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The influence of advection on zooplankton community composition in an Arctic fjord (Kongsfjorden, Svalbard)

Kate Willis [a,*], Finlo Cottier [a], Slawek Kwasniewski [b], Anette Wold [c], Stig Falk-Petersen [c]

[a] Scottish Association for Marine Science, Dunstaffnage Marine Laboratory, Oban, Argyll PA37 1QA, Scotland, United Kingdom
[b] Institute of Oceanology, Polish Academy of Sciences, Powstancow Warszawy St. 55, 81-712 Sopot, Poland
[c] Norwegian Polar Institute, N-9296 Tromsø, Norway

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Abstract

A continuous, high-resolution time series of zooplankton and hydrographic data were collected from Kongsfjorden between April and September 2002 using a sediment trap and instrumentation deployed on a mooring. The time series has, for the first time, demonstrated the close relationship between water mass advection and changes in zooplankton community structure in Kongsfjorden. Zooplankton identified in the trap samples included 31 species/genera and seven higher taxa representing ubiquitous, boreal and Arctic biogeographic origins. Correspondence Analysis (CA) identified three phases of zooplankton community composition in 2002. Phase I, from 18 April to 29 May, consisted primarily of resident *Calanus finmarchicus* and *Calanus glacialis* stage CVI females. Phase II, from 30 May to 23 June, was dominated by meroplankton, *Oikopleura* cf. *vanhoeffeni*, *C. finmarchicus* early life stages (CI to CIII), *Calanus hyperboreus* and *Themisto abyssorum*. Phase III, from 4 July to 8 September, comprised *C. finmarchicus* (predominantly CV), *C. glacialis* CV, *C. hyperboreus* CIV and a greater diversity of other copepod species, in particular, increasing numbers of *Oithona similis*. Transition between the zooplankton community phases was abrupt and clearly associated with the advection of water masses into the fjord from the adjacent shelf. Peaks of the Arctic species *C. glacialis, C. hyperboreus* and *T. abyssorum* in late May were associated with a change in the dominant fjordic water mass from local Winter Cooled Water (WCW) to an influx of Arctic Water (ArW) from the coastal current. A temperature increase of 2.75 °C in the upper water column signified the transition from Phase II to Phase III with the dominant water mass changing from ArW to Atlantic Water (AW) from the West Spitsbergen Current.
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1. Introduction

Kongsfjorden is a glacial fjord on the northwest coast of Spitsbergen in the Svalbard archipelago. It opens to the West Spitsbergen Shelf (WSS) through a common mouth it shares with the adjacent Krossfjorden (Fig. 1). The WSS is a region where Atlantic, Arctic and glacial source waters converge, mix and are exchanged (Saloranta and Svendsen, 2001), consequently, Kongsfjorden displays many sub-Arctic characteristics despite its high-latitude location at 79°N. The regional balance between the three water sources shifts seasonally such

* Corresponding author. Tel.: +44 1631 559313; fax: +44 1631 559001.
E-mail address: kate.willis@sams.ac.uk (K. Willis).

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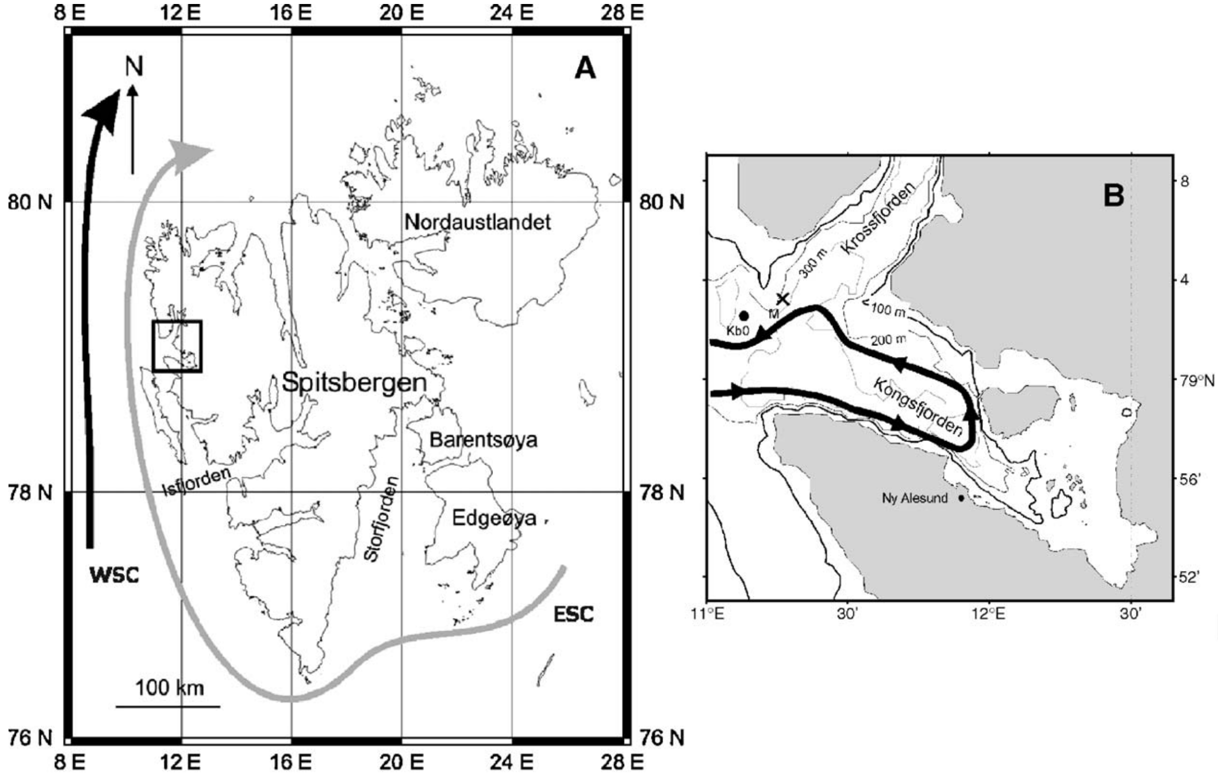

Fig. 1. (A) The Svalbard archipelago with the Kongsfjorden–Krossfjorden system on the northwest coast of Spitsbergen indicated by the box. The two major currents flowing north along the West Spitsbergen Shelf are the cold coastal current originating as the East Spitsbergen Current (ESC) and the West Spitsbergen Current (WSC) which carries warmer Atlantic Water. (B) The location of the mooring (X) and zooplankton sampling station Kb0 (●) in Kongsfjorden. The dark grey arrow in (B) shows the topographically steered currents (ArW and AW) originating from the shelf and circulating round the fjord. The mooring is located on the northern side of this circulation.

that within an annual cycle the shelf waters and adjacent fjords switch from a state of Arctic dominance (cold and fresh) to one of Atlantic dominance (warm and saline) and back (Cottier et al., 2005; Svendsen et al., 2002). Kongsfjordrenna, a submarine glacial trough, acts as a deep-water connection between the outer basin of Kongsfjorden and the shelf, so water mass exchange across the shelf–fjord boundary is not impeded topographically and advection plays a significant role in determining the physical and biological characteristics of the fjord (Hop et al., 2002; Svendsen et al., 2002). Water mass classification for the fjord and WSS, consistent with cross-shelf exchange mechanisms, was first described by Svendsen et al. (2002). A slightly modified version of this scheme, proposed by Cottier et al. (2005), is adopted in this paper.

The two principal water masses originating outside the fjord are warm, saline Atlantic Water (AW) carried in the West Spitsbergen Current (WSC), and relatively cold, fresh Arctic Water (ArW) carried by the inshore coastal current (Fig. 1A). Both currents flow northward, the former following the shelf slope and the latter on the shelf, and are separated by a frontal region at the shelf break. AW entering Kongsfjorden mixes with ArW as it crosses the shelf to form Transformed Atlantic Water (TAW) with temperature and salinity properties distinct from water in the core of the WSC.

