ORIGINAL PAPER

Impact of warm water advection on the winter zooplankton community in an Arctic fjord

Kate J. Willis · Finlo R. Cottier · Slawek Kwaśniewski

Abstract The west coast of Spitsbergen is influenced by water masses of Atlantic and Arctic origin. During the winter of January–April 2006, water temperatures on the West Spitsbergen Shelf were ~3°C warmer than typical winter conditions, leading to a coastal sea ice cover of reduced thickness, extent and duration. A sediment trap deployed from September 2005 to May 2006 in the outer basin of Kongsfjorden (NW Spitsbergen) at a depth of 115 m has provided a continuous winter time-series of zooplankton during a period of rapid increase in water temperatures. Prior to an anomalous and prolonged influx of warm Atlantic water (AW) starting at the end of January, the trap samples were dominated by the boreo-Arctic copepod *Metridia longa*. Species that increased in abundance during the influx included late stages of *Calanus finmarchicus, C. glacialis, C. hyperboreus* and *Paraeuchaeta norvegica*. The early introduction of shelf populations into the fjord, and thus increased copepod biomass relative to typical winter conditions with little advection, has implications for the marine pelagic food web and pelagic-benthic coupling.

Keywords Arctic shelf · Kongsfjorden · Sediment trap · Advection · Atlantic water · *Calanus* · *Metridia longa*

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Introduction

Kongsfjorden, a glacial fjord on the northwest coast of Spitsbergen in the Svalbard archipelago, is strongly influenced by both Arctic and Atlantic water (AW) masses (Svendsen et al. 2002), and to a lesser extent glacial discharge (Maclachlan et al. 2007). The relative dominance of these water masses changes seasonally and inter-annually such that the shelf waters and adjacent fjords switch from a state of Arctic dominance to Atlantic dominance and back (Cottier et al. 2005; Svendsen et al. 2002). The fjord opens to the West Spitsbergen Shelf (WSS) through a common mouth it shares with the adjacent Krossfjorden (Fig. 1). A submarine glacial trough, Kongsfjordrenna, acts as a deep-water connection between the outer basin of Kongsfjorden and the shelf, so there is no topographic barrier to exchange between the shelf and the fjords (Svendsen et al. 2002). Therefore advection of water masses plays a significant role in determining the physical and biological characteristics of the fjord (Hop et al. 2002). Unlike other fjords in the Nordic Seas region, the zooplankton fauna in Kongsfjorden is relatively rich and comprised of co-occurring boreal and Arctic species, which respond to variations in the distribution and dynamics of the West Spitsbergen water masses (Kwaśniewski et al. 2003; Willis et al. 2006). Consequently, the composition of the zooplankton community in Kongsfjorden is a function of hydrographic processes and the origin of the water masses. Thus, the fjord is well suited to studying the effects of climate change on water mass distribution, sea ice conditions and ecosystem function in Arctic shelf ecosystems (Hop et al. 2006).

The WSS and adjacent coastal waters are influenced primarily by water masses of Arctic origin (Saloranta and Svendsen 2001), although there are often intrusions of warm AW crossing the Arctic Front from the West

