



Zooplankton community structure; a comparison of fjords, open water and ice stations in the Svalbard area

Wojciech WALKUSZ¹, Katharina STOREMARK², Torunn SKAU³, Charlotte GANNEFORS⁴ and Marte LUNDBERG⁴

¹ *Instytut Oceanologii, Polska Akademia Nauk, ul. Powstancow Warszawy 55, 81-712 Sopot, Poland
<walwo@iopan.gda.pl>*

² *The University Centre on Svalbard, P.O.Box 156, N-9171 Longyearbyen, Norway*

³ *University of Bergen, Department of Fisheries and Marine Biology. P.O.Box 7800, N-5020 Bergen, Norway*

⁴ *Norwegian Polar Institute, The Environmental Centre, N-9296 Tromsø, Norway*

ABSTRACT: The zooplankton community structure was studied in the Svalbard area at three shelf stations: Billefjorden, Kongsfjorden and Hinlopen (Spitsbergen shelf area), and at two open water stations: Ice West and Ice East (north of Spitsbergen, in the Arctic Ocean). Two different plankton nets – WP-2 and WP-3 – were used to collect a size range of zooplankton. The Bray-Curtis similarity analysis showed differences between sampling stations based on total zooplankton abundance, species composition, and comparison of *Calanus* spp. development. Total abundance was the highest in Kongsfjorden and Hinlopen. The small omnivorous copepod *Oithona similis* Claus, 1863 was the dominating species at all localities and the Atlantic copepod *Calanus finmarchicus* (Gunnerus, 1765) was found at all stations. *Calanus* spp. development was delayed at the ice stations when compared to the shelf stations. Results are discussed in relation to differences in environmental factors among stations.

Key words: Arctic, Svalbard, zooplankton, *Calanus*, fjords.

Introduction

Zooplankton communities are primarily structured by the water masses they occupy (Falk-Petersen *et al.* 1999, Clark *et al.* 2001), but are also influenced by light intensity and primary production (Eilertsen *et al.* 1989). Approximately 75% of the pelagic primary production is grazed in the upper 300 meters of the water column (Barnes and Hughes 1999). At high latitudes the main characteristics of marine ecosystems are stable temperatures and one pronounced seasonal phytoplankton bloom as a response to cyclic changes in the light regime (Falk-Petersen

et al. 1982). At high latitudes light is strongly limited during winter, while a rapid increase in illumination in spring leads to rapid growth of phytoplankton during the spring bloom (Valiela 1995). The organisms inhabiting Arctic marine ecosystems have adapted to the seasonal variability in food supply by demonstrating high activity during the short growth period in the summer.

Among other zooplankton species, three *Calanus* species are found in Svalbard waters and they are the key species of the ecosystem (Hop *et al.* 2002, Karnovsky *et al.* 2003, Kwaśniewski *et al.* 2003). The population structure of calanoid copepods changes throughout the year according to the species' different reproductive cycles, which are influenced by temperature and food availability (Conover and Huntley 1991, Falk-Petersen *et al.* 1999). The three different *Calanus* species are considered to be indicators of the water masses they inhabit. *Calanus glacialis* Jashnov, 1955 is clearly of Arctic origin, but penetrates currents south of the Polar front (Conover 1988). *Calanus finmarchicus* is of Atlantic origin but co-occurs with Arctic species in areas of water mass convergence (Wiborg 1955, Tande 1991). *Calanus hyperboreus* Krøyer, 1838 is an Arctic deep-water species (Richter 1994, Hirche 1997) and its distribution mostly coincides with that of *C. glacialis*.

C. finmarchicus is expected to dominate in waters of Atlantic origin, whereas *C. glacialis* and *C. hyperboreus* are expected to dominate in waters of Arctic origin (Hop *et al.* 2002, Kwaśniewski *et al.* 2003).

The characteristics of the investigated area

The areas around Svalbard are influenced by both Atlantic water, originating from the warm Gulf Stream (Piechura 2001), and Arctic water from the Polar basin. Two well-defined currents influence the hydrology of the waters surrounding the West and North Coast of Spitsbergen (Fig. 1).