The occurrence of locally produced water masses within the fjord varies throughout the year. In late spring and summer glacial melt water forms a layer of Surface Water (SW) of variable thickness and temperature. Beneath this, mixing between SW and the underlying Atlantic water types (AW and TAW) produces Intermediate Water (IW). In autumn and winter two water masses are formed within the fjord; cold (<1 °C) Local Water (LW) is produced by surface cooling at the end of summer, and Winter Cooled Water (WCW) with temperatures close to freezing point, develops by convection of very cold and dense water produced by cooling and sea ice formation (Haarpaintner et al., 2001). By the end of winter, WCW exists as a relatively homogeneous water mass within the fjord and can persist in the deep basins and depressions of the fjord throughout the year.

During summer, the fjords on the west coast of Spitsbergen can undergo intense and rapid changes in hydrography, shifting from an Arctic to Atlantic Water dominated systems (Berge et al., 2005; Cottier et al., 2005). Gradual modification of vertical stratification in Kongsfjorden during spring through mixing of warmer and fresher SW erodes the density front separating the fjord waters from the shelf. This allows ArW and then Atlantic Water (TAW then AW) to penetrate into the fjord.

Advected waters enter the fjords of West Spitsbergen along their southern boundaries as a topographically constrained current (Berge et al., 2005). The dominant circulation of water within Kongsfjorden, shown schematically in Fig. 1B, is dominated by a persistent cyclonic gyre in the mid- to deep-water (Cottier et al., 2005; Basedow et al., 2004; Svendsen et al., 2002), though in the surface this can be reversed due to wind forcing and decoupling of the fresher surface water (Cottier et al., 2005; Ingvaldsen et al., 2001).

The zooplankton fauna in Kongsfjorden is relatively rich and unlike other fjords in the Nordic Seas region is comprised of co-occurring boreal and Arctic species, which respond to variations in the distribution and dynamics of the West Spitsbergen water masses (Kwasniewski et al., 2003). Species representative of Atlantic water masses include the copepods *Calanus finmarchicus* and *Oithona atlantica*, the polychaete *Tomopteris helgolandica*, the amphipod *Themisto abyssorum*, and euphausiids belonging to the genus *Thysanoessa*. Species of Arctic origin include the copepods *C. glacialis*, *C. hyperboreus* and *Metridia longa*, the amphipod *Themisto libellula*, and the pteropods *Clione limacina* and *Limacina helicina.* The three co-occurring *Calanus* species, which dominate the zooplankton numerically, originate from different bio-geographic zones. Kwasniewski et al. (2003) proposed that populations of the boreal *C. finmarchicus* and Arctic *C. glacialis* in Kongsfjorden consist of local and advected individuals, with the proportions of each varying seasonally and annually depending on the timing and volume of AW and ArW intrusions. For example, lower abundance of *C. glacialis* in 1997 relative to 1996 may have been caused by the predominance of AW in 1997, which generally has a lower abundance of this species. Kwasniewski et al. (2003) also proposed that the Arctic *C. hyperboreus* is an expatriate in the fjord, with advection of copepodids in ArW intrusions sustaining the population rather than local spawning. Although it has been assumed that advective processes account for the high zooplankton biomass present in the fjord and are very important in structuring plankton species composition (Hop et al., 2002; Kwasniewski et al., 2003; Walkusz et al., pers. comm.), still little is known about the role of water mass advection on shaping the biological communities in Kongsfjorden.

Continuous zooplankton time series are difficult to obtain in the Arctic using standard zooplankton sampling methods due to the often adverse conditions experienced. The Scottish Association for Marine Science (SAMS) and the Norwegian Polar Institute (NPI) have maintained a long-term hydrographic/biological mooring in the outer basin of Kongsfjorden to study exchange processes in the fjord. A sediment trap deployed at a depth of 65 m on the mooring from April to September 2002 in Kongsfjorden has, for the first time, provided a continuous time-series of zooplankton which, with the associated hydrographic data, has furthered our understanding of the role of advection on zooplankton community composition in the fjord.

2. Methods

2.1. Sediment trap zooplankton

A single sediment trap (Paarflux with 21 cup carousel) was deployed on a single-point mooring at the common mouth of the Kongsfjorden–Krossfjorden system at 79° 3.25′N, 11° 18.0′E in 215 m water depth (Fig. 1). The mooring was first deployed on 16 April 2002 from *RV Lance* and recovered for maintenance on 23 June 2002 by *RRS James Clark Ross*. The second deployment was from 3 July 2002 until its final recovery on 28 September 2002 by *RV Håkon Mosby*. On each deployment the sediment trap was positioned at a depth of 65 m. The sampling periods were from 18 April to 23 June, and 4 July to 8 September with a sampling frequency of 3.5 days per bottle. The trap sample bottles were pre-filled with filtered seawater containing NaCl to provide a density discontinuity relative to ambient seawater, and 2% formalin buffered with sodium borate to preserve the deposited material. All zooplankton were removed from the wet sample using small forceps with sharpened ends under a stereomicroscope. All animals removed were intact and showed no signs of decomposition, suggesting that they entered the trap actively and were subsequently killed by the preservative. Large zooplankters (amphipods, appendicularians, chaetognaths, ctenophores, euphausiids, and medusae) were sorted and identified from the sample. *Calanus* were identified to species based on morphology and prosome lengths of individual copepodite stages according to Kwasniewski et al. (2003). *Calanus* prosome lengths were measured under a stereomicroscope equipped with a calibrated ocular micrometer. Remaining copepods were identified to the lowest possible taxon.

Changes in zooplankton species composition over time were analysed by correspondence analysis (CA) using CANOCO version 4 (Ter Braak and Smilauer, 1999). Correspondence analysis is based on a unimodal response model in which the abundance of species rises and falls within a limited range of values of an environmental variable (Van Wijngaarden et al., 1995). The results are presented as ordination plots of sites (sediment trap sample dates) and species using species-centred CA in which each species is implicitly weighted by the variance of its abundance values. Species with high variance, often the abundant ones, therefore dominate the CA solution, whereas species with low variance, often the rare ones, only have minor influence (Ter Braak, 1987). Euclidean scaling was used so that resulting ordination plots were optimal for interpreting distances between sites (sample dates). Each date was considered to be a site (indicated as a point on the ordination plot) and the species abundance was not transformed. The CA ordination plots (presented separately as dates and species for clarity) summarise changes in the zooplankton community over the period the sediment trap was deployed, and the goodness-of-fit of the axes is indicated by their eigenvalues.

2.2. Zooplankton vertical distribution

The vertical distribution of *Calanus* species at Station Kb0 (see Fig. 1B), 3.5 km to the southwest of the mooring, was determined on three sampling occasions in 2002; 17 April just prior to deployment of the sediment trap on 18 April; 29–30 July; and 21–23 September, two weeks after the final sediment trap sample on 8 September. Zooplankton were collected with a Multi Plankton Sampler (MPS; square opening of 0.25 m) equipped with five nets (0.180 mm mesh) that could be closed in sequence. The filtered water volume was calculated from wire length and net mouth area assuming 100% filtration efficiency at 0.5 m s^{-1} hauling velocity. On each sampling occasion, the sampling depth strata were determined following examination of temperature and salinity distributions to identify the water masses present. Samples were preserved in 4% formaldehyde in sea water buffered with hexamine.

2.3. Hydrography

Hydrographic instrumentation on the mooring was similar for each deployment (Table 1). An upward looking 300 kHz ADCP recorded thirty bins (each bin 4 m high, the deepest centred at 145 m and shallowest at 29 m) with a standard deviation in velocity of approximately 0.5 cm s^{-1}. Two Seabird 37 Microcats were positioned at depths of 40 and 205 m respectively. Salinity and temperature measurements from the microcats were accurate to 0.01 and 0.01 °C respectively. Vemco Miniloggers had a resolution of 0.1 °C (8-bit) and 0.01 °C (12-bit) and were accurate to 0.1 °C; calibrations were confirmed in a shipboard water bath after each deployment.