Fig. 1 **a** The Svalbard archipelago with the Kongsfjorden-Krossfjorden system on the northwest coast of Spitsbergen highlighted 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 (*AW*). **b** The location of the mooring (*cross symbol*) 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
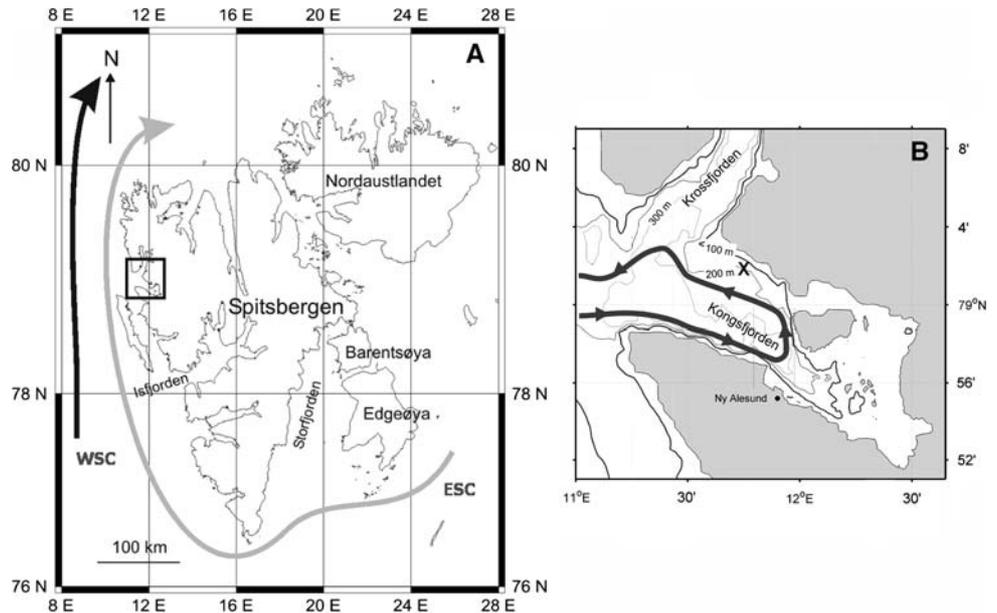
Spitsbergen Current onto the WSS and into the fjords. It is believed that the major intrusion of AW into the fjords occur primarily in the summer months, with a density front at the fjord entrance preventing winter intrusions (Cottier et al. 2005). However, during the winter of 2006, there was extensive advection of AW across the WSS and into the fjords of West Spitsbergen, which raised water temperatures by several degrees (Cottier et al. 2007).

The close relationship between water mass advection and changes in zooplankton community structure in Kongsfjorden during the summer months has been demonstrated using sediment traps (Willis et al. 2006). Although sequential sediment traps are not specifically designed to sample zooplankton they have been used to monitor zooplankton communities in regions where it is not practicable to use standard sampling methods (Hargrave et al. 1989, Forbes et al. 1992; Willis et al. 2006). With the exception of a study on *Pseudocalanus* and *Oithona* (Lischka and Hagen 2005), little is known about the winter zooplankton community in Kongsfjorden, so here we present a unique data set collected by a sediment trap in the outer basin of the fjord from September 2005 to May 2006. Crucially, it captures a distinct switch in the zooplankton community during the exceptionally warm and strongly advective conditions during the winter of 2006.

Methods

A sequential sediment trap (McLane Parflux 78H-21 with 21 cup carousel and 0.5 m^2 aperture) was moored at a depth of 115 m on the north side of the outer basin of Kongsfjorden at 79° 01.2N 11° 46.4E (Fig. 1; bottom depth ~210 m).

The sampling period was from 16 September 2005 to 17 May 2006, with a sampling frequency of one month per bottle from 16 September to 15 March, and seven days thereafter. Swimmers from the seven day samples (16 March to 19 April and 20 April to 17 May) were pooled for comparison with the monthly trap samples. Prior to deployment, sediment trap sample bottles were 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. Temperature (T) and salinity (S) were recorded during the sediment trap deployment period with Seabird 37 Microcats positioned at depths of 33 and 103 m. The microcats were accurate to 0.01°C (T) and better than 0.01 (S).

The trap samples were passed through a 300 μm mesh sieve to remove the larger swimmers. Any smaller species that may have been present in the samples (such as *Microcalanus*, *Oithona* and juvenile *Limacina helicina*) may not have been routinely retained on the sieve. All animals retained on the sieve were intact and showed no signs of decomposition, suggesting that they entered the trap actively and were subsequently killed by the preservative. All zooplankton retained on the sieve were sorted and identified. Developmental stages of *Calanus* were identified to species based on morphology and prosome lengths of individual copepodid stages according to Kwaśniewski 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. Zooplankton species are presented as numbers per trap sample, with sampling intervals of one month, starting on the 16th day of each month.

Results

Copepod abundance was highest in September, with *C. glacialis* (CV), *C. hyperboreus* (CIV), *C. finmarchicus* (CV) and *Paraeuchaeta norvegica* (CV) dominating the trap sample (Fig. 2). Other species present in low numbers in September included the amphipods *Melita palmata, Themisto abyssorum* and *T. libellula*, the chaetognaths *Sagitta elegans* and *Eukrohnia hamata*, and the decapod *Eualus gaimardii* (Fig. 3). Small numbers of *M. palmata* were also present in the October–December trap samples, while the small boreal copepod *Bradyidius similis* peaked in abundance in December (Fig. 2). Overall species abundance was lowest in the October trap sample with only small numbers of *M. palmata, C. glacialis, Metridia longa* and *P. norvegica* present. The appendicularian *Oikopleura* cf. *vanhoeffeni* peaked in abundance in November. Later life stages