The West Spitsbergen Current (WSC) carries Atlantic Water with a salinity higher than 35.0 PSU and temperature above 3.0°C (Sakshaug *et al.* 1994). The Sørkapp Current (SC) carries Arctic Water with a salinity of 34.3–34.8 PSU and temperatures below 0°C. Coastal water is recognised above the shelf by a lower salinity than Atlantic water, while the temperature is approximately the same. The WSC flows along the entire West Coast of Spitsbergen and divides into two branches northeast of the island. The eastern branch flows north and around Spitsbergen and partly contributes to the southern flowing East Spitsbergen Current (ESC). The second branch flows north- and westwards, and later flows southwards below Arctic water in the East Greenland Current (EGC) (Fig. 1).

Sea-air exchange and the process of ice formation modify the warm Atlantic inflow to the Polar Basin. These processes take place on shallow shelf areas, mainly on the eastern side of the Polar Basin (Pfirman *et al.* 1994). Due to ice

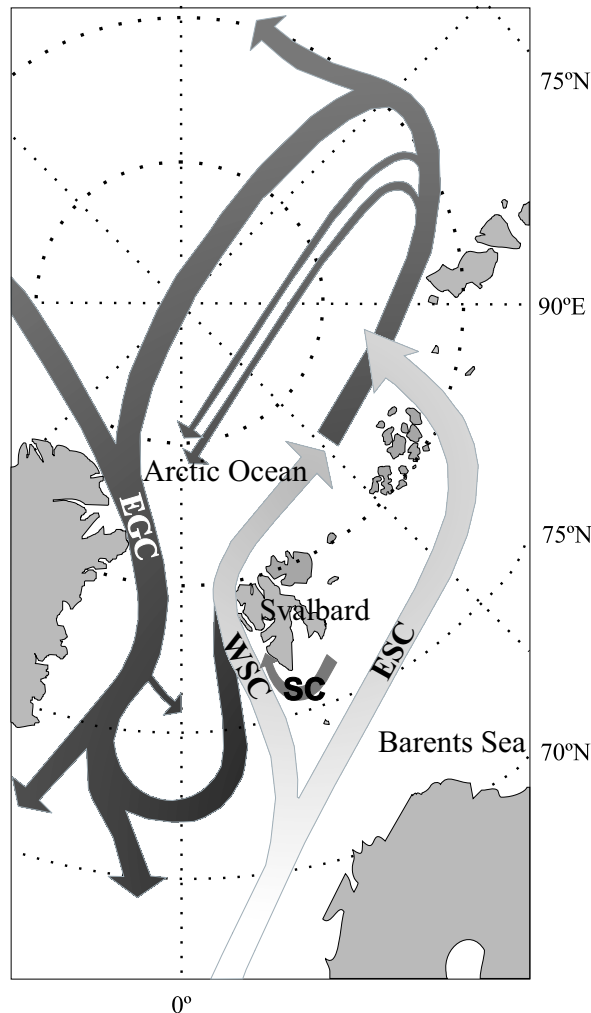


Fig. 1. Currents in the Arctic Ocean. The bright arrows indicate the warm Atlantic Water Currents and the dark arrows indicate the currents with cold and dense Arctic water. Original map was made by Vigdis Tverberg and Stig Falk-Petersen (unpublished; the map presented with authors' permission).

forming processes, cold and saline water is found in ice-covered areas. This water has high density and sinks to greater depth forming “deep water”.

Some open West Spitsbergen fjords, e.g. Kongsfjorden, are strongly influenced by warm Atlantic water (Svendsen *et al.* 2002), whereas sill fjords are influenced very little by this warm water. Due to the barrier created by a sill, the exchange of water masses will occur mostly in the upper water layer (Syvitsky *et al.* 1984, Asknes *et al.* 1989). In Billefjorden, a sill fjord, the cold and dense water that forms in the fjord basin is retained. In the Hinlopen strait cold water masses from the Polar Basin meet with warm Atlantic water. We aimed to determine, by com-

binning hydrological measurements and sampling of zooplankton at different localities in Svalbard waters, the zooplankton community structure and discuss how differences between the localities could relate to the local hydrography and bathymetry.

