# Mesozooplankton dynamics in relation to food availability during spring and early summer in a high latitude glaciated fjord (Kongsfjorden), with focus on *Calanus*

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## ARTICLE INFO

## ABSTRACT

The timing of zooplankton reproduction in relation to spring pelagic bloom is essential in determining grazers' recruitment success and the transport of biomass through the system. At high latitudes marine ecosystems are characterized by extreme seasonality with the production of autotrophes concentrated during the spring. In two consecutive years we studied mesozooplankton during spring and early summer in Kongsfjorden, Svalbard (79°N), aiming at identifying the main grazers and understanding what affects the timing in zooplankton. The main grazers were females and nauplii of holoplanktonic *Calanus*, together with meroplanktonic Cirripedia nauplii and Polychaeta larvae. The appearing of offspring and larvae showed a correlation with the spring bloom which occurred earlier in 2004 compared to 2003. The Arctic *Calanus glacialis* reproduced before its Atlantic counterpart *Calanus finmarchicus* and prior to the bloom. In the Arctic regions decreasing sea ice cover as a result of climate change is expected to alter the timing of the spring bloom which in turn will pose a need for the zooplankton to adjust their reproduction activities. Subsequently, this adjustment will influence ecosystem functioning mainly by modifying particulate organic matter and energy fluxes.

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## 1. Introduction

Zooplankton constitute the link between autotrophic pelagic producers and heterotrophic pelagic and benthic consumers in aquatic systems. They play a crucial role in the effective functioning of food webs, and have a considerable impact on the biological carbon pump (Conover, 1966; Miller, 2004; Reid et al., 2009; Richardson, 2008). The role and impact of metazoan zooplankton are determined by their composition and abundance, which depend on timing of reproduction and recruitment of species, which is strongly related to the availability of autotrophic and heterotrophic protistan food, particularly in the Arctic (Hirche, 1997; Kosobokova and Hirche, 2001; Madsen et al., 2001; Nielsen et al., 2007; Søreide et al., 2010). Arctic ecosystems are characterized by extreme seasonality, which is determined by large annual change in solar radiation, and associated pronounced variability in the water temperature and sea ice cover that limit and control primary production rates and duration (Hegseth, 1998; Leu et al., 2011; Sakshaug et al., 2009). Thus, the population dynamics of zooplankton, in relation to the

short annual pulse of food, is of great importance in such high-latitude areas, particularly for herbivorous species (Madsen et al., 2001; Niehoff et al., 2002; Nielsen and Hansen, 1995; Pesant et al., 2000; Wassmann et al., 1991). The timing of seasonal vertical migration and reproduction will determine which organisms will profit from the spring bloom, and hence will regulate the transfer of biomass (and energy) produced during this period (Durant et al., 2007; Fortier et al., 1995; Levinsen et al., 2000; Platt et al., 2003). However, studies of spring zooplankton community development in high Arctic regions, with appropriate temporal resolution, remain scarce due to logistic difficulties in acquiring adequate data sets (Carmack and Wassmann, 2006).

Of all the mesozooplankton, three calanoid copepods *Calanus finmarchicus*, *Calanus glacialis*, and *Calanus hyperboreus* are considered the key species that link primary producers to the higher trophic levels in Arctic pelagic ecosystems (Falk-Petersen et al., 2002; Hop et al., 2006; Scott et al., 2002). Studies suggest that these species in their typical domains (*C. finmarchicus* in the Atlantic domain, *C. glacialis* in Arctic shelf seas and *C. hyperboreus* in the deep parts of Arctic seas and the Arctic Ocean), individually or collectively, make up 70–90% of the mesozooplankton biomass (Ashjian et al., 2003; Hopcroft et al., 2005; Mumm et al., 1998; Richter, 1994; Wassmann et al., 2006). *Calanus* species differ in duration of their life cycles, and a 1-year cycle in *C. finmarchicus* (Tande, 1982), 1- or 2-year cycle in *C. glacialis* (Scott et al., 2000; Tande et al., 1985), and 2 up to 6 year life cycle in

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*C. hyperboreus* (Falk-Petersen et al., 2009; Hirche, 1997; Madsen et al., 2001) are typically observed in these species in Arctic ecosystems. The species show a seasonal ontogenetic vertical migration, with an ascent towards the surface during spring, which may be associated with the ice break up (Madsen et al., 2001) or may take place prior to the spring bloom (Hirche et al., 2001). Egg production, hatching success as well as growth and survival of early developmental stages are related with the available food quantity and quality (Arendt et al., 2005; Dale et al., 2001; Jonasdottir et al., 2002). However, the largest of the three species, *C. hyperboreus*, relies entirely on internal lipid reserves for its reproduction (Hirche and Niehoff, 1996; Niehoff et al., 2002), while the other two species utilize to a different extent the new production (Harris et al., 2000; Hirche and Bohrer, 1987). *C. glacialis* shows ability to exploit ice algae as a food source during early spring (Hirche and Kosobokova, 2003; Runge and Ingram, 1991; Søreide et al., 2010), whereas *C. finmarchicus* requires phytoplankton for its successful reproduction (Harris et al., 2000). *Calanus* species effectively use phytoplankton or ice algae as food source (Falk-Petersen et al., 2009; Graeve et al., 2005; Scott et al., 2002). They also feed on protistan heterotrophic plankton but the importance of this diet differs depending on life stage and season (Levinsen and Nielsen, 2002; Levinsen et al., 2000; Turner et al., 2001). *Calanus* exploit the short, productive season to build up the lipid reserves that will enable them to overwinter successfully at depth in a state of dormancy with low metabolic activity (Hirche, 1996). Towards the end of overwintering they reach sexual maturity (in either the first, second or typically the third year for *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*, respectively), and begin reproduction.

In addition to the pelagic pathways in which ice algae/phytoplankton–zooplankton–nekton components play the main roles, there are links in food webs and biological carbon pump cycles involving larval stages of benthic organisms (meroplankton), which lead in a straight line to the benthic compartment where carbon is consequently transformed (Legendre, 1996; Markus and Boero, 1998). The successful recruitment of many benthic invertebrates depends on the availability of phytoplankton as a food source, since many of those species have pelagic larval stages that can be highly abundant temporarily during spring in high latitude coastal areas (Fetzer et al., 2002; Smidt, 1979; Walkusz et al., 2009). Their ability to profit from the spring bloom depends, again, on the timing of the release of the pelagic larval stages in relation to phytoplankton succession.

An intensive study of the temporal change in the phytoplankton food quantity and quality, in terms of fatty acid composition, was carried out in Kongsfjorden (Svalbard, Norway, 78°57′ N 11°55.2′ E) during spring 2003 and 2004 (Leu et al., 2006). During these periods, zooplankton were sampled from the euphotic zone, to record the changes in the community composition during spring and summer. Previous zooplankton studies from Kongsfjorden have concentrated mainly on the summer and autumn seasons (Kwasniewski et al., 2003; Scott et al., 2000), while recently some works on seasonal variability have been published (Lischka and Hagen, 2005, 2007; Narcy et al., 2009; Walkusz et al., 2009). However, none have a sufficiently high temporal resolution to resolve the potentially large dynamics during spring bloom and post-bloom periods. Hence, the aim of this paper was to describe and quantify the tempo of development of zooplankton community in the euphotic zone during spring and early summer, and to discuss the observed regularities. Specifically, our goal was to identify the main grazers that were able to exploit the spring phytoplankton bloom, and to describe their temporal distribution, in an attempt to understand the timing of their occurrence and reproduction in relation to available food and its quality. Comparison of data collected in two consecutive years allowed some assessment of the inter-annual variability in the zooplankton development. Our aim was to pay particular attention to the *Calanus* species given their pivotal role in Arctic pelagic systems.

## 2. Materials and methods

### 2.1. Study area

Kongsfjorden is a glacial fjord on the north-west coast of Spitsbergen (Svalbard) sharing a common entrance with Krossfjorden (Svendsen et al., 2002). It is 20 km long with a width ranging from 4 to 10 km and a maximum depth of 400 m (Fig. 1). Kongsfjorden is influenced by both Atlantic and Arctic water masses and receives a discharge of freshwater and sediments from the adjacent glaciers that varies seasonally, peaking in the summer. During winter, the inner part of the fjord typically has a fast ice cover. The formation, thickness and break-up of this ice cover show strong inter-annual variations, linked to the meteorological and hydrographic conditions. A detailed review of the physical environment of Kongsfjorden is given by Svendsen et al. (2002).

In contrast to typical fjords, Kongsfjorden does not have a shallow sill at the entrance, thereby allowing a relatively free connection to the adjacent shelf through a deep channel, Kongsfjordrenna. While this might imply the likelihood of a regular exchange of water between the fjord and the shelf, recent work has shown that during winter and spring the potential for exchange becomes limited by a density front forming at the fjord entrance (Cottier et al., 2005). This control on water mass exchange typically breaks down in summer permitting modified Atlantic Waters from the West Spitsbergen Current to enter the fjord. Thus, the seasonal restriction on communication between the fjord and the shelf controls the extent to which distinct water masses are able to occupy the fjord and consequently the advection of plankton communities into the fjord (Walkusz et al., 2009; Willis et al., 2006).

### 2.2. Hydrography and in situ fluorescence

Hydrographic data for both study periods in 2003 and 2004 came from two independent sets of observations. The first was a series of CTD profiles taken at the study site down to 100 m on each day of zooplankton sampling from 17 April until 23 May in 2003, and from 10 May until 11 June in 2004, which provided vertical profiles of temperature, salinity and fluorescence. The instrumentation and data processing for these observations have been described elsewhere (Leu et al., 2006). The second set of hydrographic data was from a fixed, single-point mooring at the south shore of Kongsfjorden in an approximate position of 78°58.3′ N and 11°39′ E (Fig. 1). The first deployment of this mooring was from 23 May to 6 September 2003 in water of 260 m depth and the second from 9 September 2003 to 22 August 2004 in 270 m. Thus, the deployments spanned the majority of the zooplankton sampling period in both 2003 and 2004.

In the first deployment, temperature was recorded on 12 sensors (accuracy 0.01 °C) between depths of 10 m and 215 m with $\Delta t \leq 1$ h. During the second deployment, the same sensors were positioned between 35 m and 260 m, again recording with $\Delta t \leq 1$ h. Temperature data were linearly interpolated at 10 m intervals and 1-h time steps and then a 49-h running mean was applied to filter out temperature variations associated with tidal flow. Using the temperature record it was then possible to identify subsurface advection of water given the good relationship of water masses to temperature (Cottier et al., 2005).