(CV, CVI male and female) of the boreo-Arctic copepod *M. longa* dominated the samples from November to January, with a progressive increase in abundance over this period (Fig. 2). Peaks in abundance of later stages of *C. finmarchicus*, *C. glacialis* and the boreal *P. norvegica* occurred in February and March, corresponding with the influx of AW into the fjord (Fig. 4). A small peak in abundance of *C. hyperboreus* was also obvious in February. Abundance of *C. finmarchicus* and *C. glacialis* remained high in April, whilst *P. norvegica* was absent from the trap sample. The ostracod *Discoconchoecia elegans* peaked in abundance in January and February (Fig. 3). Other species occasionally present in the trap samples, albeit in very low numbers, included *Heterorhabdus norvegicus, Gaetanus tenuispinus, Pseudocalanus* spp., *Microcalanus* spp., *Thysanoessa* spp., *Tomopteris helgolandicus*, siphonophore fragments, and various polychaetes.

Fig. 2 Abundance of copepod developmental stages in the sediment trap deployed at a depth of 115 m in Kongsfjorden between September 2005 and May 2006. Trap sampling periods are one month, beginning on the 16th day of each month. Developmental stages are copepodid stages CIII to CVI males (*M*) and females (*F*). The *arrows in the top figures* indicate the start of the AW influx. Note: *y*-axis scales are different
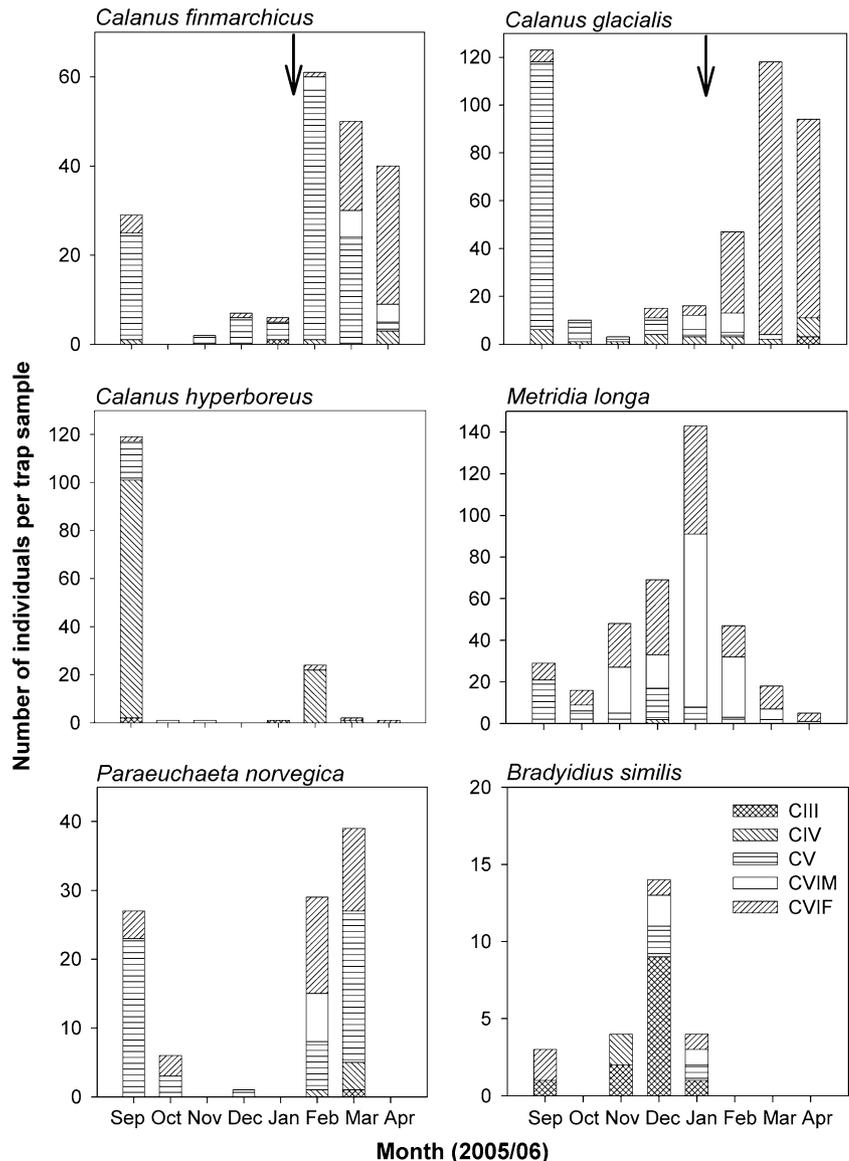
Fig. 3 Abundance of zooplankton swimmers in the sediment trap deployed at a depth of 115 m in Kongsfjorden between September 2005 and May 2006. Trap sampling periods are 1 month, beginning on the 16th day of each month. The *arrows in the top figures* indicate the start of the AW influx. Note: *y*-axis scales are different
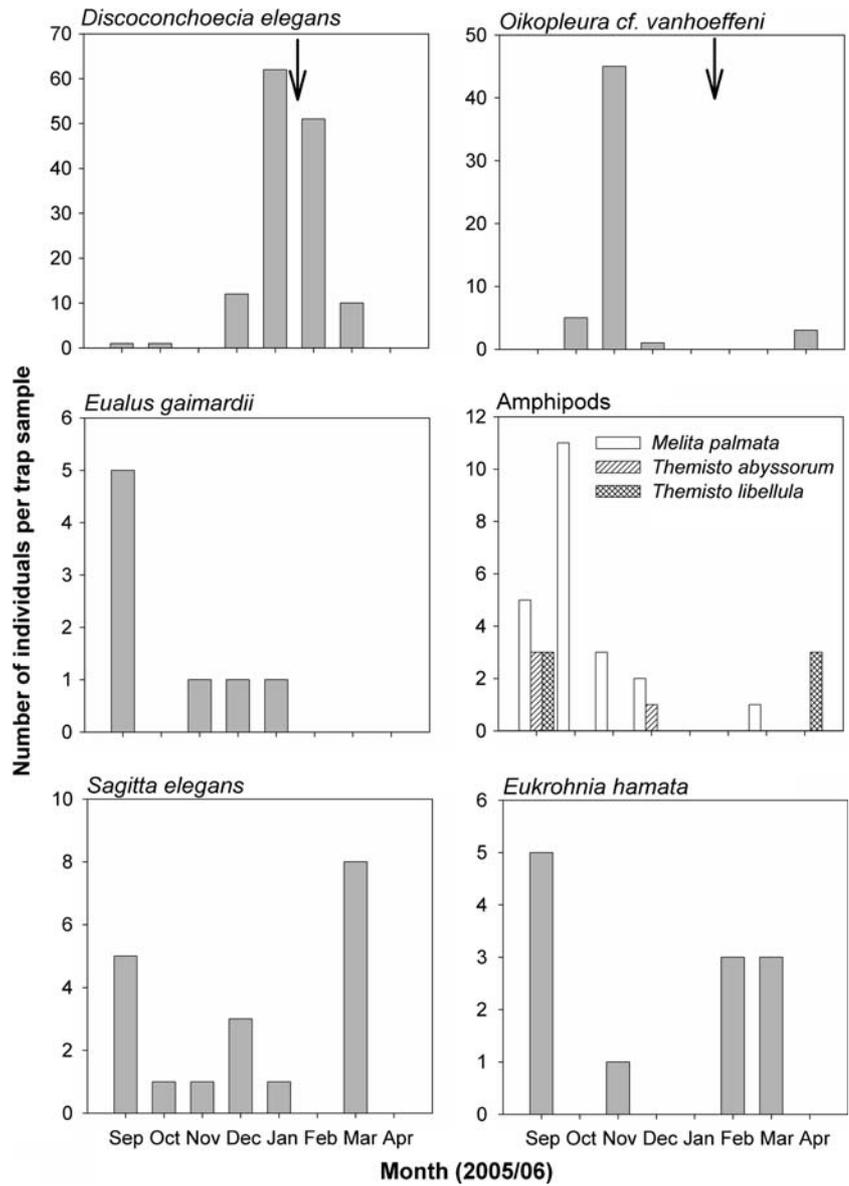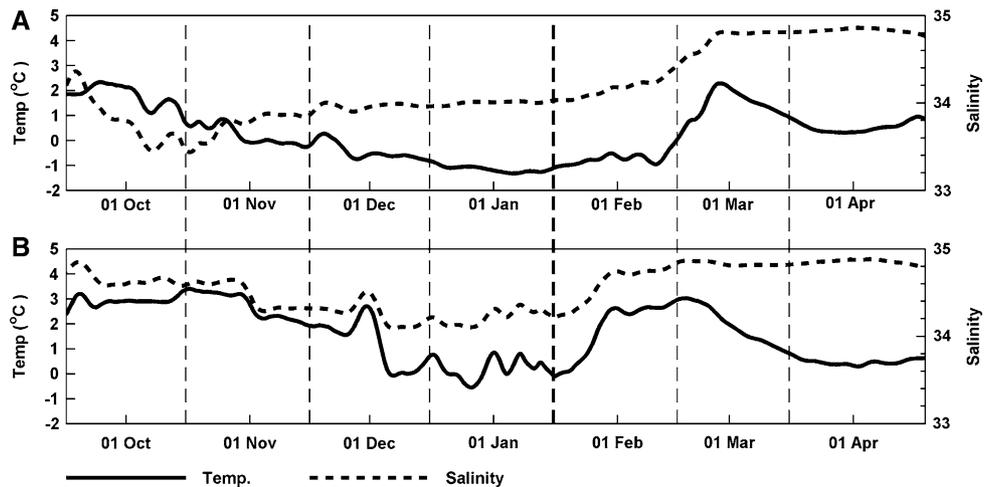