Materials and methods

Sampling of the zooplankton communities was conducted from R/V *Jan Mayen* from 11 to 24 September 2002 in five localities including two fjords (Kongsfjorden and Billefjorden), the strait Hinlopen, and in the open water (Ice stations East and West) (Fig. 2, Table 1).

Table 1

List of sampling stations.

| Station name | Geographical position | Echo depth |
|-----------------|------------------------------|------------|
| Billefjorden | 78°39'48'' N 16°44'06'' E | 189 m |
| Kongsfjorden | 78°59'55'' N 11°30'11'' E | 359 m |
| Ice West | 81°12'43'' N 01°18'32'' E | 1612 m |
| Hinlopen strait | 79°37'08'' N 18°59'28'' E | 327 m |
| Ice East | 81°39'38'' N 18°31'45'' E | 2456 m |

At each station a CTD (SEABIRD) probe was deployed. Conductivity and temperature profiles were measured from the surface to the bottom. Using standard plankton nets WP-2 (opening 0.25 m², mesh size 180 µm) and WP-3 (opening 1 m², mesh size 1000 µm) the entire water column was sampled in the two fjords and Hinlopen, but only the upper 300 m were sampled at the open sea stations. At each station two samples were taken: one with WP-3 and one with WP-2 net (in total 10 samples). We assumed 100% filtering efficiency. All samples were preserved in formaldehyde (4% solution in seawater, buffered with borax). Individuals larger than 1 cm were picked out and identified before the rest of the sample was divided into subsamples, using a micropipette or a box splitter, and subjected to detailed identification until more than 300 individuals were counted. If one species was very numerous it was necessary to enumerate more individuals of other taxa to obtain the assumed accuracy (Harris *et al.* 2000). Most of the organisms were identified to the species level, with some exceptions e.g. Harpacticoida, Ostracoda and Copepoda nauplii. *Calanus* species were identified to developmental stages on the basis of prosome length given in existing literature (Unstad and Tande 1991).

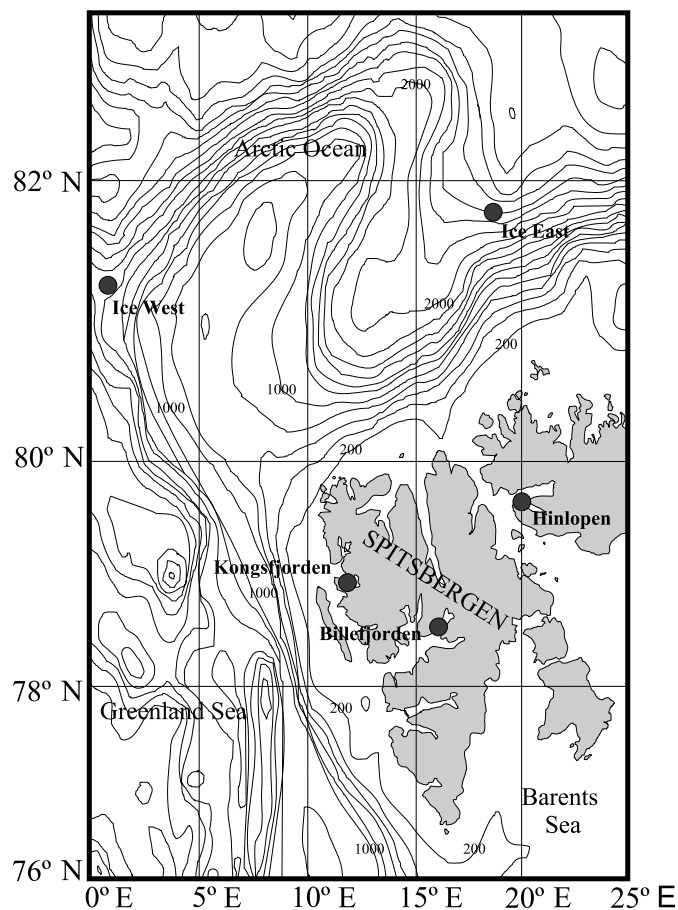


Fig. 2. Map of Spitsbergen and the five different sampling locations.
 Source: www.aquarius.geomar.de.