In 2003 (17 April–23 May) the water was thermally homogeneous down to 100 m, with temperature less than −0.7 °C (Leu et al., 2006) during the early part of the sampling period, indicative of the persistence of Winter Cooled Water formed the previous winter (Nilsen et al., 2008; Svendsen et al., 2002). Water temperature was still homogenous and cold (T < 1 °C) during the middle part of the sampling (Leu et al., 2006) while it first increased notably (T > 1–3 °C) only in mid-June at depths below 100 m and two weeks later also in the surface layer (Fig. 2A). The surface layer warming continued through July, and water with T > 3 °C was present in the upper 50 m on our final sampling in 2003.
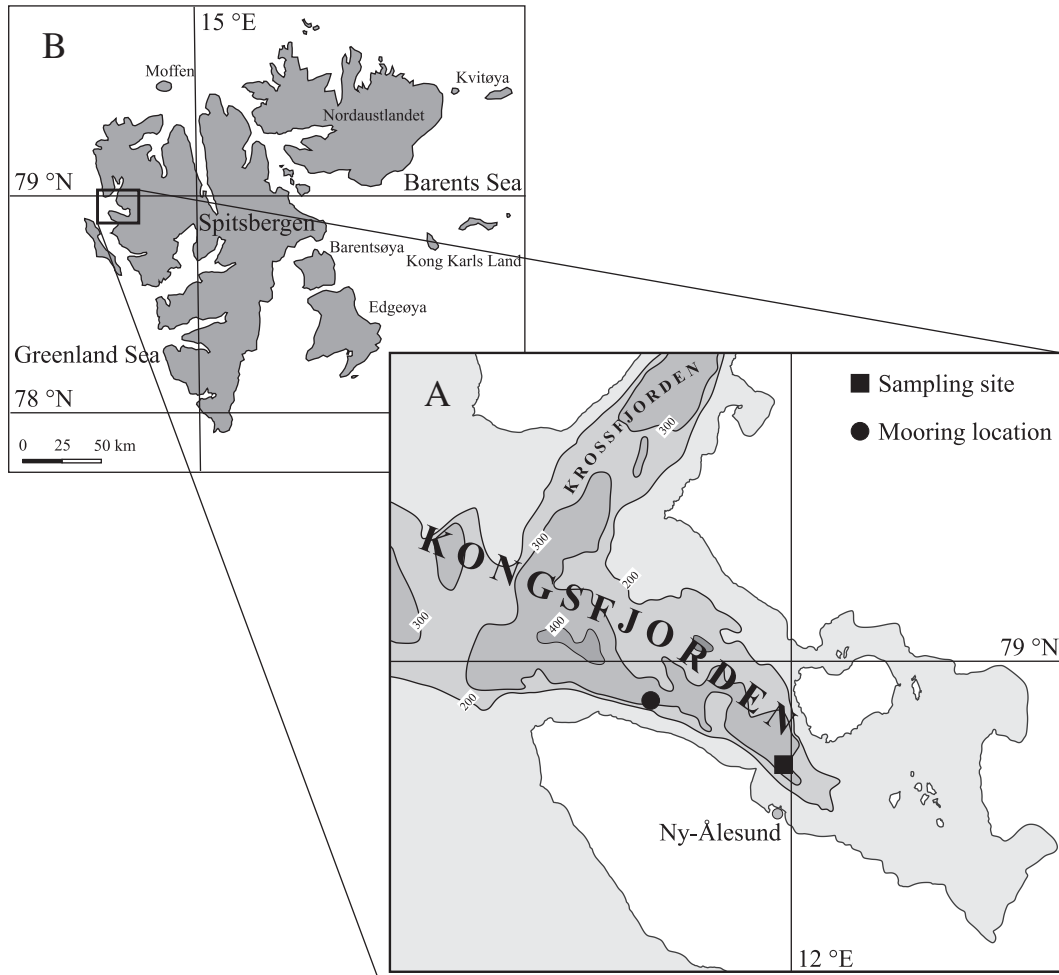
**Fig. 1.** (A) Map of Kongsfjorden area with sampling site (square) and mooring location (circle) indicated. (B) Map of Svalbard archipelago with location of Kongsfjorden indicated by a frame.

In 2004 the temperature in the water column during the zooplankton sampling was characterized by subtle thermohaline stratification during the period 10 May to 11 June, with warmer (T > 1 °C) and fresher water in the surface 20 m that started to develop after mid-May due to melting of the sea ice (Leu et al., 2006). The measurements from the mooring (Fig. 2C) suggest that the temperature was uniform in the upper 100 m prior to this study, with warmer water gradually occupying the deeper part of the fjord during the study period. The mooring was only able to record temperatures below 35 m depth but during the zooplankton sampling period there was no evidence of the temperature in the upper 100 m increasing above 1 °C until the final sampling day.

As a proxy for food availability in the euphotic zone during the development of zooplankton community in spring we used the in situ fluorescence measurements conducted along with CTD profiles at the study site on each day of zooplankton sampling from 17 April until 23 May in 2003, from 10 May until 11 June in 2004, and on a few additional days during these periods when the zooplankton was not sampled, as well as the results of parallel fluorometrical measurements of chlorophyll *a* (Chl *a*) concentrations and phytoplankton identifications in sea water samples (see Leu et al., 2006 for details on instrumentation and data processing). The time series of Chl *a* concentrations presented here (Fig. 2B and D) are based on Seapoint chlorophyll fluorometer measurements. The raw instrument readings were interpolated onto a regular 1 metre interval in the depth range from 0.5 m to 49.5 and we present the mean of these values for each observation day within 50–0 m layer, expressed

in mg m$^{-3}$ The plots show time variation of fluorometrically measured Chl *a* concentrations, which agree well with the Chl *a* concentrations in the sea water samples (Leu et al., 2006). In 2003, during the zooplankton sampling in April–May, the measurements detected the development of a spring bloom, with a peak in Chl *a* concentrations in mid May (up to 10 mg m$^{-3}$), and the phytoplankton biomass during this time was dominated by diatoms (Fig. 2B, Leu et al., 2006). In 2004 (Fig. 2D) the in situ fluorescence measurements showed low Chl *a* concentrations (with maximum a little above 2 mg m$^{-3}$ at the beginning of May), generally a post bloom situation, with the phytoplankton biomass dominated by flagellates (Leu et al., 2006).

### 2.3. Zooplankton sampling

Zooplankton samples analysed in this study were collected in two consecutive years: in 2003, from 17 April to 19 July (14 samples), and in 2004, from 10 May to 8 June (9 samples). Samples were collected from the upper layer (50–0 m) in vertical hauls, from a small boat using a hand operated WP-2 net (mouth area 0.25 m$^2$, mesh size 0.180 mm: Tranter and Fraser, 1968) except for the sample from 8 June 2004, which was taken from RV *Lance* and with Multi Plankton Sampler type Midi towed vertically (mouth area 0.25 m$^2$, mesh size 0.180 mm). The sampling took place in the mid part of the fjord, in a vicinity of the long-term monitoring station K3 (78°57′ N, 11°55.2′ E), towards the inner fjord, in the neighbourhood of Ny-Ålesund (Fig. 1).
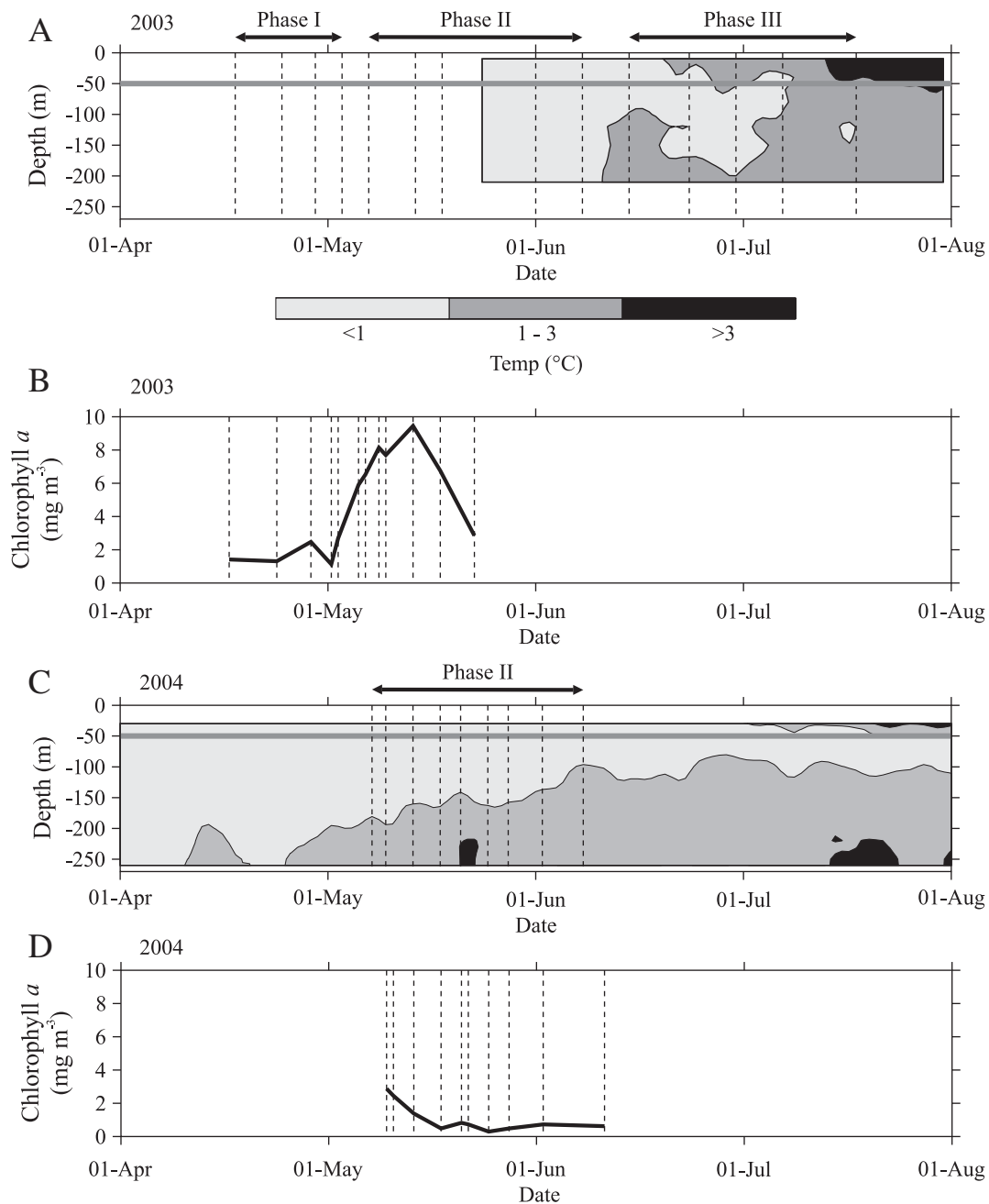
**Fig. 2.** Temperature (°C) changes in Kongsfjorden during (A) 2003 and (C) 2004 derived from sensors on the mooring, and chlorophyll a concentrations (mg m⁻³, mean for 50–0 m layer) during (B) 2003 and (D) 2004, derived from in situ fluorescence measurements on days of zooplankton sampling. The vertical dashed lines indicate dates of zooplankton sampling (in A and C) and dates of vertical temperature, salinity and fluorescence measurements (in B and D). The horizontal grey lines indicate the depth limit of zooplankton sampling and the fluorescence measurements in this study.