Fig. 4 Time series of temperature and salinity recorded at the **a** upper (33 m) and **b** lower (103 m) microcats. A 3.5-day box filter has been applied to the data. *Vertical broken lines* indicate the sampling periods for each sediment trap bottle starting on 16 September 2005 and ending on 17 May 2006. The *heavy broken line* indicates the start of the AW influx and transition period in zooplankton species composition

The hydrographic conditions at the location of the mooring were captured by the microcats (33 and 103 m) and the temperature and salinity time series are shown in Fig. 4. From September through to mid-January, the temperature at both microcats decreased from approximately 3 to −1°C, with small temperature fluctuations in early January at the lower microcat. Salinity at the upper microcat (33 m) decreased throughout September and then remained relatively stable at ∼34 from early November through to early February (Fig. 4a). At the lower microcat (103 m), salinity was initially around 34.8 reducing to 34.2 through December (Fig. 4b). From mid-January, as indicated by the heavy broken line in Fig. 4, both temperature and salinity increased at the lower microcat. A similar increase, beginning late in February, was also observed in the upper water column. At the end of February and in early March, both upper and lower microcats recorded water of ∼3°C and salinity 34.9, indicating the presence of AW in the fjord (Swift 1986). This was followed by a period of intense cooling of the entire water column during March and April through increased surface heat flux.

Discussion

There is an increasing body of information detailing changes in the physical environment of the Arctic in response to climate warming, whereas, there is little information available on associated changes in the biotic communities. The deployment of a sediment trap in Kongsfjorden has provided us with the first winter time series of the larger zooplankton species composition in the fjord. Furthermore, the winter of 2006 was unusual across the WSS in that there was extensive transport of AW across the shelf starting at the end of January. This inflow raised water temperatures by more than 3°C, reduced the extent and thickness of the sea ice cover, and transported zooplankton species onto the WSS and into Kongsfjorden, and presumably into other West Spitsbergen fjords.

The basis of the winter cross-shelf advection was an unusual pressure system over northern Europe bringing sustained southerly winds during December and January followed by a wind reversal and a sustained period of northerly winds. These meteorological conditions generated sustained up-welling at the shelf edge, leading to advection of AW across the WSS (Cottier et al. 2007). The effect was further enhanced by increases in northward transport of AW (Walczowski and Piechura 2007). The underlying cause of the meteorological conditions is beyond the scope of this paper; however, we do not attribute it to changes in the North Atlantic Oscillation index as the winter value for 2005–2006 does not show any strong anomaly.