The moored instruments were used to record changes in temperature (T) and salinity (S) during the periods the sediment trap was deployed. A continuous record of T and S approximately 25 m above the sediment trap opening was obtained from the upper microcat at a depth of 40 m. Mean T and S were calculated for the 3.5 day duration of each sediment trap sample. At each mooring deployment and recovery, a water column CTD profile was taken at the site. For full details of seasonal hydrography see Cottier et al. (2005).

3. Results

3.1. Sediment trap zooplankton

Zooplankton taxa identified in the sediment trap samples included 31 species/genera and seven higher taxa representing ubiquitous, boreal, and Arctic biogeographic origins (Table 2). The most common taxa in the

Table 1
Details of the instrumentation used on each mooring deployment, including the number of instruments, deployment depths and sampling frequency

Instrument	Sample interval	Deployment 1		Deployment 2	
		Quantity	Depth (m)	Quantity	Depth (m)
Seabird microcat	4 min	2	40, 205	2	45, 205
Minilog-8 bit	16 min	4	30, 65, 150, 175	3	30, 35, 55
Minilog-12 bit	12 min	6	35, 55, 70, 100, 120, 155	6	70, 120, 130, 150, 180, 205
RDI 300 kHz ADCP	4 min	1	150	1	150
24-bottle sediment trap	3.5 d/bottle	1	65	1	65

Table 2
List of taxa identified in sediment trap samples from Kongsfjorden in 2002 and their biogeographic origin

Taxon	Biogeographic origin	Taxon	Biogeographic origin
Holoplankton			
Calanus finmarchicus	Boreal	*Oikopleura* cf. *vanhoeffeni*	Boreo-Arctic
Calanus glacialis	Arctic	*Fritillaria borealis*	Boreal
Calanus hyperboreus	Arctic	*Sagitta elegans*	Ubiquitous
Pareuchaeta norvegica	Boreo-Arctic	*Eukrohnia hamata*	Arctic
Metridia longa	Arctic	*Hyperia galba*	Boreo-Arctic
Pseudocalanus minutus	Boreo-Arctic	*Themisto libellula*	Arctic
Pseudocalanus acuspes	Boreo-Arctic	*Themisto abyssorum*	Subarctic-Boreal
Microcalanus spp.	Boreo-Arctic	*Clione limacina*	Arctic
Oithona similis	Ubiquitous	*Limacina helicina*	Arctic
Oithona atlantica	Boreal	*Tomopteris helgolandica*	Boreal
Triconia borealis	Boreo-Arctic	*Thysanoessa longicaudata*	Boreal
Cyclopoida		*Thysanoessa inermis*	Boreal
Harpacticoida			
Aeginopsis laurentii	Arctic	**Meroplankton**	
Halitholus cirratus	Boreal	*Pagurus pubescens* larvae	
Aglantha digitale	Boreo-Arctic	Cirripedia nauplii/cypris	
Sarsia spp.		Polychaeta larvae	
Hydromedusae			
Siphonophora		**Benthic**	
Mertensia ovum	Arctic	*Eualus gaimardii*	Boreo-Arctic
Beroë cucumis	Ubiquitous	*Chaetozone* spp.	

samples were the three *Calanus* species, *C. finmarchicus, C. glacialis*, and *C. hyperboreus*, the cyclopoid copepod *Oithona similis*, chaetognaths (*Sagitta elegans*), appendicularian (*O.* cf. *vanhoeffeni*), amphipods (*Hyperia* and *Themisto* spp.) and meroplankton (Cirripedia and polychaete larvae).

The CA ordination plots clearly identify three phases of zooplankton community composition in the outer basin of Kongsfjorden during 2002 (Figs. 2 and 3). Phase I from 18 April to 29 May includes sediment trap samples 1 to 12, excluding samples 5 and 7, which had very low abundance (Fig. 2). Phase II from 30 May to 23 June includes samples 5, 7, and 13 to 19. Phase III from 4 July to 8 September comprises samples 20 to 38.

The species characterising the zooplankton community during Phase I were *C. finmarchicus* stage CVI (females and males), *C. glacialis* CV and CVIF, and low numbers of *Hyperia galba* (Fig. 3). Phase II was dominated primarily by meroplankton, *O.* cf. *vanhoeffeni*, *C. finmarchicus* and *C. glacialis* early life stages (CI to CIII), *C. hyperboreus*, copepod nauplii, and *T. abyssorum*. The Phase III zooplankton community consisted of *C. glacialis* CV, *C. finmarchicus* CIV and CV, *C. hyperboreus* CIV and a greater diversity of other copepod species. In particular, *O. similis* increased in abundance towards the end of Phase III, as indicated by the separation of samples 36 to 38 from earlier samples (Fig. 2).

Of the three co-occurring *Calanus* species in Kongsfjorden, *C. finmarchicus* and *C. glacialis* were most abundant in the trap samples (Fig. 4). In Phase I,

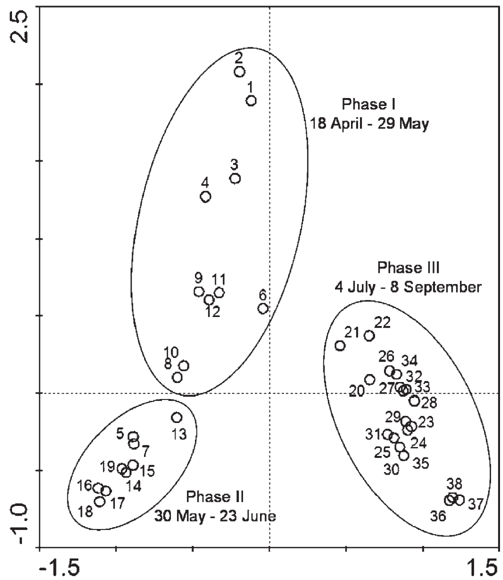

Fig. 2. Ordination diagram (CA) illustrating Phases I, II and III in zooplankton community composition in Kongsfjorden between 18 April and 8 September 2002. Of the total variance, 73% is explained on the horizontal axis and 56% on the vertical axis. Sediment trap samples are shown as open circles, with the phases and associated time periods indicated by the contours. The species responsible for the ordination are shown in Fig. 3.

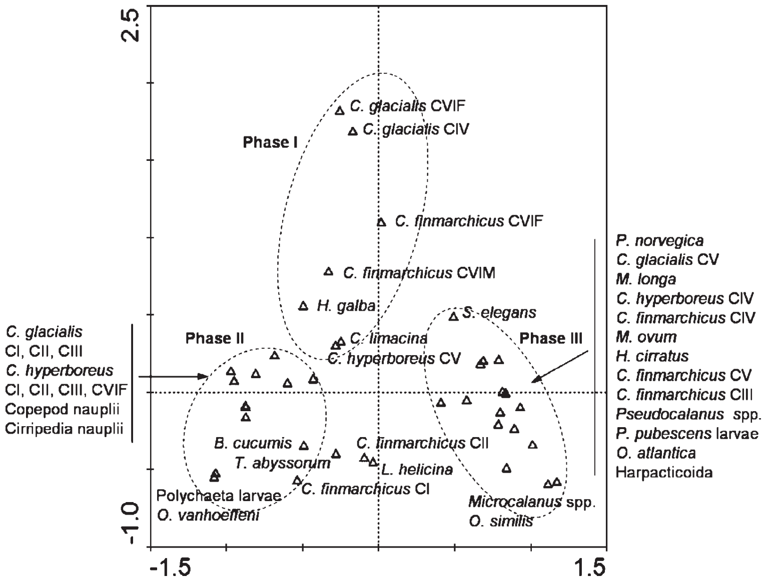

Fig. 3. Ordination diagram (CA) illustrating changes in zooplankton species composition in Kongsfjorden between 18 April and 8 September 2002. Phases I, II and III shown in Fig. 2 are indicated by the broken contours. CI to CVI are *Calanus* copepodite stages I to VI females (F) and males (M). Only those species well explained by the ordination are shown; species in the centre of the diagram have been omitted.