Samples were preserved in 4% solution of buffered formaldehyde in seawater, and stored in 250 ml polypropylene wide-mouth bottles. Sorting and identification of zooplankton were carried out following the procedures described by Postel (2000). Abundant samples were examined by sub-sampling method with aliquots obtained with 2 ml automatic pipette, with the pipette tip cut at 5 mm diameter to allow free collection of mesozooplankton (an equivalent of the Stempel pipette). The large (total length > 5 mm) organisms (macrozooplankton) were always sorted out before taking sub-samples and identified and counted in their entirety. Samples with low abundance were also

**Table 1**
Length of prosome [LP, mm] boundary values of the copepodid stages used for *Calanus* species identification. mts. 5 — 5th metasome segment. AF — copepodid CVI female.

| Stage | *C. finmarchicus* | *C. glacialis* | *C. hyperboreus* |
|---|---|---|---|
| CI | ≤0.75 | 0.75–1.0 | >1.0 |
| CII | <1.1 | 1.1–1.4 | >1.4 |
| CIII | ≤1.6 | 1.6–2.1 | >2.1 |
| CIV | <2.2 | 2.2–2.9 | >3.1, mts. 5 pointed |
| CV | <2.9 | 2.9–4.0 | >6.0, mts. 5 pointed |
| AF | <3.2 | 3.2–4.6 | >7.6, mts. 5 pointed |

**Table 2**
Zooplankton abundance [ind.m$^{-3}$] in Kongsfjorden in 50–0 m layer in 2003. 0 — estimated abundance <1 ind.m$^{-3}$. Empty cell — species/taxon absent.

| Taxon\Date | 17 April | 24 April | 29 April | 3 May | 7 May | 14 May | 18 May | 1 June | 8 June | 15 June | 24 June | 1 July | 8 July | 19 July |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Calanus finmarchicus* AF | 11 | 4 | 4 | 4 | 3 | 1 | 0 | 0 | 3 | 1 | 5 | 7 | 1 | 8 |
| *C. finmarchicus* CV | 2 | 2 | 3 | 2 | 0 | 1 | 0 | | 0 | 0 | 1 | 2 | | 51 |
| *C. finmarchicus* CIV | 2 | 1 | 2 | 2 | 1 | 0 | | | 0 | 0 | 8 | 32 | 20 | 181 |
| *C. finmarchicus* CIII | 1 | 1 | 2 | 1 | 0 | 0 | | | 3 | | 18 | 28 | 50 | 172 |
| *C. finmarchicus* CII | | | 1 | | | | | 0 | 10 | 1 | 38 | 92 | 64 | 99 |
| *C. finmarchicus* CI | | | | | | | 0 | 1 | 22 | 6 | 68 | 206 | 76 | 89 |
| *Calanus glacialis* AF | 10 | 4 | 5 | 4 | 0 | | | | 0 | | 2 | 0 | | |
| *C. glacialis* CV | | 0 | 2 | 0 | | 0 | | | 0 | 1 | 2 | 19 | 56 | 147 |
| *C. glacialis* CIV | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 10 | 40 | 126 | 392 | 460 |
| *C. glacialis* CIII | | 1 | 3 | 1 | | 0 | | 1 | 34 | 29 | 308 | 364 | 362 | 139 |
| *C. glacialis* CII | | | 1 | | | | 0 | 0 | 31 | 40 | 428 | 202 | 118 | 21 |
| *C. glacialis* CI | | | | | 1 | 2 | 2 | 2 | 102 | 47 | 312 | 79 | 50 | 7 |
| *Calanus hyperboreus* AF | | | | | | | | | | | | | | |
| *C. hyperboreus* CV | | | | | | | | | | | | 0 | | 0 |
| *C. hyperboreus* CIV | | | 0 | | | | | | | | 4 | 11 | 12 | 17 |
| *C. hyperboreus* CIII | | 0 | | | | | | 0 | 0 | 3 | 12 | 0 | 2 | |
| *C. hyperboreus* CII | | | | | | 0 | 0 | | | | | | | |
| *C. hyperboreus* CI | | | | | 2 | 1 | 3 | 1 | 8 | | 2 | | | |
| *Pseudocalanus* spp. AM | | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 5 | 0 | 2 | 2 | 0 | |
| *P. minutus* AF | 2 | 2 | 2 | 3 | 1 | 1 | 0 | 0 | 2 | 2 | 2 | 2 | 6 | 11 |
| *P. acuspes* AF | 0 | 0 | | 0 | 0 | 2 | 2 | 0 | 14 | 3 | 22 | 8 | 4 | 0 |
| *Pseudocalanus* spp. CV | 11 | 9 | 16 | 3 | 5 | 9 | 2 | 0 | 10 | 1 | 6 | 43 | 46 | 106 |
| *Pseudocalanus* spp. CIV | 15 | 20 | 4 | 3 | 3 | 1 | 0 | | 2 | 1 | 22 | 36 | 28 | 90 |
| *Pseudocalanus* spp. CIII | 22 | 9 | 5 | 4 | 1 | 0 | 0 | 2 | 16 | 1 | 19 | 19 | 20 | 139 |
| *Pseudocalanus* spp. CII | 2 | 3 | | 0 | 0 | 0 | 0 | 3 | 11 | | 22 | 28 | 48 | 297 |
| *Pseudocalanus* spp. CI | | | | 0 | 0 | 0 | 0 | 2 | 21 | 1 | 12 | 55 | 188 | 457 |
| *Microcalanus* spp. | 1 | 4 | 40 | | | | | | | | 2 | | 4 | |
| *Oithona similis* | 22 | 134 | 437 | 470 | 58 | 22 | 46 | 102 | 187 | 50 | 104 | 169 | 496 | 935 |
| Calanoida nauplii | 112 | 81 | 71 | 71 | 265 | 590 | 573 | 230 | 1071 | 180 | 1431 | 1390 | 732 | 875 |
| Cirripedia nauplii | 752 | 342 | 152 | 313 | 16 | 2878 | 5520 | 890 | 3129 | 214 | 1955 | 657 | 808 | 7 |
| Polychaeta larvae | 42 | 188 | 55 | 93 | 5 | 390 | 274 | 65 | 901 | 176 | 513 | 248 | 60 | 0 |
| *Fritillaria borealis* | 10 | 1 | 3 | 2 | 36 | 426 | 574 | 83 | 870 | 6 | 537 | 164 | 16 | |
| Others | 7 | 7 | 14 | 10 | 12 | 15 | 66 | 26 | 151 | 21 | 123 | 190 | 488 | 384 |

examined in their entirety. When possible, zooplankton were identified to species or genus level (most of the copepods), whereas the remaining taxa were identified to the lowest possible taxonomical level. For larger copepods that were collected representatively (e.g. *C. finmarchicus*, *C. glacialis*, *C. hyperboreus*, and *Pseudocalanus* spp.), copepodid developmental stages were identified as well. *Calanus* were identified to species for each copepodid stage, based on prosome length and morphology (Table 1 after Kwasniewski et al., 2003). Filtered water volume was estimated from the net opening and the sampling layer thickness, assuming maximum theoretical filtration efficiency of the nets. During the sampling clogging was not found to be causing serious problems. The zooplankton abundance presented throughout the paper is expressed as a number of individuals per m$^3$ within the 50–0 m layer. Dry mass of zooplankton was calculated using data on abundance and species- and stage-specific dry mass data compiled from various sources (for details see Kwasniewski et al., 2010), and throughout this paper the dry mass (DM) is expressed as mg dry mass per m$^3$ within the 50–0 m layer.

The nauplii developmental time $D_n$ (i.e. from hatching to CI) was calculated based on Belehradek's temperature function: $D = a \, (T - \alpha)^b$ (Corkett et al., 1986; Mauchline, 1998), where D is the duration time in days, T is the temperature in °C and a, b and $\alpha$ are fitted constants. For *C. finmarchicus* $D_n$ was calculated with $a = 1408$, $b = -1.64$ and $\alpha = 7.36$ (Corkett et al., 1986), for $T = 0$ °C. For *C. glacialis* $D_n$ was calculated with $a = 8825$, $b = -2.05$ and $\alpha = 12.97$ (Mauchline, 1998), for $T = 0$ °C.

### 2.4. Statistical analysis

To identify the patterns of changes in zooplankton composition and abundance, a correspondence analysis (CA) was applied, using the CANOCO software (ter Braak and Smilauer, 2002). The dissimilarity between samples in CA is based on the chi-square metric, implying that any two samples with identical relative abundances are judged to be identical. Log-transformed absolute abundance data ($y' = \log(A \times y + B$: $A = 1$ and $B = 1$) of the full species dataset were used in the analysis; for *Calanus* and *Pseudocalanus* species the different developmental stages were included as well to improve the temporal resolution of the development of the zooplankton community studied.