Prior to the AW influx, the zooplankton sediment trap community was dominated by the boreo-Arctic copepod *M. longa*, with peaks of *O. vanhoeffeni* and *D. elegans* in November and January, respectively. There is no historical information on the community composition of the larger zooplankton species in Kongsfjorden during winter. However, the species composition in the trap samples was comparable to that in four sediment traps moored at similar depths on the shelf break of the Canadian Beaufort Sea during the winter of 1987–1988 (Forbes et al. 1992). As in the Beaufort Sea traps, calanoid copepods, and in particular *M. longa* females, dominated the Kongsfjorden trap samples. Unlike *Calanus*, *M. longa* remains active in the upper water column during the autumn and winter (Grønvik and Hopkins 1984; Båmstedt and Ervik 1984; Båmstedt et al. 1985), and its abundance progressively increased in the trap samples from October through to January, but then declined considerably following the AW influx in February. In two of the Beaufort Sea traps an overall trend of increasing *M. longa* abundance was apparent from November through to March (Forbes et al. 1992). Likewise, in Balsfjorden, Norway, *M. longa* increased in abundance throughout autumn and early winter, peaking in December (Barthel 1995).

From mid January 2006, there was a significant shift in species composition when the fjord's resident zooplankton community was augmented by expatriate species transported into the fjord from the WSS in the AW influx. Conspicuous peaks in abundance of *C. finmarchicus, C. glacialis, C. hyperboreus* and *P. norvegica* were associated with this influx. Given the timing of the AW influx in February, we must consider the possibility that the abundance peaks observed in the trap samples were unrelated to it, and instead reflect increasing copepod migratory activity towards the end of the Arctic winter, and seasonal migrations. However we suggest that for the AW indicator species in particular, this is unlikely. The existence of regular synchronised diel vertical migration (DVM) throughout most of the winter months has been identified in data from an ADCP (300 kHz) deployed during winter in Kongsfjorden at the same location as the sediment trap (not during the sampling period reported here), although the species responsible are unknown. This would suggest that the February abundance peaks are unlikely to represent the onset of synchronised DVM following its cessation during the Arctic winter. Instead, given that DVM behaviour occurs through winter, we would expect the abundances of the migrating species to remain relatively stable in the sediment trap samples throughout the deployment period, which was obviously not the case.

The peak of *P. norvegica* in the trap samples was clearly associated with the AW influx as this copepod resides in deep water during the winter (Baliño and Aksnes

1993; Skarra and Kaartvedt 2003), below the sediment trap sampling depth. Further south in Oslofjord, *P. norvegica* females were reported to be at their deepest (100–200 m) in February and March by Skarra and Kaartvedt (2003), with little evidence of DVM. We do not know exactly when the *Calanus* species begin their seasonal ascent to the surface following diapause in Kongsfjorden. It is likely that *C. glacialis* ascends earlier in the season than *C. finmarchicus* as it reproduces well before the spring bloom. In Lurefjord (western Norway), 80% of the immature *C. glacialis* females were located in the top 100 m of the water column by the end of February (Niehoff and Hirche 2005), and Arnkværn et al. (2005) estimated that reproduction started in late February/early March in Billefjorden, Svalbard. Thus, the increased abundance of *C. glacialis* in the February sediment trap sample is likely to reflect the combined influences of seasonal migration and shelf water advection.

Reproduction occurs later in *C. finmarchicus* and tends to coincide with the spring phytoplankton bloom (Diel and Tande 1992). Low-rate pre-bloom spawning by *C. finmarchicus* has been observed in AW in the Barents and Norwegian Seas (Melle and Skjoldal 1998; Hirche et al. 2001), and may also occur in Billefjorden (Arnkværn et al. 2005), where females peaked in abundance at the end of March. Thus, we suggest that the *C. finmarchicus* in the February sediment trap sample are likely to be individuals from the WSS transported into the fjord in the AW influx. The small peak of *C. hyperboreus* in February is harder to explain, but it was probably also due to the advection of shelf waters into the fjord. This oceanic species over-winters at depths greater than 1,000 m in the West Spitsbergen Current (WSC) south of Svalbard (Hirche 1997), where it does not begin the spring ascent until April. The high abundance of *Calanus* in the September sediment trap sample may be related to their seasonal descent in late summer.

Species associations in Kongsfjorden respond to variations in the distribution and dynamics of the regional water masses, with the proportions of each varying seasonally and inter-annually depending on the timing and volume of Atlantic and Arctic Water intrusions (Kwaśniewski et al. 2003; Willis et al. 2006). Copepod biomass in the fjord is generally augmented during influxes of water masses from the WSS in late spring and summer. Consequently, it is unlikely that the spring phytoplankton bloom in April–May is heavily grazed under normal conditions in the fjord. Changing patterns of atmospheric circulation may enhance coastal up-welling and advection of water masses from the shelf edge into the west Spitsbergen fjords throughout the year. The effect would be a change in the zooplankton species composition and biomass on the shelf and in the fjords, with ensuing impacts on the marine pelagic foodweb and the vertical flux of biogenic matter.