The zooplankton communities were compared between stations with respect to taxonomic composition and abundance using hierarchical clustering, Bray-Curtis similarity, and average linkage (Systat 9 software) (Field *et al.* 1982).

Results

Hydrography

Four sampling stations – Kongsfjorden, Ice West, Ice East and Hinlopen – were strongly influenced by the inflow of Atlantic Water (Fig. 3).

In Kongsfjorden Atlantic water was mixed with water of Arctic shelf origin and locally produced fjord water. At the Ice station West, Arctic Water was present

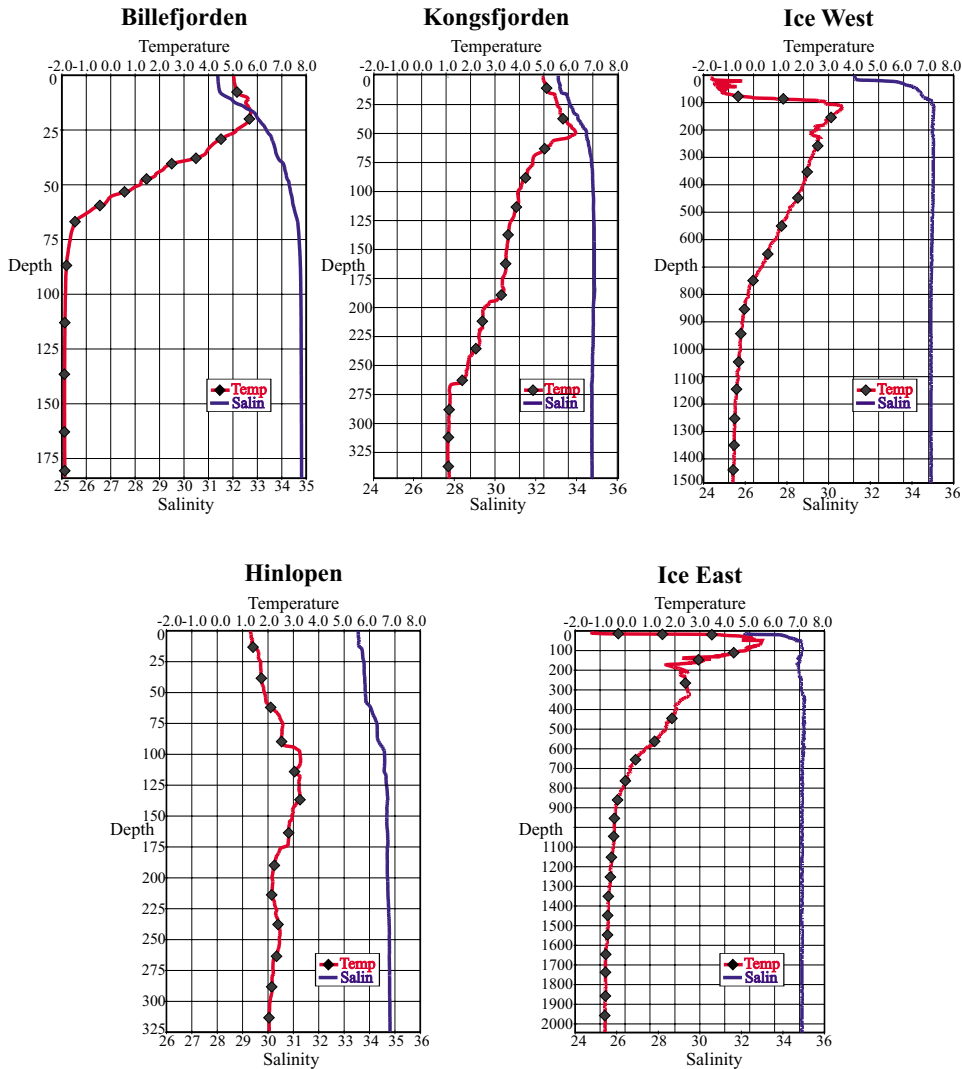


Fig. 3. Temperature and salinity measured at the five different stations.

in the upper 100 m and Atlantic Water was found below 100 m. At Ice station East, there were generally two layers present. The surface layer, the upper 50 m, had a lower salinity and lower temperature than the deeper saline water. The temperature in the deeper layer decreased down to 1000 m, where it became stable. In Hinlopen the mixing of water masses of Atlantic and Barents Sea/Arctic Ocean origin resulted in water masses gaining the characteristics of Arctic Surface Water (Smith 1990).