## 3. Results

### 3.1. Zooplankton community composition and abundance

During the entire study 38 zooplankton taxa were identified, all known from earlier studies in Kongsfjorden or other Spitsbergen fjords. Copepoda were the most diverse group (10 species), with Amphipoda (5), Decapoda (4) and Cnidaria hydromedusae (4) following. The numerically dominating zooplankton during spring 2003 and 2004 in the upper 50 m of Kongsfjorden were copepods (including nauplii stages), Cirripedia nauplii and Polychaeta larvae (Tables 2, 3). Together they accounted for more than 85% of the total abundance in all samples. In 2003, three major phases in the zooplankton composition and abundance time-series were identified (Fig. 3). During phase I (early spring/ pre-bloom: Leu et al., 2006), from 17 April to 3 May, the zooplankton was characterized by low total absolute abundances (788–1030 ind.m$^{-3}$) and predominance of small copepods *Oithona similis*, *Pseudocalanus* spp. and *Microcalanus* spp., together with a varying fraction of Cirripedia nauplii (Fig. 4A). During phase II (spring/main bloom) from 7 May to 8 June, the absolute abundances of small copepods did not change substantially (Table 2), but their relative abundances decreased because Cirripedia nauplii occurred in highest numbers (maximum 5520 ind.m$^{-3}$ on 18 May), thereby accounting for up to 80% of the zooplankton total abundance. Due to large variability in Cirripedia nauplii, the total zooplankton abundances during this phase were strongly variable, changing by a factor of

**Table 3**
Zooplankton abundance [ind.m$^{-3}$] in Kongsfjorden in 50–0 m layer in 2004. 0 — estimated abundance <1 ind.m$^{-3}$. Empty cell — species/taxon absent.

| Taxon\Date | 8 May | 10 May | 14 May | 18 May | 21 May | 25 May | 28 May | 2 June | 8 June |
|---|---|---|---|---|---|---|---|---|---|
| *Calanus finmarchicus* AF | 15 | 15 | 26 | 11 | 21 | 55 | 19 | 24 | 16 |
| *C. finmarchicus* CV | 6 | 5 | 9 | 14 | 5 | 13 | 2 | 6 | 4 |
| *C. finmarchicus* CIV | 0 | 3 | | | 0 | | | | 8 |
| *C. finmarchicus* CIII | 1 | 1 | | | 0 | | | 6 | 114 |
| *C. finmarchicus* CII | | | | 1 | 7 | 10 | 10 | 30 | 92 |
| *C. finmarchicus* CI | | 5 | 8 | 4 | 24 | 14 | 15 | 23 | 218 |
| *Calanus glacialis* AF | 4 | 3 | 2 | 4 | 3 | 13 | 0 | 6 | 4 |
| *C. glacialis* CV | 1 | 3 | 4 | 11 | 6 | 19 | 18 | 24 | |
| *C. glacialis* CIV | 14 | 8 | 4 | 14 | 5 | 10 | 6 | | 28 |
| *C. glacialis* CIII | 2 | | | 4 | 0 | 2 | 17 | 53 | 362 |
| *C. glacialis* CII | | 1 | 10 | 46 | 69 | 31 | 30 | 72 | 482 |
| *C. glacialis* CI | 80 | 85 | 174 | 248 | 217 | 32 | 58 | 71 | 1032 |
| *Calanus hyperboreus* AF | | | | | | | | | |
| *C. hyperboreus* CV | | | | | | | | 0 | 4 |
| *C. hyperboreus* CIV | | | | | | | | 0 | |
| *C. hyperboreus* CIII | | | | | | | | 18 | 22 |
| *C. hyperboreus* CII | | 2 | 1 | 39 | 43 | 35 | 34 | 78 | 24 |
| *C. hyperboreus* CI | 33 | 65 | 89 | 146 | 74 | 15 | 6 | 10 | 4 |
| *Pseudocalanus* spp. AM | 333 | 91 | 58 | 97 | 93 | 16 | 22 | 14 | 8 |
| *P. minutus* AF | 183 | 53 | 22 | 66 | 40 | 12 | 14 | 18 | 100 |
| *P. acuspes* AF | 27 | 11 | 10 | 7 | 6 | 5 | 6 | 6 | |
| *Pseudocalanus* spp. CV | 659 | 153 | 18 | 65 | 36 | 8 | 13 | 4 | 34 |
| *Pseudocalanus* spp. CIV | 161 | 30 | 9 | 13 | 6 | | | 4 | 22 |
| *Pseudocalanus* spp. CIII | 35 | 1 | 2 | 7 | 5 | 0 | 4 | 22 | 112 |
| *Pseudocalanus* spp. CII | | | 6 | 54 | 12 | 19 | 15 | 24 | 74 |
| *Pseudocalanus* spp. CI | 11 | 38 | 35 | 123 | 34 | 38 | 6 | 20 | 76 |
| *Microcalanus* spp. | | | | | | | | | 10 |
| *Oithona similis* | 79 | 182 | 210 | 177 | 131 | 162 | 111 | 136 | 252 |
| Calanoida nauplii | 3612 | 3817 | 4688 | 3901 | 3581 | 1959 | 1002 | 1537 | 2990 |
| Cirripedia nauplii | 10,801 | 4379 | 3401 | 15,222 | 1549 | 1600 | 446 | 1456 | 13,712 |
| Polychaeta larvae | 694 | 226 | 508 | 1225 | 194 | 168 | 139 | 211 | 832 |
| *Fritillaria borealis* | 46 | 26 | 27 | 99 | 55 | 123 | 74 | 26 | |
| Others | 58 | 41 | 55 | 50 | 33 | 120 | 138 | 130 | 219 |

List of taxa included as "Others": *Acartia longiremis, Oithona atlantica, Triconia borealis*, Harpacticoida, Ostracoda, *Themisto libellula, T. abyssorum, Apherusa glacialis, Onisimus* sp., Amphipoda, Isopoda, Euphausiacea (including nauplii, calyptopis and furcilia), *Pagurus pubescens, Hyas araneus*, Decapoda (including Caridea), Bivalvia (veliger), *Limacina helicina*, Clione limacina, Echinodermata (larvae), *Oikopleura* c.f. *vanvoeffeni, Parasagitta elegans, Eukrohnia hamata, Aeginopsis laurentii, Aglantha digitale, Rathkea octopunctata, Sarsia princeps*, Beroe cucumis, Pisces (larvae).

eight (410–7065 ind.m$^{-3}$). During phase III (early summer/post-bloom, 15 June–19 July), the zooplankton absolute abundances stabilized at a higher level (795–6016 ind.m$^{-3}$). The large herbivorous copepods, represented mainly by *C. glacialis* and *C. finmarchicus*, became more numerous and made up 30% of the total abundance (1090 ind.m$^{-3}$ and 600 ind.m$^{-3}$, respectively, with all copepodid stages included). In the course of phase III smaller copepods were systematically becoming important again, and *Pseudocalanus* spp. and *O. similis* reached their highest abundances, 1100 and 935 ind.m$^{-3}$, respectively, on the last day of sampling (19 July). Of the other zooplankton organisms, the appendicularian *Fritillaria borealis* was abundant mainly through phase II (up to 870 ind.m$^{-3}$ on 8 June), but it also appeared later at reasonably high abundance (maximum 537 ind.m$^{-3}$ on 24 June). During the entire sampling period in 2003 other taxa that were present in notable numbers were *Limacina helicina* during phases I and II, Euphausiacea nauplii and calyptopis during phases II and III, and Echinodermata larvae and Cirripedia cyprids during phase III.

The sampling period in 2004 was shorter (8 May–8 June), and took place during the post-bloom period (Leu et al., 2006). Zooplankton abundances varied between 2205 and 21,647 ind.m$^{-3}$ (Table 2), and the same taxa identified as being most important in 2003 accounted for >90% of the total community abundance in 2004, with Cirripedia nauplii and Copepoda nauplii predominating (Fig. 4B) and a notable contribution of Polychaeta larvae, *C. finmarchicus* and *C. glacialis*, as well as other copepods (*Pseudocalanus* spp. and *O. similis*). The relative composition of the zooplankton in 2004 mostly resembled the composition during phase II in 2003, whereas the total zooplankton abundances were much higher, mainly due to higher numbers of Copepoda and Cirripedia nauplii. Also similar to the previous year, Cirripedia nauplii in 2004 showed distinct peaks in abundance (8 May, 18 May and 8 June), but it was only the

peak on 8 June that was associated with a steep increase in abundances of other zooplankters (both *Calanus* species and Polychaeta larvae).

### 3.2. Stage composition and abundance of C. glacialis and C. finmarchicus

In mid-April 2003, *C. glacialis* population found in the uppermost 50 m of Kongsfjorden consisted almost exclusively of adult females, with some CIII–CV copepodids originating most likely from the previous years (Fig. 5A). After 7 May, females of *C. glacialis* disappeared and were not found in the 50–0 m layer until the end of this study except on one occasion (1 July). The first occurrence of CI was recorded on 7 May, and CI dominated the population throughout this month. From the beginning of June, copepodids CII–CIV of the new generation increased in relative abundance, ultimately accounting for 97% of *C. glacialis* population in the upper 50–0 m layer in mid-July, with copepodid CIV dominating at 59% on the last day of sampling. The absolute abundance of *C. glacialis* in 2003 remained low until nearly the end of phase II (June 1), ranging from 1 to 11 ind.m$^{-3}$ (Fig. 5A). The abundance of this species started to increase towards the beginning of phase III, peaking at over 1000 ind.m$^{-3}$ on 24 June, with the young copepodid stages being the most numerous at that time.