For example, it has been proposed that the lipid rich Arctic *Calanus* species will decrease in abundance in an AW dominated system, with a consequent decline in birds such as the little auk (*Alle alle*), which feed on them (Karnovsky et al. 2003). Obviously, this is not yet the case in Kongsfjorden, as *C. glacialis* abundance increased in the sediment trap following the AW influx. *C. glacialis* is an Arctic shelf species (Conover 1988), hence its association with the shelf waters advected into the fjord. However, its distribution does appear to be correlated with temperature, as females and copepodite stage V tend to avoid water temperatures above 5°C (Kosobokova 1998; Niehoff and Hirche 2005). Similarly, Hirche (1997) questions whether *C. hyperboreus* is able to reproduce successfully in the warmer waters of the WSC. Therefore, in a future Arctic likely to be increasingly dominated by warmer AW, it is still possible that the Arctic *Calanus* species may decline in abundance. Finally, under ice free conditions such as those experienced during the winter of 2006, phytoplankton production will dominate over ice algae production, and grazing by zooplankton will reduce the export of primary production to the benthos, retaining it in the water column and driving the food web away from the benthic community (Carroll and Carroll 2003).

References

Arnkværn G, Daase M, Eiane K (2005) Dynamics of coexisting *Calanus finmarchicus, Calanus glacialis* and *Calanus hyperboreus* populations in a high-Arctic fjord. Polar Biol 28:528–538

Baliño BM, Asknes DL (1993) Winter distribution and migration of the sound scattering layers, zooplankton and micronekton in the Masfjorden, western Norway. Mar Ecol Prog Ser 102:35–50

Båmstedt U, Ervik A (1984) Local variations in size and activity among *Calanus finmarchicus* and *Metridia longa* (Copepoda, Calanoida) overwintering on the west coast of Norway. J Plankton Res 6:843–857

Båmstedt U, Tande KS, Nicolajsen H (1985) Local variations in size and activity among *Calanus finmarchicus* and *Metridia longa* overwintering on the west coast of Norway. J Plankton Res 6:843–857

Barthel C-G (1995) Zooplankton dynamics in Balsfjorden, northern Norway. In: Skjoldal HR, Hopkins C, Erikstad KE, Leinaas HP (eds) Ecology of fjords and coastal waters. Elsevier, Amsterdam, pp 113–126

Conover RJ (1988) Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the Northern hemisphere. Hydrobiologia 167/168:127–142

Carroll ML, Carrol J (2003) The Arctic Seas. In: Black KD, Shimmield GB (eds) Biogeochemistry of marine systems. Blackwell, London, pp 127–156

Cottier FR, Tverberg V, Inall ME, Svendsen H, Nilsen F, Griffiths C (2005) Water mass modification in an Arctic fjord through cross-shelf exchange: the seasonal hydrography of Kongsfjord, Svalbard, J Geophys Res (Oceans) 110:c12005, doi: 10.1029/2004JC002757

Cottier FR, Nilsen F, Inall ME, Gerland S, Tverberg V Svendsen H (2007) Wintertime warming of an Arctic shelf in response to large-scale atmospheric circulation. Geophys Res Lett 34:L10607, doi:10.1029/2007/GL029948

Diel S, Tande K (1992) Does the spawning of *Calanus finmarchicus* in high latitudes follow a reproducible pattern. Mar Biol 113:21–31

Forbes JR, Macdonald RW, Carmack EC, Iseki K, O'Brien MC (1992) Zooplankton retained in sequential sediment traps along the Beaufort Sea shelf break during winter. Can J Fish Aquat Sci 49:663–670

Grønvik S, Hopkins CCE (1984) Ecological investigations of the zooplankton community of Balsfjorden, northern Norway: generation cycle, seasonal vertical distribution, and seasonal variations in body weight and carbon and nitrogen content of the copepod *Metridia longa* (Lubbock). J Exp Mar Biol Ecol 80:93–107

