q_{10} of 2.04 calculated from data by Pinchuk & Hopcroft (2006) (see 'Materials and methods'). The original experimental temperatures are presented in parentheses for each study

Stage	<i>Thysanoessa</i> spp.			<i>Thysanoessa inermis</i>			<i>Euphausia superba</i>	
	This study (5–8°C)	Buchholz et al. (2012) (4°C)	Pogodin (1980) (7–8°C)	Lindley & Williams (1980) (6–10°C)	Pinchuk & Hopcroft (2006) (5°C)	Pinchuk & Hopcroft (2006) (12°C)	Ikeda (1984) (0°C)	McWhinnie & Denys (1978) (1.5°C)
Egg	0	0	0	0	0	0	0	0
Nauplius	3	4.5		11	2	6	6–9	3
Metanauplius	16				6	14	14	8–14
Calyptopis	22		15–16	30–41	10	29	21–37	
Furcilia	63				33	44	44–89	

Table 4. Growth and biometrical parameters of krill larvae at different development periods. Length (mean \pm SD), carbon weight and daily growth rates. Daily rations in % body carbon d^{-1} . –: no data

Date (2010)	Stage	n	Length (mm)	Weight (μ g C)	Growth rate (d^{-1})	Daily ration (% d^{-1})
May 10	Nauplius	127	0.46 \pm 0.03	3.5	–	–
May 18	Metanauplius	150	0.50 \pm 0.01	4.0	0.017	5.2
Jun 3	Calyptopis	221	1.68 \pm 0.5	25.7	0.117	37.2
Jul 18	Furcilia	269	4.90 \pm 1.2	123.0	0.035	10.6
Full period	–	–	–	–	0.052	15.9

increases in calyptopis and furcilia abundance later in the season (130 and 42 ind. m^{-3} , respectively) (Fig. 7D,E). Eggs developed into nauplii within 3 d, and those developed into metanauplii within 16 d from spawning. After 22 d, the larvae had developed to the calyptopis stage and after 63 d to the furcilia stage (see 'Materials and methods', Table 3).

Larval growth rates were highest from metanauplius to calyptopis (0.12 d^{-1} , or 37 % body carbon d^{-1}), while the overall daily growth rate for the whole period across all developmental stages was 0.052 d^{-1} , or 16 % body carbon d^{-1} (Table 4). Mortality rates calculated from the maximum average egg and larval abundances (ind. m^{-3}) were calculated as 25 % for egg to nauplius, 48 % by the calyptopis stage and 83 % from egg to furcilia.

DISCUSSION

Our data show that development stages of krill are a key plankton community component in Greenland coastal waters. In general, crustacean nauplii are the most numerous metazoan group in the seas (Bjørnberg 1984) and the most important first prey for the majority of fish larvae (Pedersen & Fossheim 2008).

However, knowledge about the ecology of nauplii is limited (Kjørboe & Sabatini 1995, Turner 2004, Jung-Madsen et al. 2013), particularly for the ecology of Arctic krill nauplii (Drobysheva 1987, Dalpadado & Skjoldal 1991). Here, we provide a first description of the spatial and seasonal distribution of krill larvae in SW Greenland.

Spawning, maturity and seasonal distribution of larvae

A clear succession from egg to calyptopis was documented in Kapisigdlit fjord. Krill eggs increased in abundance during late April and early May, following initiation of spawning. Spawning by species of *Thysanoessa* has previously been observed in April and May in Iceland (Astthorsson 1990, Gislason & Astthorsson 1995), the Barents Sea (Dalpadado & Skjoldal 1991), the North Sea (Lindley & Williams 1980) and the St. Lawrence estuary (Plourde et al. 2010). During April to May, surface water temperature increased from 1°C to approximately 5°C in the inner part of the fjord, and a phytoplankton bloom was apparent (Stn K4).

In the Godthåbsfjord system, the population of krill consists of *Thysanoessa raschii*, *T. inermis*, *T. longicauda* and *Meganyctiphanes norvegica* (Agersted & Nielsen 2014). However, the absence of smaller individuals and non-fertilized females of *M. norvegica* suggests that this species does not reproduce in the fjord but is advected from outside the fjord (Agersted & Nielsen 2014). Astthorsson (1990) and Falk-Petersen & Hopkins (1981) suggest a similar influx of *M. norvegica* to the Isafjord-deep and Balsfjorden,

respectively. The spawning in Kapisigdlit is therefore assumed to be that of *Thysanoessa* spp. Several authors have suggested that spawning of *Thysanoessa* spp. coincides with the onset of the phytoplankton spring bloom (Einarsson 1945, Berkes 1976, Lindley & Williams 1980, Falk-Petersen & Hopkins 1981, Astthorsson 1990, Gislason & Astthorsson 1995, Dalpadado 2006, Plourde et al. 2010), which is further supported by the present results.