The stage development of *C. finmarchicus* population in 2003 followed a similar pattern to the one observed for the Arctic *C. glacialis*, although its timing was delayed (Fig. 5B). The relative abundance of *C. finmarchicus* females decreased after their predominance in early spring, but contrary to *C. glacialis* there were still some individuals present in the uppermost 50 m of the fjord until mid-July, accounting for 1–10% of the population. The first occurrence of *C. finmarchicus* copepodid CI was observed on 18 May, 11 days later than in *C. glacialis*. By the end of the sampling in
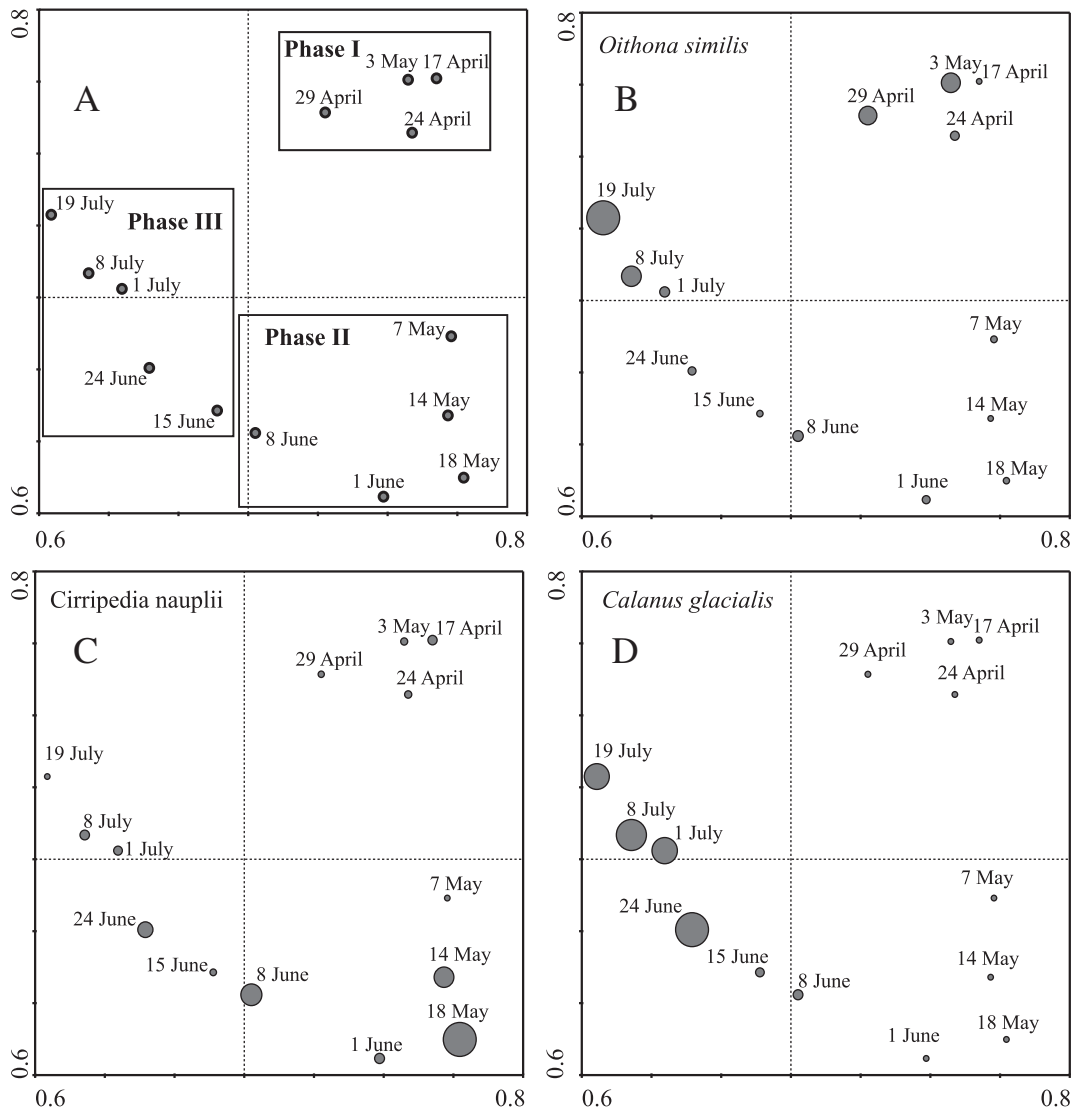
**Fig. 3.** (A) Correspondence analysis (CA) of zooplankton community composition by sampling dates in 2003, with individual graphs illustrating time distribution of taxa characteristic for the identified phases, namely: (B) *Oithona similis* (phase I), (C) Cirripedia nauplii (phase II) and (D) *Calanus glacialis* (phase III).

mid-July, the predominating stage of *C. finmarchicus* were CIII and CIV (approx. 30% each). The abundance of *C. finmarchicus* was low until the beginning of phase III, with a notable increase occurring one week later than in the case of its Arctic counterpart (Fig. 5B). The maximum abundance of this species was delayed even more, as it was observed only on the last day of our sampling (July19).

In 2004, *C. glacialis* CI accounted for 80% of the population on the first day of sampling, 8 May (Fig. 6A). This predominance of CI lasted until the middle of the observation period (25–28 of May) when the next stages, CII and CIII, started to contribute important fractions of the population. During the study in 2004 the overall population abundance of *C. glacialis* did not show substantial modification until the last day of sampling on 8 June.

Similar to the previous year, the timing of reproduction of *C. finmarchicus* in 2004 was delayed noticeably compared to the timing of *C. glacialis* (Fig. 6B). Females of *C. finmarchicus* species were a considerable fraction of the population almost until the end of sampling (2 June) and the proportion of CI of this species increased to 50% of the total species abundance only by 8 June. The first appearance of *C. finmarchicus* CI in 2004, however, was observed 8 days earlier than in 2003. There was a tendency to increasing proportions of CII and CIII of this species from 28 May onwards. Likewise in

*C. glacialis*, the population abundance of *C. finmarchicus* did not vary substantially until the last day of sampling.

### 3.3. Temporal changes of zooplankton biomass

In 2003, during phase I the average zooplankton dry mass (DM) in the 50–0 m layer was $23 \pm 9$ mg DM m$^{-3}$. During this phase the most important zooplankters in the 50–0 m layer were *C. glacialis* and *C. finmarchicus* (all copepodid stages included) as well as Cirripedia nauplii (Table 4). The remaining fraction of the biomass consisted predominantly of large but scarce chaetognaths, decapods larvae or hydromedusae. The biomass in phase II was considerably larger but more variable ($62 \pm 47$ mg DM m$^{-3}$). During this phase the biomass was dominated by Cirripedia nauplii, with considerable fractions due to Copepoda nauplii and large zooplankters, and less contribution from both *Calanus* species. During phase III the biomass increased again ($134 \pm 88$ mg DM m$^{-3}$) with the main biomass constituent being *C. glacialis*, with a notable fraction of *C. finmarchicus* and *Pseudocalanus*. The contribution of Cirripedia nauplii, and Copepoda nauplii was reduced, while that of other zooplankton remained nearly constant.
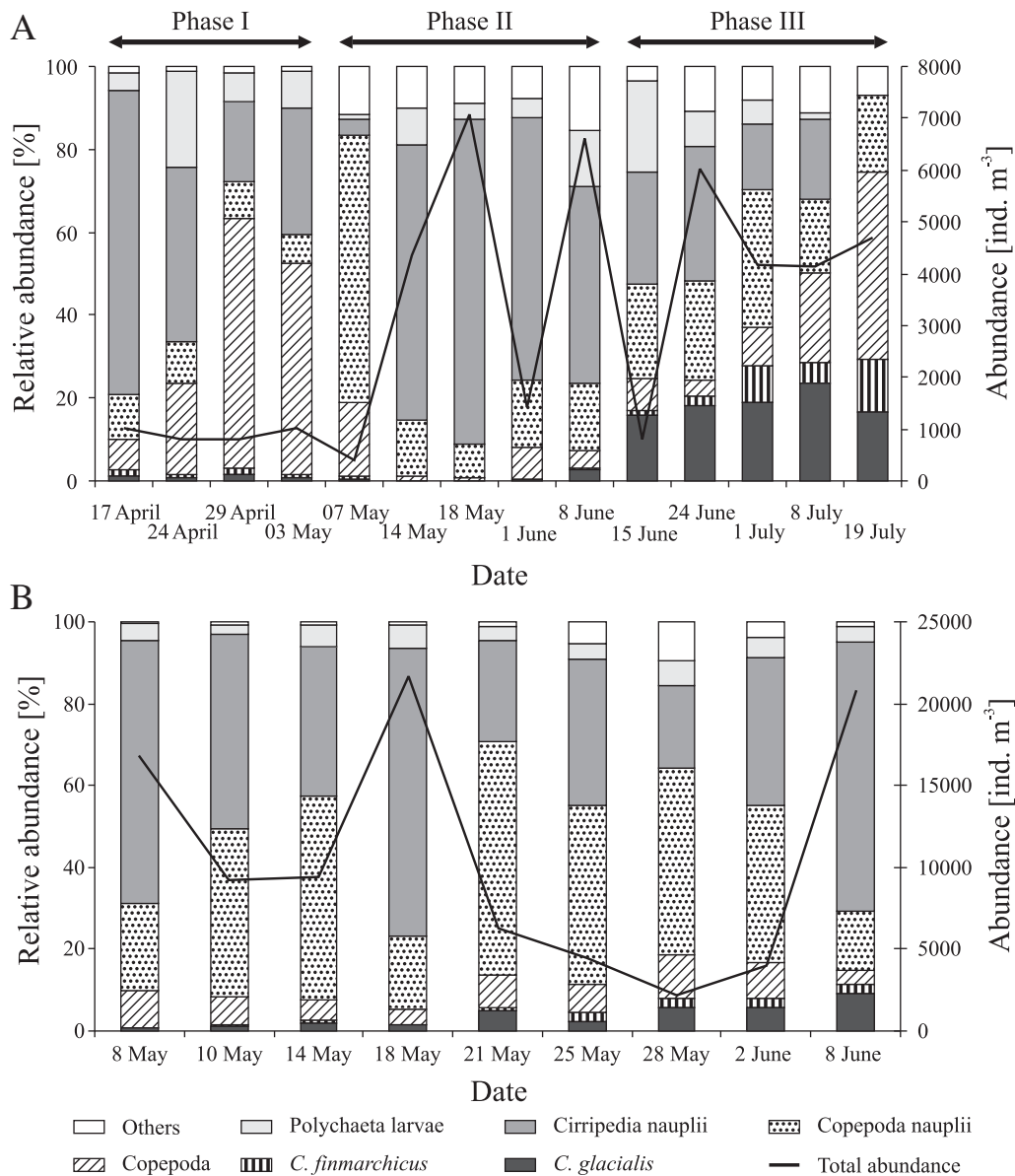
**Fig. 4.** Relative abundance of major taxonomic components and total abundance of zooplankton community in Kongsfjorden (50–0 m) during (A) spring and summer 2003 and (B) spring 2004.

In 2004, the average total zooplankton biomass was $188 \pm 136$ mg DM m$^{-3}$ (Table 4), and was dominated by Cirripedia nauplii, while the remaining fraction consisted of mainly *C. glacialis*, *C. finmarchicus*, Copepoda nauplii and other zooplankters.