Hargrave BT, von Bodungen B, Conover RJ, Fraser AJ, Vass WP (1989) Seasonal changes in sedimentation of particulate material and lipid content of zooplankton collected by sediment trap in the Arctic Ocean off Heiberg Island. Polar Biol 9:467–475

Hiche H-J (1997) Life cycle of the copepod *Calanus hyperboreus* in the Greenland Sea. Mar Biol 128:607–618

Hirche H-J, Brey T, Niehoff B (2001) A high-frequency time series at ocean Weather ship station M (Norwegian Sea): population dynamics of *Calanus finmarchicus*. Mar Ecol Prog Ser 219:205–219

Hop H, Pearson T, Hegseth EN, Kovacs KM, Wiencke C, Kwaśniewski S, Eiane K, Mehlum F, Gulliksen B, Wlodarska-Kowalczuk M, Lydersen C, Weslawski JM, Cochrane S, Gabrielsen GW, Leakey RJG, Lønne OJ, Zajaczkowski M, Falk-Petersen S, Kendall M, Wängberg S-A, Bischof K, Voronkov AY, Kovaltchouk NA, Wiktor J, Poltermann M, di Prisco G, Papucci C, Gerland S (2002) The marine ecosystem of Kongsfjorden, Svalbard. Polar Res 21:167–208

Hop H, Falk-Petersen S, Svendsen H, Kwaśniewski S, Pavlov V, Pavlova O, Søreide JE (2006) Physical and biological characteristics of the pelagic system across Fram Strait to Kongsfjorden. Prog Oceanogr 71:182–231

Karnovsky NJ, Kwaśniewski S, Weslawski JM, Walkusz W, Beszczyńska-Möller A (2003) Foraging behaviour of little auks in a heterogeneous environment. Mar Ecol Prog Ser 253:289–303

Kosobokova KN (1998) New data on the life cycle of *Calanus glacialis* in the White Sea (based on observations of its genital system development). Oceanology 38:347–355

Kwaśniewski S, Hop H, Falk-Petersen S, Pedersen G (2003) Distribution of *Calanus* species in Kongsfjorden, a glacial fjord in Svalbard. J Plankton Res 25:1–20

Lischka S, Hagen W (2005) Life histories of the copepods *Pseudocalanus minutus, P. acuspes* (Calanoida) and *Oithona similis* (Cyclopoida) in the Arctic Kongsfjorden (Svalbard). Polar Biol 28:910–921

Maclachlan SE, Cottier FR, Austin WEN, Howe JA (2007) The salinity:δ^{18}O water relationship in Kongsfjorden, western Spitsbergen. Polar Res 26:160–167

Melle W, Skjoldal HR (1998) Reproduction and development of *Calanus finmarchicus, Calanus glacialis* and *Calanus hyperboreus* in the Barents Sea. Mar Ecol Prog Ser 169:211–228

Niehoff B, Hirche H-J (2005) Reproduction of *Calanus glacialis* in the Lurefjord (western Norway): indication for temperature-induced female dormancy. Mar Ecol Prog Ser 285:107–115

Saloranta TM, Svendsen H (2001) Across the Arctic front west of Spitsbergen: high-resolution CTD sections from 1998–2000. Polar Res 20:177–184

Skarra H, Kaartvedt S (2003) Vertical distribution and feeding of the carnivorous copepod *Paraeuchaeta norvegica*. Mar Ecol Prog Ser 249:215–222

Svendsen H, Beszczyńska-Möller A, Hagen JO, Lefauconnier B, Tverberg V, Gerland S, Ørbæk JB, Bischof K, Papucci C, Zajaczkowski M, Azzolini R, Bruland O, Wiencke C, Winther J-G, Dallmann W (2002) The physical environment of Kongsfjorden-Krossfjorden, an Arctic fjord system in Svalbard. Polar Res 21:133–166

Swift JH (1986) The Arctic waters. In: Hurdle BG (ed) The Nordic Seas. Springer, New York, pp 124–156

Walczowski W, Piechura J (2007) Pathways of the Greenland Sea warming. Geophys Res Lett 34:L10608, doi:10.1029/2007GL029974

Willis KJ, Cottier F, Kwaśniewski S, Wold A, Falk-Petersen S (2006) The influence of advection on zooplankton community composition in an Arctic fjord (Kongsfjorden, Svalbard). J Mar Syst 61:39–54