from 18 April to 30 May, CVI females dominated and low numbers of *C. hyperboreus* stages CI to CII were occasionally present in the trap. There was a second peak of *C. glacialis* at the end of Phase I in late May. During Phase II, *C. glacialis* abundance was very low and *C. finmarchicus* consisted of a range of development stages (CI to CVI females). *Calanus hyperboreus* (primarily stages CVI and CV) peaked in abundance at the beginning of Phase II in early June. Following the mooring turnaround between 23 June and 4 July, a distinct difference in the stage composition of the three *Calanus* species was apparent. For the period 4 July to 8 September (Phase III), *C. finmarchicus* was the most abundant *Calanus* species, and CV was the most prevalent *C. finmarchicus* and *C. glacialis* life stage, whilst CIV was the predominant *C. hyperboreus* life stage (Fig. 4). *C. finmarchicus* stages CIV and CVIF were also present in the trap samples throughout most of this period, along with low numbers of other life stages.

Of the other zooplankton present in the trap samples, meroplankton and appendicularians were most abundant from April to June (Phase I and II), but were virtually absent in Phase III from July to September (Fig. 5). A peak in abundance of the boreal appendicularian *Fritillaria borealis* occurred over the transition period from Phase I to II. In Norwegian coastal waters this species undergoes population maxima in April/May and July/August (Wiborg, 1955). Hyperiid amphipods were present in many of the trap samples throughout the deployment period, albeit in relatively low abundance (Fig. 5). The Arctic hyperiid *T. libellula* was present during Phase I, whereas the boreo-Arctic *T. abyssorum* peaked in abundance at the beginning of June (Phase II). *O. similis* increased in abundance during the second deployment period (Phase III), with high numbers (>160 per trap sample) occurring in late August/early September (Fig. 5).

3.2. Zooplankton vertical distribution

Total zooplankton abundance at Kb0 was much lower in April, than in July and September (Fig. 6). In contrast to the sediment trap samples, abundance of all three *Calanus* species in April was very low in the net samples at Kb0 (*C. hyperboreus* was absent) with only a few individuals present in the upper water column. Abundance had increased considerably by July with *C. finmarchicus* present in high numbers throughout the water column, *C. glacialis* peaking in abundance at the surface, and *C. hyperboreus* located at depth (Fig. 6). The increase in abundance in the net samples at Kb0 was more pronounced than in the sediment trap because of high abundance in the trap samples in April. In September, *C. finmarchicus* and *C. hyperboreus* abundance and distribution were similar to that seen in July, whilst *C. glacialis* were most abundant at depth. Of the other zooplankton, the most frequently occurring and abundant taxa at Kb0 were also present in the sediment

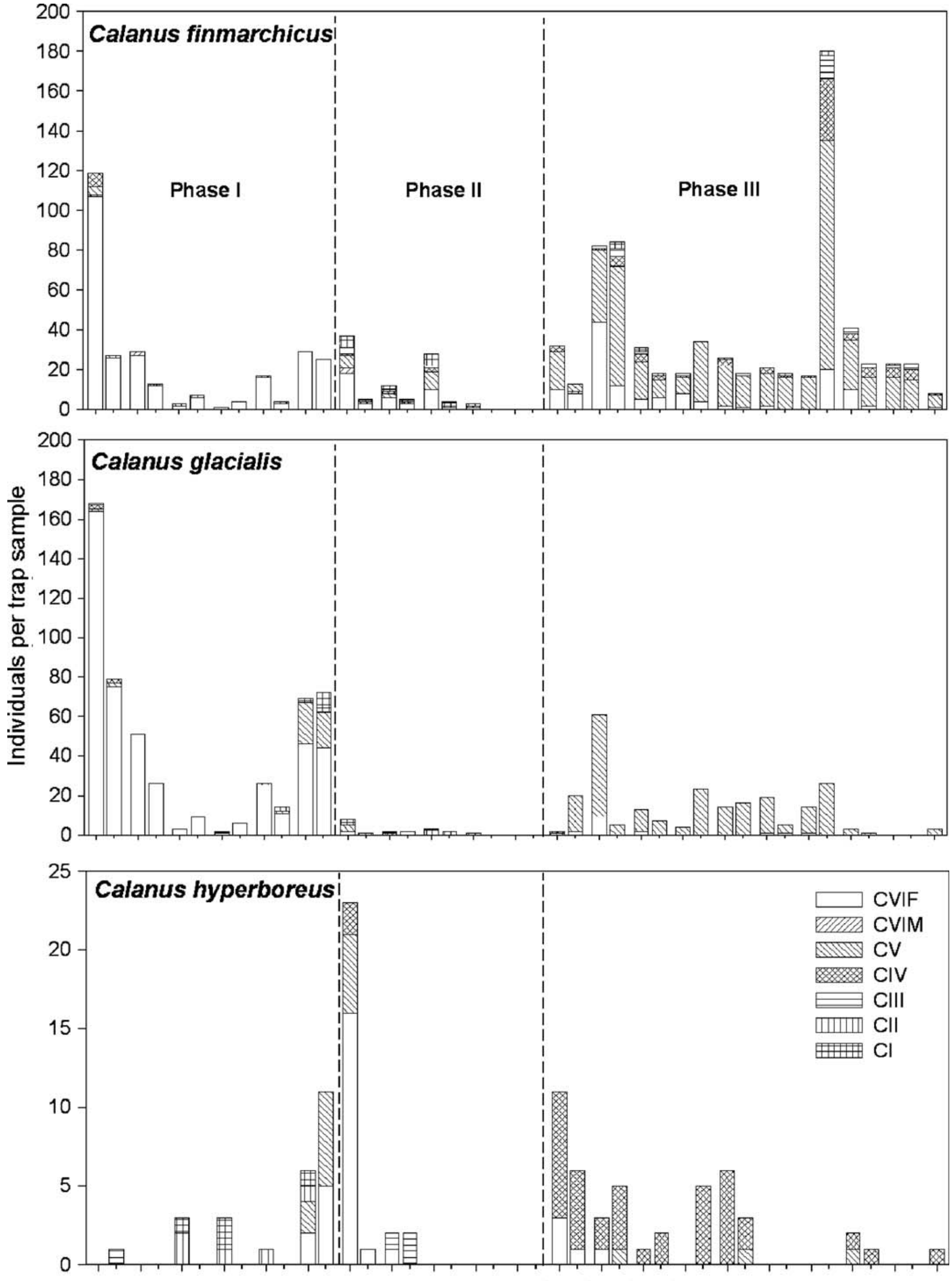

Fig. 4. Abundance of *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* development stages in the sediment trap deployed at a depth of 65 m in Kongsfjorden between April and September 2002. Phases I, II and III shown in Fig. 2 are indicated by the vertical broken lines. Developmental stages are copepodite stages CI to CVI females (F) and males (M). Note: *y*-axis scales are different.

trap, although not in high numbers, namely, *M. longa*, *O. similis*, *Pseudocalanus* spp. and *Microcalanus* spp., *Triconia borealis*, and Cirripedia nauplii. Of these, *Pseudocalanus* spp., *O. similis* and Cirripedia nauplii generally preferred the surface waters, while the others occurred at greater depths at Kb0.