## 4. Discussion

### 4.1. Zooplankton community dynamics

The intensive sampling in 2003 and 2004 revealed considerable changes in the zooplankton community in Kongsfjorden during spring and early summer, which manifest as the changes in the composition as well as the abundance of taxa. The results show that the community changes took place in a stepwise manner, rather than a gradual evolution. However, the individual taxa that played roles in the community dynamics showed differing temporal distribution patterns (such as the high variability observed in Cirripedia nauplii or the gradual increase and decrease as observed in *Calanus* copepodids). Information on Kongsfjorden zooplankton community variability was presented in a study by Willis et al. (2006), who collected samples with sediment

traps over a period of 5 months. Although not directly comparable, both this study and Willis et al. (2006) suggest similar patterns in zooplankton community seasonal dynamics, featuring characteristic events such as presence of females of both *Calanus* species preceding the appearance of Cirripedia nauplii, longer presence of females of *C. finmarchicus* than females of *C. glacialis* in the upper part of the water column or re-emergence of *O. similis* in higher abundance beginning at early summer. A high temporal resolution study on zooplankton in Young Sound (East Greenland) showed that during spring–early summer period meroplankton composition and abundance can change very rapidly there, although different taxa were involved (Polychaeta, Gastropoda, Bivalvia: Nielsen et al., 2007). The lack of Cirripedia nauplii may result from a lower population abundance of this crustacean in Young Sound, most likely due to longer presence of sea ice and ice scouring along the coast. On the other hand, a study from Southwest Greenland (Smidt, 1979), revealed the important role of Cirripedia nauplii in the zooplankton community in Gothåbsfjord, where they were present from mid April until June, and displayed wide fluctuations and short term maxima in April or May depending on the year. *C. glacialis* preceding *C. finmarchicus* in initiating reproduction and in development
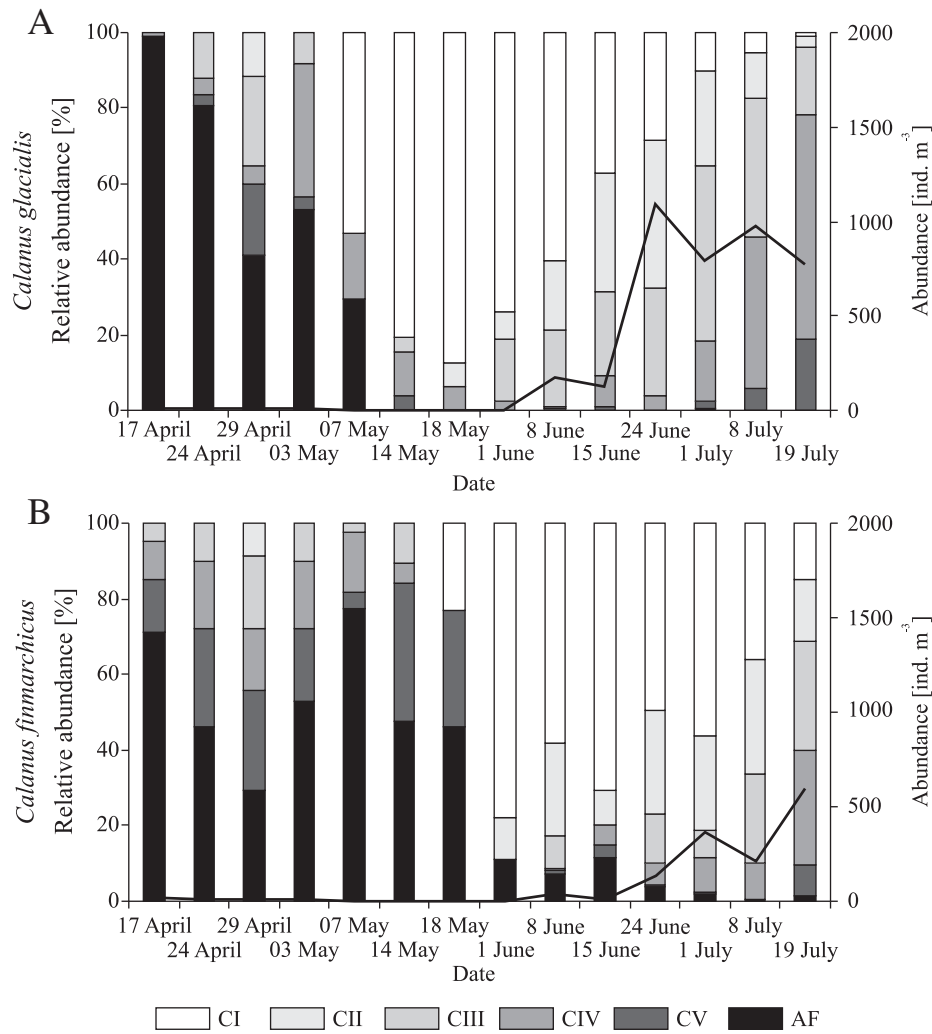
**Fig. 5.** Stage composition and total abundance of (A) *C. glacialis* and (B) *C. finmarchicus* in Kongsfjorden (50–0 m) during spring and summer 2003.

was also observed during the spring–summer transition in Disko Bay, west Greenland (Madsen et al., 2001; Niehoff et al., 2002), and the temporal evolution of individual copepodids observed there suggested a gradual change in community structure.

The changes observed in the zooplankton community during this study coincided with changes in the environmental variables potentially important for zooplankton seasonal development (Fig. 2, Leu et al., 2006). In phase I that encompassed the second half of April 2003 the zooplankton community in the upper 50 m of the fjord was moderately abundant and predominated by small size copepods (*O. similis*, *Pseudocalanus*, occasionally *Microcalanus*). During that time the water was very cold (below −0.7 °C) and homogenous (Leu et al., 2006; Lischka and Hagen, 2005; Rokkan Iversen and Seuthe, 2011), hydrologically indicative of a post-winter state. The fluorescence measurements (Fig. 2B) showed low levels of Chl *a*, suggesting the primary producers functioning in a pre-bloom phase (Leu et al., 2006; Rokkan Iversen and Seuthe, 2011). In May–early June the zooplankton become much more abundant, although in a fluctuating manner, and the main zooplankton components changed to Cirripedia and Copepoda nauplii, with considerable contribution from Polychaeta larvae and *F. borealis*. Concurrently, the water temperature increased slowly and an intense bloom occurred as indicated by high Chl *a* values measured during that period (up to 10 mg m$^{-3}$: Fig. 2B, Leu et al., 2006). In second half of June–first weeks of July the zooplankton abundance was still high, but less variable, and during that time the most conspicuous feature was the predominance of copepodids of *C. glacialis*, along with systematically increasing

proportion of *C. finmarchicus*, *Pseudocalanus* and *O. similis*, while the role of meroplankton and nauplii was decreasing. During that period the water temperature was also systematically increasing (Fig. 2A), while the phytoplankton was most likely passing between post bloom and summer stratified conditions, with decreasing production of phytoplankton and increasing production of bakterioplankton (Rokkan Iversen and Seuthe, 2011). The predominance of Cirripedia and Copepoda nauplii in May 2004 suggest that the observed zooplankton community mostly resembled that during phase II in 2003, however, the water temperature during May 2004 was higher (Fig. 2C, Leu et al., 2006), and the phytoplankton was found to be in a post-bloom phase (Chl *a* ~ 2 mg m$^{-3}$: Fig. 2D, Leu et al., 2006).

### 4.2. Potential grazers of the spring bloom

Effective utilization of the spring bloom is an important process in Arctic marine ecosystems (Leu et al., 2011; Wassmann et al., 2006). The changes in the zooplankton community time-series presented here enable two major questions of ecological significance to be discussed: (i) which of the numerically dominant grazers exploit the phytoplankton biomass most effectively, and (ii) does the timing of reproduction in the species match the dynamics of the available food source? The first of these questions also concerns the fate of the pelagic primary production produced during the spring bloom, since the autotrophic biomass either supports the recruitment of benthic organisms or is retained in the pelagic system depending on who are the dominant
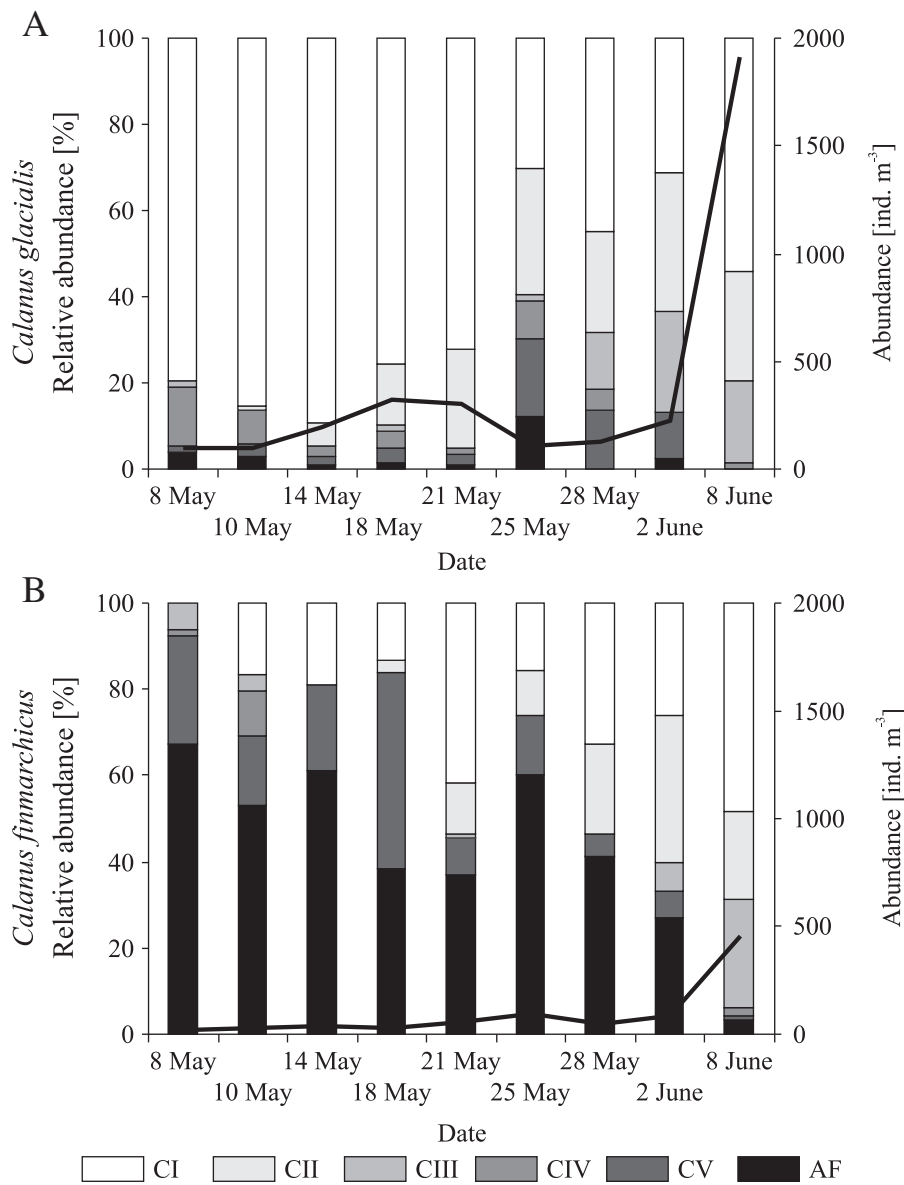
**Fig. 6.** Stage composition and total abundance of (A) *C. glacialis* and (B) *C. finmarchicus* in Kongsfjorden (50–0 m) during spring 2004.

grazers. In addition, the timing of reproduction compared to the timing of the bloom may also be important for successful development of zooplankton because of the nutritional quality of the bloom, which can be quantified in terms of relative amount of polyunsaturated fatty acids, and was usually found to be highest during the early phase of the bloom (Leu et al., 2006; Parrish et al., 2005).