During the study period, there was a second peak in egg abundance at the beginning of July, indicating a second spawning event, as described by MacDonald (1928) for *T. raschii* in the Firth of Clyde. The second spawning period observed in the present study correlates with the subsurface phytoplankton bloom, with a maximum chl *a* level of $>10 \mu\text{g chl } a \text{ l}^{-1}$ at Stn K4. It is possible that the second spawning event observed here can be attributed to *T. raschii*. Studies have documented later spawning in *T. raschii* compared to *T. inermis* in the Gulf of St. Lawrence and the Balsfjorden (Berkes 1976, Falk-Petersen & Hopkins 1981, Plourde et al. 2010), and Drobysheva (1987) showed a prolonged spawning season for *T. raschii* in the Barents Sea, which could lead to less interspecific competition. Agersted & Nielsen (2014) found that females of *T. raschii* were fertilized, that is they carried spermatophores, during the study period in June 2010, whereas *T. inermis* females with spermatophores were much less abundant. The 2 time-separated peaks in egg abundance could therefore be related to spawning by *T. inermis* and *T. raschii*, respectively. However, in the future, species molecular identification of eggs will be necessary to support this hypothesis.

Egg and nauplius abundances were highest in the shallow, warmer inner fjord (Stns K5 and K6), despite the outward-moving flow of the subsurface layer (Mortensen et al. 2011). Similarly, Einarsson (1945) and Astthorsson (1990) reported spawning of *T. raschii* in the inner parts of Seydisfjord, Reydarfjord and Isafjord-deep on Iceland. The inner parts of fjords have weaker mixing and greater inputs of nutrient-rich runoff, resulting in stratification and favourable growth conditions for phytoplankton (Astthorsson 1990, Mortensen et al. 2011). Chlorophyll data were only available from Stn K4. However, Kjellerup et al. (unpubl.) found the highest chl *a* concentrations during April 2010 at the inner station (Stn K6, $3.5 \mu\text{g chl } a \text{ l}^{-1}$), possibly explaining why spawning primarily took place there.

Spawning occurred in the surface layers where food concentrations were highest. Multinet samples showed eggs to be concentrated in the upper 50 m, as previously described for *Thysanoessa* spp. in Scottish

waters by Mauchline & Fisher (1969). Development times showed cumulative development from egg to nauplius within 3 d and to metanauplius within 16 d. Temperature is known to have a positive effect, with a higher temperature resulting in faster development (Ikeda 1984, Ross et al. 1988, Pinchuk & Hopcroft 2006). The present results are comparable to earlier findings on development times for *Thysanoessa* spp. (Buchholz et al. 2012) and *Euphausia superba* (McWhinnie & Denys 1978, Ikeda 1984) and are supported by findings suggesting development time of *T. raschii* egg to nauplius within 3 d at 3°C (M. D. Agersted unpubl. data). It should be emphasized, however, that the development times presented in Table 3 originate from different experimental procedures and conditions, e.g. *in situ* data are affected by fluctuations in temperature, compared to controlled laboratory experiments. Furthermore, a recent study by Bi et al. (2011) suggests that stage-specific development times for stage-structured marine organisms can be biased when the methodologies used only consider information on survivors.

Calyptopis larvae were dispersed more evenly along Kapisigdlit fjord than the younger stages (Fig. 5D). Kapisigdlit has a classical estuarine circulation, driven by freshwater input from land. As the main sources of freshwater are located in the inner parts of the fjord, the mean water advection out of the fjord is in the surface layer, while an inflow of water is present in the layers below (Swailethorp et al. 2014). The early development from egg to first calyptopis (CI) depends exclusively on internal energy reserves, after which feeding becomes critical. The CI stage only can survive for a maximum of 1 to 2 wk without food (Ikeda 1984, Siegel 2000, Gao et al. 2013). As a result, calyptopis stages are expected to ascend toward the surface, where food concentration is higher (Gao et al. 2013). Tidal advection and currents, therefore, most likely drive dispersal of calyptopis larvae from the inner region out into the fjord. Development time from egg to calyptopis was 22 d, which subsequently meant that calyptopes started to ascend toward the surface in early and mid-June (Table 3). This supports the theory of advection-driven dispersal, since during the season in which calyptopes increased, there was strong advection out of the fjord from a sudden freshwater outflow caused by the breakup of the ice in the Kapisigdlit River. That would have carried these later-stage larvae out into the fjord.

Modelling of krill movement in the Scotia Sea has suggested that krill can be dispersed by advection (Murphy et al. 2004), and a recent study on cod lar-

vae (*Gadus morhua*) in Kapisigdlit illustrates similar patterns in their distribution (Swailethorp et al. 2014). Any changes in tidal advection and timing or magnitude of freshwater input must therefore be considered likely to influence larval distributions and transport through the fjord system. Furthermore, since the duration of the non-feeding stages from hatching to moulting into CI is temperature dependent (Pinchuk & Hopcroft 2006), future climate changes could result in shorter durations of early non-feeding stages. Development time of *Thysanoessa* spp., derived from the succession observed in the fjord of larval stages from egg to furcilia, was comparable to that of the Antarctic *E. superba* (Table 3).