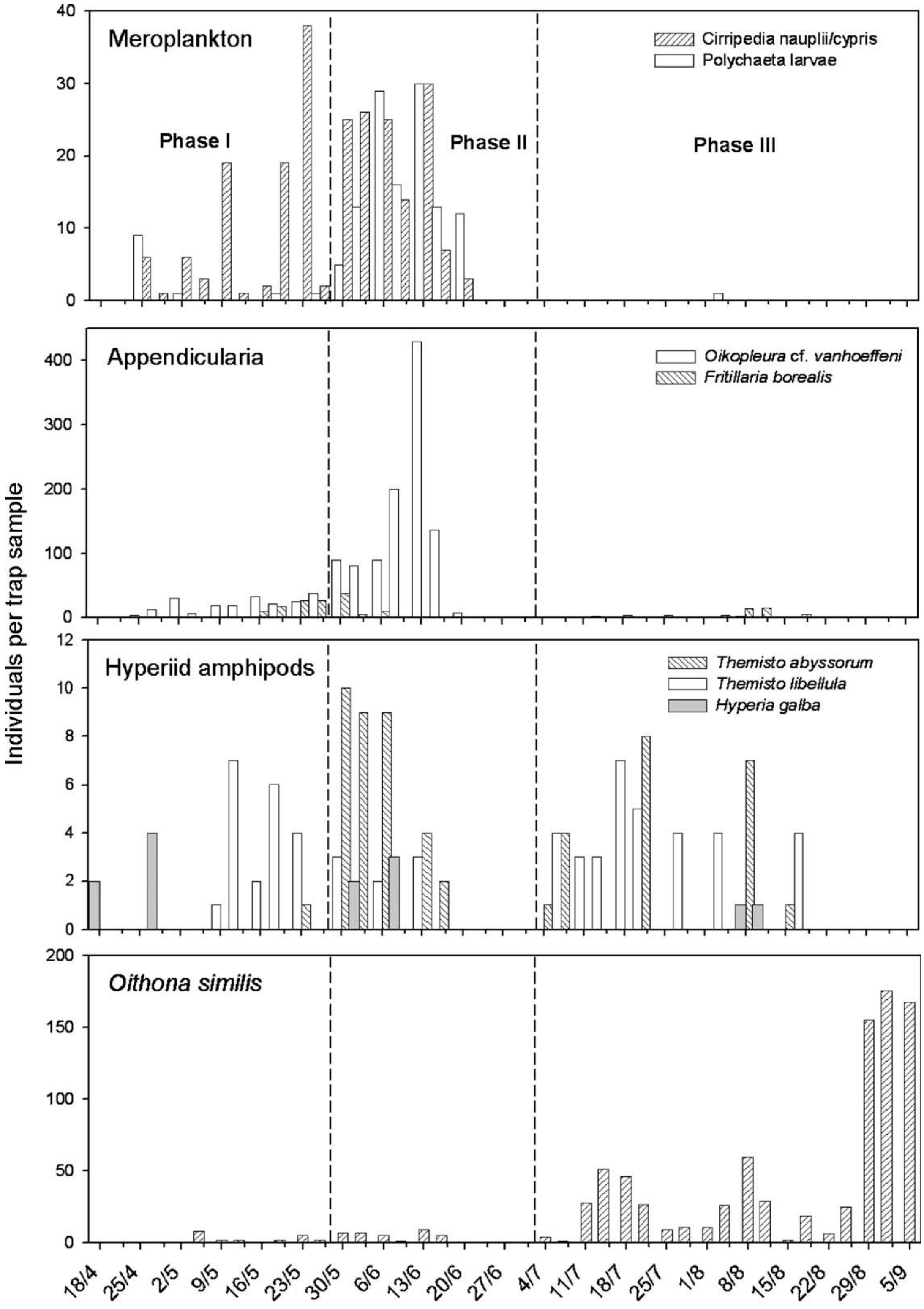

Fig. 5. Abundance of meroplankton, appendicularians, hyperiid amphipods and *Oithona similis* in the sediment trap deployed at a depth of 65 m in Kongsfjorden between April and September 2002. Phases I, II and III shown in Fig. 2 are indicated by the vertical broken lines. Note: *y*-axis scales are different.

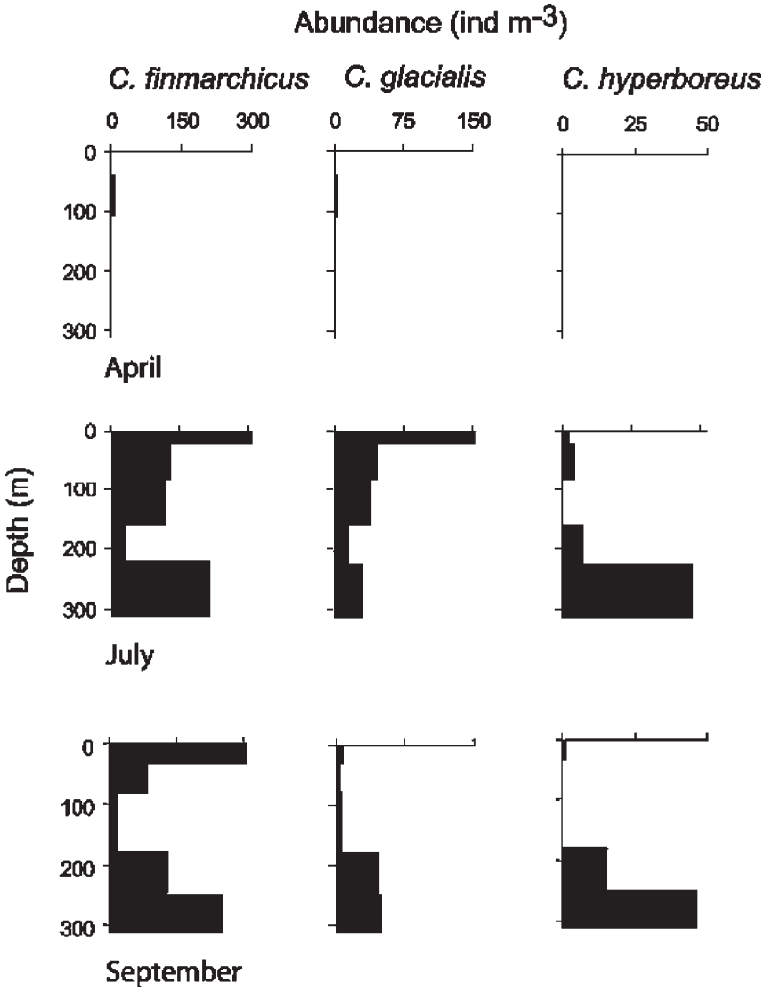

Fig. 6. Vertical distribution of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* at station Kb0 at the entrance to Kongsfjorden in April, July and September 2002. Note: *x*-axis scales are different.

3.3. Hydrography

The ADCP recorded steady southwest currents confirming the occurrence of a persistent cyclonic circulation within the fjord with the mooring located on the northern side of the gyre (Fig. 1B). For further details refer to Cottier et al. (2005). CTD casts indicate that the hydrography of the fjord changed markedly over the observational period between April and September (Fig. 7). In April, at the start of Phase I, the water was isothermal with a very weak salinity gradient. In June, at the end of Phase II, ArW occupied the water above the sediment trap, with TAW below. By September, at the end of Phase III, the sediment trap was located in the middle of the AW layer, which extended from 25 to 100 m, with TAW remaining in the deep water.

The *T* and *S* time series measured by the microcat at 40 m during zooplankton community Phase I showed remarkably little temporal variation, with values of temperature (<0 °C) and salinity (ca. 34.5) indicative of the presence of local WCW (Fig. 8). During Phase I temperature increased by only 1 °C over 6 weeks due to surface warming and vertical mixing. Mean differences in the temperature and salinity between each 3.5 day period in Phase I were 0.13 °C and 0.016 respectively.