In this study, the abundant zooplankton of phase I (April) were smaller copepods, largely dominated by *Pseudocalanus* spp. and *O. similis*, as well as females of *C. glacialis* and *C. finmarchicus*. This suggests that they might be important grazers on small size phytoplankton, protistan heterotrophic plankton as well as bacteria (nano- and microplankton), that are considered the main food source for the larger grazers during pre-bloom phase (Leu et al., 2006; Rokkan Iversen and Seuthe, 2011). Lischka and Hagen (2007) found diatom marker fatty acids in *P. minutus* sampled during spring, indicating a herbivorous diet. This was confirmed by Thor et al. (2005) who found that the vertical distribution of *Calanus* and *Pseudocalanus* was significantly correlated with Chl *a* concentrations, whereas other dominating species (*Metridia longa*, *O. similis*) did not show this correlation. In accordance with Lischka and Hagen (2005),

**Table 4**
Zooplankton biomass [DM, mg m$^{-3}$] in Kongsfjorden in different phases of the community development (average and SD), and relative biomass of selected taxa (average and SD).

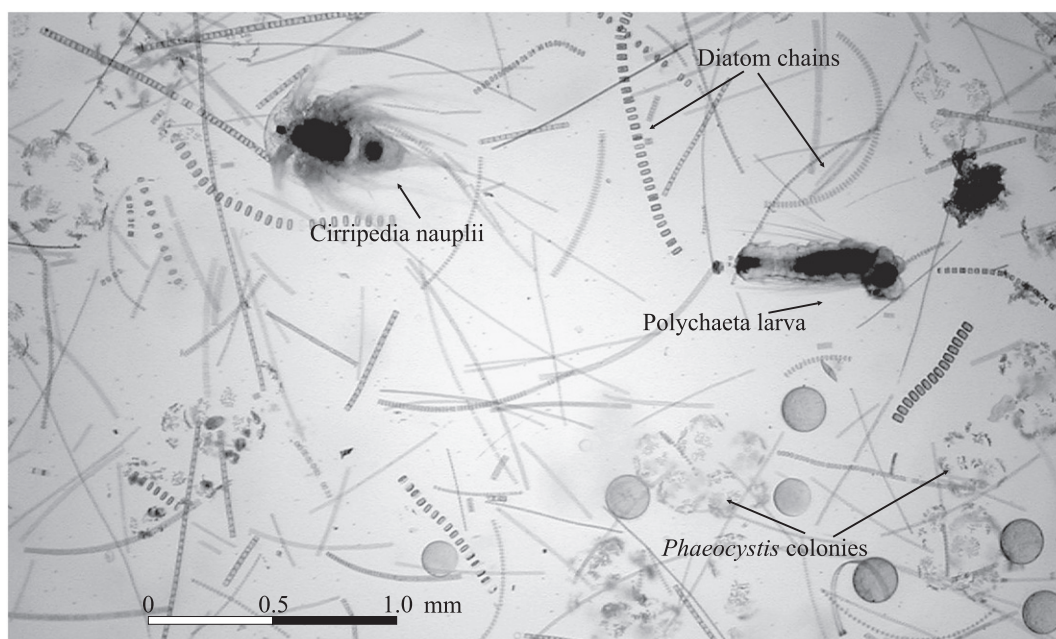|  | 2003 | | | 2004 |
|---|---|---|---|---|
|  | Phase I | Phase II | Phase III | Phase II |
| DM [mg m$^{-3}$] | 23.1 ($\pm$9.3) | 62.0 ($\pm$46.6) | 133.7 ($\pm$87.5) | 187.8 ($\pm$135.9) |
| DM [%] | | | | |
| *C. glacialis* | 34.8 ($\pm$8.4) | 4.0 ($\pm$6.4) | 57.1 ($\pm$18.7) | 15.3 ($\pm$11.5) |
| *C. finmarchicus* | 9.9 ($\pm$1.8) | 4.8 ($\pm$9.6) | 5.7 ($\pm$4.7) | 7.1 ($\pm$5.0) |
| Other Copepoda | 4.4 ($\pm$3.1) | 1.8 ($\pm$2.4) | 4.0 ($\pm$0.6) | 3.6 ($\pm$1.7) |
| Copepoda nauplii | 1.5 ($\pm$0.2) | 8.3 ($\pm$10.7) | 3.6 ($\pm$1.9) | 8.5 ($\pm$5.0) |
| Cirripedia nauplii | 33.1 ($\pm$9.8) | 69.7 ($\pm$35.0) | 18.0 ($\pm$16.1) | 52.6 ($\pm$22.7) |
| Polychaeta larvae | 3.4 ($\pm$2.6) | 3.2 ($\pm$2.5) | 2.7 ($\pm$3.4) | 1.8 ($\pm$0.6) |
| Other zooplankton | 12.9 ($\pm$4.4) | 8.2 ($\pm$7.1) | 8.9 ($\pm$4.7) | 11.2 ($\pm$7.5) |

**Fig. 7.** Size comparison of Cirripedia nauplii, Polychaeta larva and the dominating phytoplankton species (colonies) during peak spring bloom (7 May 2003). Scale approximate.

*Pseudocalanus* seemed to be reproductively active during May and June, as suggested by the presence of adult males and females during that period. Until mid-May, the population in this study was dominated by CIV and CV copepodid stages, most likely representing the overwintering population, which developed into adults that year, feeding on the pre-bloom nano- and microplankton. Elevated numbers of CI *Pseudocalanus* started to appear in mid-June which is in accordance with the notion that copepods of this genus usually reach their highest abundances later in the year (Walkusz et al., 2009). Our supposition of the role of *O. similis* as an important grazer in the zooplankton community prior to the bloom is in line with the findings by Narcy et al. (2009), who showed that these cyclopoid copepods started increasing their lipid store before the Chl *a* maximum in the water, possibly feeding on the pre-bloom microbial food. The presence of females of *C. glacialis* and *C. finmarchicus* during that time suggest that it might not be the bloom which triggers spawning, however in both species egg production tends to be higher in the presence of food (Harris et al., 2000; Hirche and Bohrer, 1987; Hirche and Kosobokova, 2003; Søreide et al., 2010). Spawning with the expectation of food being supplied during the main bloom and the successive primary production might be a strategy to spread risk of mortality and to extend the growth period in situations when food is limited rather than in surplus (Hirche et al., 2001). However, in natural conditions this may result in a situation when the development of a population may show delays, and one may observe accumulation of life stages if the offspring that needs to feed (*Calanus* nauplii at stage N3: Campbell et al., 2001; Irigoien et al., 2003) experiences lack of adequate food in sufficient quantity because of mismatch between primary production and *Calanus* reproduction.

During phase II of the zooplankton development, and concurrently with the phytoplankton bloom, Copepoda nauplii, most likely of herbivorous *Calanus* and *Pseudocalanus* species increased markedly in abundance, and constituted a considerable fraction of the community. Despite their small size, they might be well adapted to exploit the high quality diatom-dominated food available. Turner et al. (2001) showed that copepod nauplii had high weight-specific clearance rates for diatoms. In another study, Irigoien et al. (2003) found feeding efficiencies of *C. finmarchicus* nauplii to be highest for large cells (diatoms), and very low for flagellates. Although the bloom was not directly sampled in 2004, the fatty acid composition of *C. glacialis* copepodids collected during the post-bloom period showed diatom-marker fatty

acids in their lipids (Wold et al., 2007), possibly pointing to their diatom diet. The development of nauplii stages to copepodid stage I represents an important bottleneck in the life cycle of copepods and diatoms as a food source seem to be essential for the success of this development (Campbell et al., 2001; Hirche et al., 2001; Irigoien et al., 2003; Turner et al., 2001). The timing of the occurrence of CI of *C. glacialis* and *C. finmarchicus* observed during this study strongly supports this notion. In 2003, these young stages started to be present in high numbers during phase III after the bloom, most likely as a result of successful development of nauplii.

However, in terms of both abundance and biomass, it was the meroplanktonic Cirripedia nauplii that were the most important during the peak period of the spring bloom. It remains uncertain to what extent Cirripedia nauplii are able to graze the colonies of chain-forming diatoms (see Fig. 7 for comparison of sizes) that made up >70% of the spring bloom's biomass (Leu et al., 2006), although high clearance rates of barnacle nauplii for diatoms (20 μm cell size) have been described by Turner et al. (2001) in West Greenland. In their study, barnacle nauplii showed a more distinct herbivorous diet preference than *Calanus* spp. nauplii during the post-bloom period. The abundances of the meroplanktonic Cirripedia nauplii were extremely high (particularly in 2004, up to 15,000 ind.m$^{-3}$), but at the same time very variable. Similarly, Polychaeta larvae, another potential grazer of the bloom, reached high abundances that varied from one sampling day to another by a factor of five. A possible explanation for this remarkable patchiness might be that these larval stages are usually released in pulses, resulting in the presence of large patches. After their release, they will move to the surface (as a result of positive phototaxis), where good feeding conditions are available (Barnes and Klepal, 1972; Lang et al., 1979, 1980; Marsden, 1990; Martynova and Gordeeva, 2010; Singarajah et al., 1967). Here their distribution may be subjected to subsequent modifications due to tidal currents and wind-driven water motion.