Growth rates and mortality of krill development stages

The overall larval growth rate for the complete development period was 0.05 d^{-1} . The highest growth rate found was during the development of calyptopes (0.12 d^{-1}), corresponding to a daily ration of 37% body carbon d^{-1} (Table 4). Smith (1991) found growth rates for *T. inermis* larvae in the Bering Sea during late April to May (0.045 to 0.06 d^{-1}) and June (0.01 to 0.013 d^{-1}) and noticed that growth rates of calyptopis stages were higher (maximum of 0.15 d^{-1}) than those of nauplii, which also seems to be the case in this study (Table 4). In Pakhomov et al. (2004), daily growth rates of *E. superba* furcilia were up to 5.7% of body carbon, being half of those found in the present study (Table 4). Growth rates are generally controlled by food availability (Pinchuk & Hopcroft 2007), which could explain the difference in growth rates of furcilia in this study from those estimated by Pakhomov et al. (2004), where food concentration was lower. However, both a difference in temperature and the fact that Pakhomov et al. (2004) worked in a different region on a different species could also affect this.

Mortality from eggs to larvae was generally low, with 25% mortality from egg to nauplius, 48% from egg to calyptopis and 83% from egg to furcilia. Mortality of *Thysanoessa* spp. has typically been greater than that observed here, with estimates of 98% for the 0+ age group in the Barents Sea (Drobysheva 1987), 93 to 97% from egg to furcilia in the North Sea in Lindley & Williams (1980), 97% in Lindley (1980) and 98% in Lindley (1978). It is possible that a relatively good larval survival could be a result from living in a fjord (with relatively few predators and competitors) compared to open seas. This is impor-

tant information, since the mortality rate affects the recruitment and later population size (Siegel 2000). The estimated mortalities are based on the assumption that the fjord is a closed system; obviously, advective processes contribute to the calculated mortality rates.

Spatial distribution of krill larvae in the Godthåbsfjord system

In Godthåbsfjord, all developmental stages were found throughout the fjord's length. The cruise represents only a snapshot in time. However, together with the seasonal data, new knowledge of the krill larval community in this region is provided.

During June, calyptopis larvae had developed to maximum numbers in Kapisigdlit, which corresponds to the equally high relative abundance of calyptopes observed throughout the Godthåbsfjord. This is further supported by the cumulative development times calculated from larval abundance estimates in Kapisigdlit, which indicate that krill development had reached the calyptopis stages by the time of the Godthåbsfjord transect. Furthermore, the high egg abundance observed in the central and inner regions of the Godthåbsfjord (Stns GF5 to GF8) can most likely be related to the second spawning event observed in Kapisigdlit. The peak in egg abundance at Stn GF8 may be from spawning by the dominating *T. raschii* (Table 1 in Agersted & Nielsen 2014). This supports the hypothesis that either *T. raschii* have prolonged spawning or spawn later than *T. inermis* (Berkes 1976, Falk-Petersen & Hopkins 1981, Drobysheva 1987, Plourde et al. 2010). Offshore abundance of older stages (furcilia larvae) was higher than in the fjord. As suggested by Agersted & Nielsen (2014), eggs and larvae found offshore are most likely *T. longicaudata*. Even though Agersted & Nielsen (2014) did not identify larvae to species during their study, they found fertilized females of *T. longicaudata*, which suggests that spawning had occurred. Nevertheless, *T. longicaudata* have been observed spawning at 9 to 10°C (Williams & Lindley 1982), which is 7 to 8°C higher than temperatures in the offshore region during the time of our sampling. As the West Greenland Current impacts the offshore region of Fyllas Bank (Buch 1990), it is perhaps more likely that the northward-flowing current transported *T. longicaudata* eggs and larvae to the offshore region, as also suggested in Agersted & Nielsen (2014). From this, it seems likely that the main spawners in the fjord at this time of year are the

dominating *T. raschii*, whereas the *T. longicaudata* seem to be the spawners offshore.

Knowledge and understanding of the reproductive cycle and the factors controlling recruitment are essential in population ecology. However, despite their importance, no previous studies have investigated them for the krill populations in Greenland waters. Here, we document a clear succession from egg to furcilia, with 2 distinct spawning events in the innermost parts of the fjord correlated with the major phytoplankton blooms. Tidal advection and freshwater input determine the distribution of larvae, advecting older stages away from spawning sites like the innermost part of Kapisigdlit. Future changes in timing and magnitude of phytoplankton blooms and meltwater runoff will influence the distribution and growth conditions of krill larvae but also determine the spawning season and recruitment success of the population. Climate-mediated changes in the spatial and seasonal patterns of krill reproduction and larval development will have substantial implications for higher trophic levels in Greenland waters, including the coastal fjords.

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