The hydrographic transition from Phase I to II was very abrupt in the upper water column (as indicated by points A and B in Fig. 8, which represent consecutive trap samples). Temperature was used as the criterion to distinguish between Phases and between Phase I and II it increased by over 1 °C, an order of magnitude greater than the mean change of 0.13 °C during Phase I. In contrast, salinity increased by only 0.03 between Phase I and II. The temperature change was indicative of a change in dominant water mass in the fjord from local WCW to ArW advected from the shelf. The ArW then

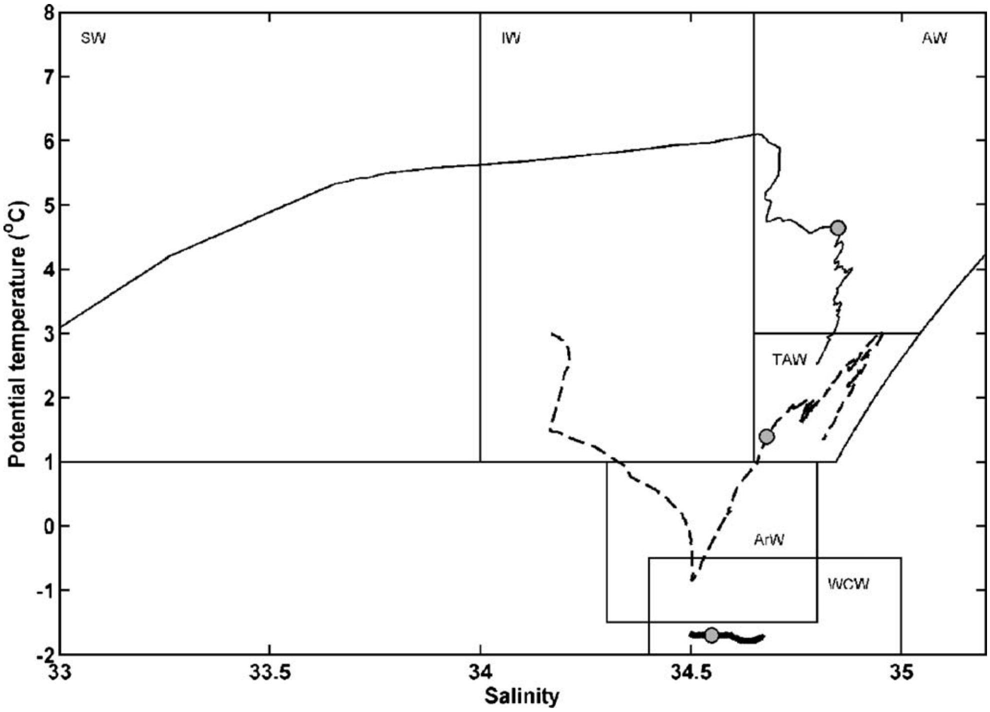

Fig. 7. *T–S* diagram of vertical CTD profile data obtained at the mooring site in 2002 during mooring deployment and recovery: April (heavy solid line) is the start of Phase II, June (dashed line) is the end of Phase II, September (light solid line) is the end of Phase III. The grey circles indicate the depth of the sediment trap in the CTD profiles. The data are superimposed on the water mass domains described in the Introduction; Winter Cooled Water (WCW); Arctic Water (ArW); Transformed Atlantic Water (TAW); Atlantic Water (AW); Intermediate Water (IW); Surface Water (SW).

dominated throughout Phase II with temperature and salinity relatively well constrained; mean differences between 3.5 day periods were 0.35 °C and 0.06 respectively. Towards the end of Phase II, there was an increase in both parameters as indicated by data point C (Fig. 8).

A massive hydrographic transition from Phase II to III is illustrated by data points C and D, which are separated by a period of 11 days when the mooring was removed for servicing. Again, temperature is used as the criterion for identifying this transition, with an increase of 2.75 °C between Phases II and III compared to a mean change of only 0.35 °C during Phase II. The increase indicates a change in water mass dominance from ArW to AW in the upper water column. During the final period of Phase III, temperature increased by about 2 °C, and salinity decreased by ca. 0.5 due to the increased influence of glacial melt and run-off.

Changes in the temperature structure of the water column at the time of each Phase transition are shown in Fig. 9. At the end of Phase I, the water column temperature was sub-zero and homogenous with predominantly WCW (Fig. 9A). The change during the transition to Phase II on 30 May was abrupt, with water temperature increasing at a rate and depth greater than could be accounted for by simple atmospheric warming. Water warmer than WCW, principally ArW, was advected into the upper water column across a depth interval from approximately 25 to 100 m, with the greatest temperature change (>3 °C) occurring at a depth of ca. 75 m, just below the sediment trap. At the end of Phase II, the hydrography of the deep water also changed as the water column became occupied first by ArW and then TAW. Between Phases II and III (Fig. 9B), temperature increased considerably in the upper water column (above ca. 140 m) due to a substantial intrusion of AW. In the deep water TAW remained as the dominant water mass during the transition to Phase III.

4. Discussion

4.1. Advection and zooplankton community composition

Physical processes such as advection are known to influence productivity, community composition, age structure, biomass and distribution of zooplankton in fjordic systems (Matthews and Heimdal, 1980; Lindahl

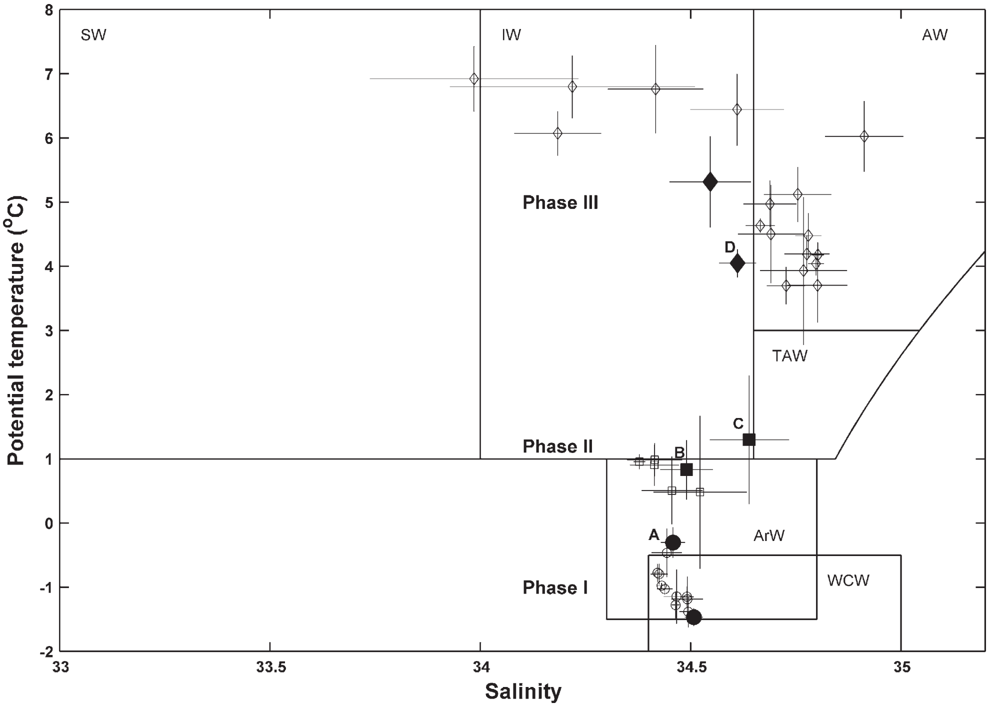

Fig. 8. *T*–*S* diagram showing temperature and salinity (mean ± S.D.) measured at 40 m for the 3.5 day period of each sediment trap sample. The data are categorised according to the three phases of zooplankton community composition shown in Fig. 2; Phase I (○); Phase II (□); and Phase III (◇). Filled symbols represent the first and last samples in each phase; last sample Phase I (A); first sample Phase II (B); last sample Phase II (C); first sample Phase III (D). Water mass domains are as per Fig. 7.

and Henroth, 1988; Aksnes et al., 1989; Basedow et al., 2004). This is particularly true in Kongsfjorden, where it has been proposed that the proportions of zooplankton species with different biogeographic origins respond to and represent changes in the distribution and dynamics of water masses to the west of Spitsbergen and their intrusion into the fjord (Hop et al., 2002; Kwasniewski et al., 2003). Annual sampling at fixed stations in Kongsfjorden since 1996 has shown seasonal variation in the proportions of the co-occurring *Calanus* species, and it has been assumed that changes in environmental conditions observed throughout the year were responsible (Hop et al., 2002; Kwasniewski et al., 2003; Walkusz et al. pers. comm.). In the current study, the concurrent high resolution zooplankton and hydrographic time series have clearly shown the close relationship between advection events and changes in zooplankton community structure in the fjord, in particular the abrupt nature of the transition between phases.