The importance of younger copepodids, at first of *C. glacialis*, and later of *C. finmarchicus* and other copepods, in the post bloom and summer stratified productivity condition (phase III), indicates that these grazers most likely do not rely on new primary production. They are, however, capable of effective development utilizing phytoplankton growing based on regenerated nutrients, as well as protistan heterotrophic plankton building an effective microbial community during that period (Rokkan Iversen and Seuthe, 2011; Seuthe et al., 2011).

### 4.3. Timing of reproduction of dominant species in relation to the spring bloom

The timing of the spawning relative to food availability is a crucial moment in the animal's life cycle, particularly for zooplankton (Cushing, 1990; Durant et al., 2005). After this, development is greatly determined by water temperature and food availability. Usually the spawning cannot be observed directly, but it is possible to back-calculate its beginning by referring to the time of first appearance of CI stages. Based on information provided by Corkett et al. (1986), and Mauchline (1998), we calculated the nauplii developmental time $D_n$ (i.e. the time from hatching to CI), for *C. glacialis* and *C. finmarchicus* in 2003, for the mean temperature in the habitat during the discussed growth period (0 °C). For *C. glacialis* $D_n$ was estimated as 47 days while for *C. finmarchicus* it was 53 days. In 2003, *C. glacialis* CI were first recorded in early May suggesting that the first spawning for this species had occurred around 20 March, whereas the earliest spawning for *C. finmarchicus* had probably occurred around 10 April. However, a substantial increase in total abundances for both species, associated with a marked increase in the relative abundances of the smallest copepodid stages, was observed later, on 8 June and 24 June, respectively. We therefore conclude that in 2003 mass spawning of *C. glacialis* began in mid-April, before the biomass peak of the spring bloom (Hirche and Kwasniewski, 1997; Kosobokova, 1999; Søreide et al., 2010), while that of *C. finmarchicus* took place at the beginning of May, when the highest Chl *a* values were found in the euphotic zone of Kongsfjorden (Leu et al., 2006). *C. glacialis* developed faster in Kongsfjorden than *C. finmarchicus* — a consequence of both earlier spawning and a shorter developmental time at the same low temperature. Since the spawning of *C. glacialis* took place before the biomass peak of the spring bloom, their nauplii stages were able to exploit the spring bloom fully, and additionally profited from the better nutritional quality of the food produced during the early phase (Leu et al., 2006). *C. finmarchicus* mass spawning took place well after the start of the spring bloom, probably due to the need of the reproducing females to fuel spawning with additional phytoplankton food, thereby confirming the findings of Tande et al. (1985) and Hirche et al. (1997).

Previous studies from Kongsfjorden have revealed that *Calanus* abundances are usually higher during summer compared to spring (Walkusz et al., 2009; Willis et al., 2006). Our study concurred with that, and showed in addition that in the arctic ecosystem where two sibling species co-occur, *C. glacialis* is more abundant than *C. finmarchicus* during spring time. However, the abundances of both species increased only during June, and by then the bulk of autotrophic biomass was gone. This suggests that food sources other than the phytoplankton from the spring bloom in the uppermost 50 m, were obviously of considerable importance for the development of copepodids up to their first overwintering stage — CV in *C. finmarchicus*, CIV in *C. glacialis* and CIII in *C. hyperboreus* (Kwasniewski et al., 2003; Scott et al., 2002). Indications of a more omnivorous diet of *Calanus* under post-bloom conditions were presented by Ohman and Runge (1994), Levinsen et al. (2000) or Möller et al. (2006), and this feeding habit was recently confirmed by means of stable isotope analysis by Søreide et al. (2008).

In 2004, CI already made up 80% of *C. glacialis* population on the first sampling day, 8 May. It is unlikely that collection of this sample coincided with the first appearance of CI in the population in that year, so from this observation alone the start of reproduction could not be calculated. However, judging from the population's relative CI abundance (80% on 8 May 2004 vs. 50% on 7 May 2003) we assume that spawning in 2004 took place earlier than in 2003. At the same time, because the water temperature in 2004 was higher in the upper 50 m, compared with the same period in 2003, the earlier appearance of CI could have been the result of both earlier spawning and faster development. Timing of reproduction synchronized with the productivity cycle of autotrophs, and the capability to respond quickly and make use of the favourable feeding and living conditions (higher temperature) seems to be behavioural features well established in both *Calanus* species. Several studies

have shown, for example, that adult females of *C. glacialis* are able to utilize the ice algal bloom for their gonad maturation and egg production, thereby enabling their offspring to take advantage of the later occurring pelagic bloom (Leu et al., 2011; Madsen et al., 2001; Runge and Ingram, 1991). In Rijpfjorden (north-east Svalbard) Leu et al. (2011) observed the highest abundances of *C. glacialis* CI copepodid stage during the biomass peak of the pelagic bloom in July, whereas in Kongsfjorden an increase in CI was seen long after the peak of the spring bloom. We suspect that this delay was due to the absence of ice algae during the early part of *C. glacialis* development during this study.

The mass occurrence of meroplanktonic larval stages of Cirripedia and Polychaeta coincided well with the biomass peak of the spring bloom, indicating a very close coupling between the development of phytoplankton and reproduction of these benthic organisms (Highfield et al., 2010; Starr et al., 1991; Turner et al., 2001). It remains to be seen, though, how the meroplanktonic larvae will be able to adapt to a potential timeshift of the spring bloom in the future — and whether or not this will change fundamentally the extent of pelagic–benthic coupling.

### 4.4. Inter-annual differences and the role of advection

As found in earlier studies (Basedow et al., 2004; Cottier et al., 2005; Kwasniewski et al., 2003; Svendsen et al., 2002; Walkusz et al., 2009; Willis et al., 2006), advection from the shelf and neighbouring West Spitsbergen Current plays important role in shaping both hydrography and zooplankton community composition in Kongsfjorden. Cottier et al. (2005) postulated that warm subsurface waters in Kongsfjorden originate from the West Spitsbergen Shelf and contain a substantial proportion of Atlantic Water (T > 3 °C) originating from the West Spitsbergen Current. In our dataset, we found an increase in zooplankton abundances that can be linked in time to the advection of warmer water in mid-June 2003 as indicated by the temperature increase measured at the mooring. However, the increase in zooplankton numbers that was seen on 8 June was rather a result of a recruitment of the local populations, since it consisted mainly of taxa, which were the main constituents of the zooplankton during phase II, including Copepoda nauplii that could eventually contribute to the increase in *C. glacialis* and *C. finmarchicus* in the next phase.

In 2004, a water mass of Atlantic origin was already detected before 1 May at depths below 150 m. In general, advection from the shelf, where seasonal development of the pelagic system may start earlier (Walkusz et al., 2009), could have happened earlier and been stronger in that year. As a result, the abundances of zooplankton, particularly those of Copepoda and Cirripedia nauplii, were higher at the same time of the year in 2004 compared to 2003. Contrary to 2003, *C. finmarchicus* AF were more abundant in the fjord during spring 2004 than *C. glacialis*, suggesting a greater influence of Atlantic origin water in 2004. At the time of sampling, however, there were higher numbers of CI of *C. glacialis* than of *C. finmarchicus*. Higher water temperatures, as well as earlier phytoplankton development (Leu et al., 2006) and in general an earlier start of the seasonal development of Kongsfjorden pelagic system, would have contributed to a faster development of the new *Calanus* generations in 2004. Besides, reproduction typically takes place later in *C. finmarchicus* than in *C. glacialis*, as was observed in 2003. An advection from the seaward part of the fjord might have contributed to a measurable increase of zooplankton abundances by the last sampling day in 2004 (8 June) as well. This notion is supported by Leu et al. (2006), who showed the intrusion of Atlantic Water between 75 and 100 m depth at this time.

## 5. Conclusions

We conclude that the stages of *C. glacialis* and *C. finmarchicus* that could profit most from the high-quality food available during the spring bloom were spawning females and nauplii stages. Development from CI to the respective first overwintering stages has to rely

on food sources other than large diatoms dominating the spring bloom. In the areas of co-occurrence *C. glacialis* reproduces earlier than *C. finmarchicus*, and can therefore exploit the bloom more effectively. High abundance of meroplanktonic organisms during the peak of the bloom, suggest good matching between their reproduction and food availability. However, the importance of this group as chain diatom grazers still needs to be evaluated. Similar to previous works, we also found apparent indications of the importance of advection in shaping the structure of fjordic pelagic systems. We believe that the contrasting advection regimes in 2003 and 2004 may account for the observed differences in the abundances between the two studied years. Advection during 2004 started earlier and transported greater volumes of Atlantic Waters that resulted in higher abundance of *C. finmarchicus* females. On the other hand, the substantial increase of *C. glacialis* CI at the very end of study period in 2004 suggests that Arctic water resident on the shelf was involved in the advection. In 2004, there was drifting sea ice observed along the entire West Spitsbergen Shelf, which indicated the presence of Arctic water from the South Cape Current.

Our results suggest that individual phases of zooplankton seasonal development in Kongsfjorden during spring and early summer may last for approximately four weeks, while the switching over between phases can occur within one to two weeks. This indicates that sampling with time resolution of a month or less is needed in order to adequately assess the role of the zooplankton in functioning of food webs or ecosystems during the spring and early summer period.

It is likely that Kongsfjorden pelagic ecosystem will change as a consequence of the warming trend at high latitudes. Since the fjord is typically influenced by modified Atlantic water, with a mix of Arctic shelf waters, increased advection of the Atlantic-type water may cause a shift from Arctic to more temperate condition, with higher winter temperatures and year-round fjord-shelf exchange, as has been seen during more recent years (Cottier et al., 2007; Wallace et al., 2010; Willis et al., 2008). Based on the results of our study, we postulate that this may result in an earlier start to the zooplankton community seasonal development, increasing role of boreal *C. finmarchicus* and growing interspecific competition between this and arctic *C. glacialis* species. In addition, if the abundance of meroplankton in the warmer ecosystem will be increasing, the growing role of meroplankton in the pelagic-benthic coupling may compensate weaker retention of particulate organic matter in the water column, typically suggested as characteristic of temperate ecosystems, as a result of importance of the meroplankton in utilizing the phytoplankton bloom, as suggested by this study.

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