In 2002, the zooplankton community in the outer basin of Kongsfjorden, as represented by the species present in the sediment trap samples, could be grouped into three distinct species associations (Phases I, II and III) demarcated by major advection events when distinct water masses crossed the West Spitsbergen Shelf and occupied the fjord. Between April and September 2002, there were two substantial and rapid changes in water mass characteristics (predominantly temperature) detected at the mooring. The rapidity and magnitude of the hydrographic changes recorded at the mooring can only be explained by advection of water masses through the outer basin of the fjord on account of the mooring location with respect to the dominant fjord circulation (Fig. 1B). Previous studies have also shown that advected water masses can penetrate far into the fjord (Berge et al., 2005; Cottier et al., 2005; Svendsen et al., 2002), and that the cyclonic gyre in the outer basin can retain zooplankton within the fjord (Basedow et al., 2004).

The first intrusion in late May was indicative of ArW crossing the front between the shelf waters and the predominantly WCW in the fjord. ArW and TAW were recorded in the deep water only towards the end of June (Fig. 7 and Cottier et al., 2005). The second major intrusion, beginning in mid-June, caused a shift in water mass dominance from ArW to AW (Fig. 9B) and was characterised by a significant increase in

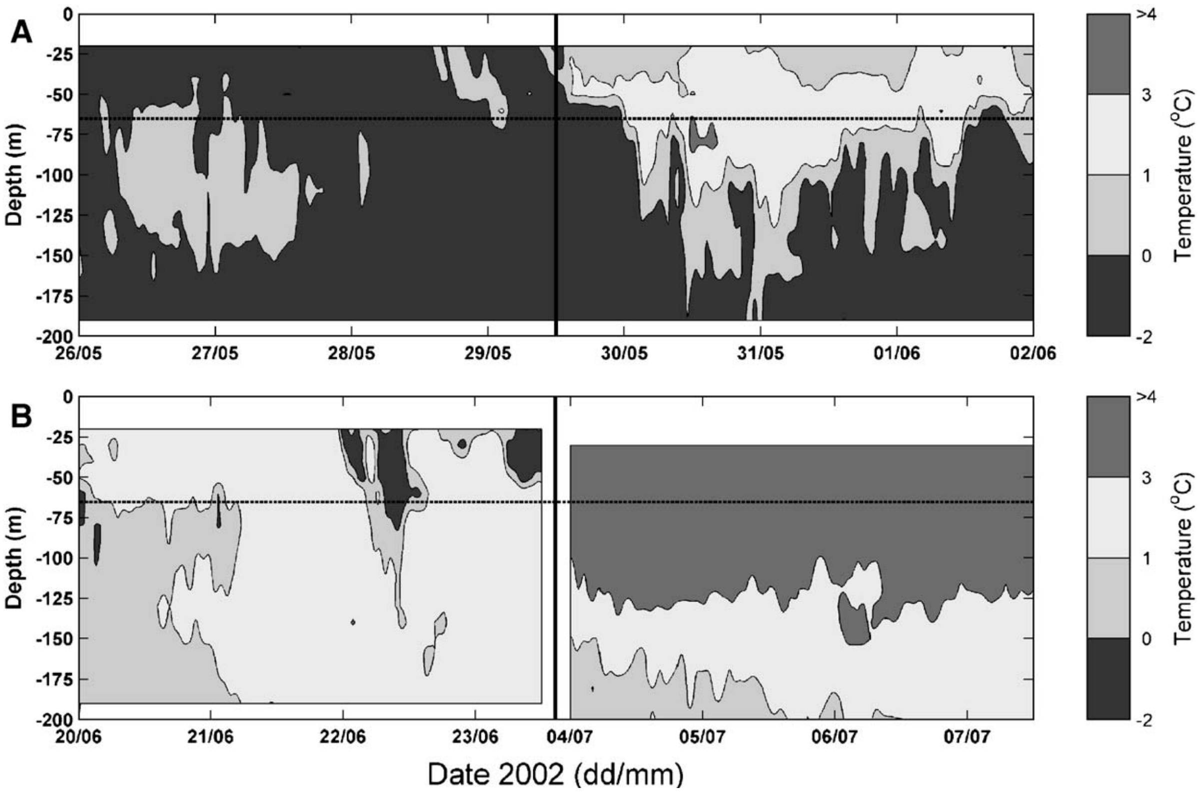

Fig. 9. Contour plot of the vertical temperature profile measured at the mooring site for the 3.5 days preceding and following the transition between the three phases: (A) Temperature profiles during the transition from Phase I to II (samples A and B in Fig. 8) and (B) during the transition from Phase II to III (samples C and D in Fig. 8). The solid vertical line demarcates the time of transition between phases according to the opening/closing of sequential sample bottles. The broken horizontal line indicates the depth of the sediment trap. Note; the break in the time series between Phases II and III as indicated along the date axis of (B).

temperature in the upper water column indicating extensive exchange of water between the shelf and the fjord. Atlantic Water then dominated the upper water column between 25 and 100 m until the mooring was retrieved in September. Although advection did modify the deep water the most significant water mass exchanges recorded at the mooring occurred in the upper 100 m within which the sediment trap was located.

Changes in zooplankton community composition were closely associated with the water mass intrusions. During Phase I, when the fjord was filled with local WCW and isolated from the ArW on the shelf, the zooplankton community comprised species with both boreal and Arctic origins, although Arctic species dominated. The presence of species from warmer biogeographic regions illustrates that boreal species are able to survive in the fjord over the Arctic winter. The abundant female *C. finmarchicus* and *C. glacialis* present in the trap in mid-April represent resident populations which would have overwintered in the fjord as CVs. The presence of large numbers of females in the surface waters indicates spawning activity by both species, with female abundance declining soon after the trap was deployed.

The ArW intrusion in late May was accompanied by an abrupt change in zooplankton community composition, with distinct peaks in abundance of Arctic and boreo-arctic species during the transition period from Phase I to II. The Phase II zooplankton community consisted of earlier life stages of all three *Calanus* species, albeit in low abundance, indicating earlier spawning by *Calanus* on the shelf than in the fjord. Higher numbers of copepod nauplii and meroplankton (Polychaeta and Cirripedia larvae) advected from the shelf were also present in the trap samples.

The Phase III zooplankton community comprised species of both boreal and Arctic origins, representing a mixture of those species advected into the fjord in the AW intrusion in late June/early July and those species already present in the fjord. The zooplankton community was dominated by the boreal *C. finmarchicus* and a greater diversity of copepod species from both boreal and Arctic regions.

Unexpectedly, the last sediment trap sample (early September) contained a considerable number (10) of the decapod shrimp *Eualus gaimardii*. The presence of this benthic species (Weslawski, 1987, 1991) in the sediment trap was surprising. However, it has been shown to display a mostly pelagic feeding habit in Isfjorden, Svalbard, preying mainly on copepods and amphipods (Birkely and Gulliksen, 2003), which would perhaps explain its presence in the sediment trap.

4.2. Use of sediment traps to sample zooplankton

The sediment trap samples have provided the first high resolution time series of change in zooplankton community composition that can be related directly to advection events in Kongsfjorden. However, given the deployment depth of the sediment trap (65 m), changes in species abundance should realistically only be considered to reflect changes in community composition and abundance in the surface layers (0 to 65 m). Distinct aggregations of *Calanus* consisting of different developmental stages have been shown to occupy different depth layers in the fjord with younger copepodids (CI–CIV) in the surface and intermediate layers and older copepodids in the bottom layers (Kwasniewski et al., 2003). Consequently, we would not expect species and life stages resident at greater depths to be present in the trap samples, unless they were undergoing regular (diel) vertical migrations (DVM). Thus, we acknowledge that the results are likely to be biased towards species present in the upper water column.

However, comparison with data on zooplankton vertical distributions collected close to the mooring at station Kb0 using MPS has enabled us to ascertain whether the trends observed in the sediment trap time series can be considered as representative of the zooplankton community in the outer basin of Kongsfjorden. Given the similarity in trends shown at Kb0 and in the sediment trap samples, we are confident that the trap provides a reliable representation of the temporal changes in zooplankton community composition within the outer basin of Kongsfjorden. It is possible that zooplankton behaviour such as DVM may have influenced species abundance in the sediment trap due to an increased likelihood of encountering the trap during regular downward migrations. However, it is becoming increasingly recognised that Arctic zooplankton do not undergo synchronised DVM under the midnight sun (Hansen et al., 1990; Blachowiak-Samolyk et al., 2006). In the Marginal Ice Zone (MIZ) of the Barents Sea, Blachowiak-Samolyk et al. (2006) found little evidence of DVM during a period of midnight sun (May 1999) and instead suggested that temporal changes in vertical distribution were the result of patchiness and changes in the physical environment particularly with respect to water mass distributions. Furthermore, many of the numerically abundant taxa such as copepod nauplii, *Pseudocalanus* spp., *O. similis*, and the three *Calanus* species were concentrated in the upper 50 m of the water column in the MIZ. Of the dominant taxa, only *Microcalanus* spp., *M. longa* and *T. borealis* were concentrated at depths greater than 50 m (Blachowiak-Samolyk et al., 2006). It is also possible that if the sediment trap had been deployed deeper in the water column, the abrupt transitions between zooplankton phases, as a result of the two major advection events, may have passed undetected as the most profound effects of the intrusions were initially restricted to the upper water column where the sediment trap was located (see Fig. 9). Thus, it is more likely that physical processes (water mass advection) and seasonal ontogenetic migrations were the primary influences on species composition of the sediment trap samples in Kongsfjorden.

4.3. Calanus population dynamics

Walkusz et al. (pers. comm.) suggest that the resident *C. finmarchicus* population is unable to maintain continuity as they observed very low numbers throughout the fjord in April. Instead, they suggest that the population is maintained by advection of Atlantic Water into the fjord. Therefore, the high numbers of CVI female *C. finmarchicus* and *C. glacialis*, along with a few male *C. finmarchicus*, present in the sediment trap samples in mid-April were somewhat unexpected, and indicate development from resident overwintering stocks. Furthermore, the different life histories of *C. finmarchicus* and *C. glacialis* have been assumed to result in segregated spawning in the fjord, thus reducing the potential for competition between the species. *C. finmarchicus* has a one year life cycle (Tande, 1982; Tande et al., 1985; Scott et al., 2000) and overwinters as stage CV. Low lipid levels found previously in overwintering *C. finmarchicus* CVs in Kongsfjorden suggest that to develop and reproduce in spring a period of feeding is required to allow development to stage CVI females and therefore spawning occurs during or after the spring bloom (Scott et al., 2000). Whereas *C. glacialis* spawns prior to the spring bloom (Smith, 1990; Hirche and Kattner, 1993; Scott et al., 2000) and has a one-to-two year life cycle (MacLellan, 1967; Tande et al., 1985; Conover and Siferd, 1993) and survives winter as stages CIV and CV. Following the second overwintering period, the lipid rich CVs are able to develop to females and spawn prior to or during the spring phytoplankton bloom (Scott et al., 2000). They may also utilise other energy sources such as heterotrophic material and ice algae allowing egg production before the onset of the spring bloom. The fact that high numbers of females of both species were present in the trap samples in mid-April suggests simultaneous spawning of the resident fjord populations.

In 2002, the spring phytoplankton bloom, which was dominated by diatoms, occurred between 18 and 26 April off Ny-Ålesund (H. Hodal, Univ. Tromsø, pers. comm.). During the bloom *Calanus* biomass in the fjord was still relatively low, and according to the sediment trap data the resident *Calanus* population was towards the end of spawning activity. This would suggest that the spring peak in primary production in the fjord was not utilised by *Calanus* as new populations from the shelf were not advected into the fjord until late May in the ArW intrusion. This has implications for pelagic–benthic coupling as zooplankton grazing is possibly the single most important factor regulating the amount of organic material sinking to the benthos in Kongsfjorden (Hop et al., 2002).

It is clear from our results that the resident *Calanus* populations were augmented by shelf populations. New populations of all three *Calanus* species were advected into the fjord in the ArW and AW intrusions as abundances and developmental stage compositions changed rapidly following each intrusion. A progression of *C. finmarchicus* developmental stages was observed in the sediment trap samples, beginning with the ArW intrusion at the end of May, although abundances were low. Following the AW intrusion, stage CV was the most abundant *C. finmarchicus* and *C. glacialis* developmental stage, though low numbers of CVI females and earlier stages of *C. finmarchicus* were also present throughout Phase III.

As proposed by Kwasniewski et al. (2003), it is unlikely that *C. hyperboreus* is able to maintain a resident population in the fjord during winter, therefore, the higher abundances of older life stages after mid-May represent advected individuals. Although low numbers of *C. hyperboreus* CI and CII were occasionally present in the trap in April and May (the product of winter spawning in the fjord), the population consisted primarily of advected CIV throughout most of the sediment trap deployment period. Thus, it is likely that *C. hyperboreus* either does not develop beyond this stage in the fjord, or that later stages avoid the surface waters due to temperature preferences. The overall low abundance of *C. hyperboreus* in the sediment trap samples reflects its preference for the cold water in the deeper basins of the fjord.

4.4. Implications of climate change

Current evidence for global climate change indicates that Arctic regions will experience the greatest effects (Fleming et al., 1997; Wlodarska-Kowalczuk and Weslawski, 2001; Sturm et al., 2003). Fjords on the west coast of Spitsbergen, which experience Atlantic, Arctic and freshwater inputs, are likely to be particularly sensitive to changes in oceanic and terrestrial conditions resulting from global climate change.

Kongsfjorden has a tendency to shift from an Arctic state (WCW and ArW dominated) to an Atlantic state (TAW and AW dominated) in June and July, and the degree to which AW occupies the fjord shows considerable inter-annual variation giving rise to 'warm' and 'cold' years in the fjord (Cottier et al., 2005). Variability in the northward transport of Atlantic Water is thought to be related to changes in atmospheric circulation as indicated by the North Atlantic Oscillation (NAO) index (Orvik et al., 2001; Saloranta and Haugan, 2001). During positive NAO phases, there is a strong northward flow of Atlantic Water (Dickson et al., 2000) and increased transport of boreal species (Berge et al., 2005; Skreslet and Borja, 2003). Future predictions provide conflicting scenarios with some forecasting an increase in the transport of Atlantic Water through Fram Strait (Zhang et al., 1998), while others predict a decrease in flow and cooling of Arctic regions (Hansen et al., 2001). Regardless, it is anticipated that future changes in oceanic fluxes will produce an adjustment of the hydrographic balance in Arctic shelf regions, with changes in the balance of associated species, and ensuing effects on ecosystem functioning.

4.5. Conclusions

The high-resolution time series of zooplankton and associated hydrographic data have, for the first time, clearly shown the close relationship between water mass advection from the adjacent shelf into Kongsfjorden and change in zooplankton community structure associated with these events. Three phases of zooplankton community composition were apparent in the fjord in 2002. The abrupt transitions between zooplankton phases occurred simultaneously with the influx of Arctic Water and Atlantic Water in late May and early July respectively.

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