The CTD profile from Billefjorden showed a division of the water column into two main layers. The surface layer, down to 60 m, was characterised by warmer

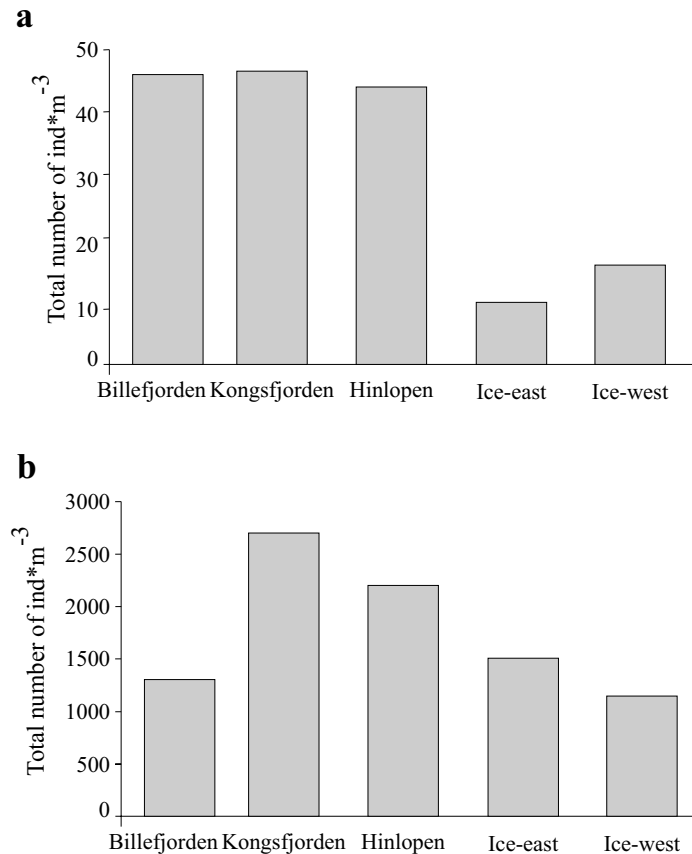


Fig. 4. Total zooplankton abundance as a number of individuals per m³ at the different stations collected by WP-3 (a) and WP-2 (b).

and less saline water, having characteristics of a fjords' surface water (Svendsen *et al.* 2002). Below these water masses typical winter-cooled water was found; the product of ice formation and brine release.

Total zooplankton abundance

Copepoda (22 species) was the major group identified in our studies both in terms of number of species and abundance (Table 2). Chaetognatha, Bivalvia veligers, *Limacina helicina* (Phipps, 1774) and *Aglantha digitale* (O.F. Müller, 1776) were the other taxa that occurred most regularly. Most of the taxa were present at all stations, but their relative abundances varied between locations.

The number of organisms sampled by the WP-2 net was 50–100 times higher than that sampled by the WP-3 net (Fig. 4).

Total abundance of organisms sampled by the WP-3 net was of the order of 45 ind·m⁻³ in Billefjorden, Kongsfjorden and Hinlopen, and much lower at the two ice stations (Fig. 4a). Total abundance of organisms sampled by the WP-2 net was

Table 2
 List of taxa found in all five localities – data from both, WP-3 and WP-2.

| Copepoda: | Others: |
|---|--|
| <i>Acartia longiremis</i> (Lilljeborg, 1853) | <i>Aglantha digitale</i> (Müller, 1776) |
| <i>Bradydus similis</i> (Sars, 1902) | <i>Apherusa glacialis</i> (Hansen, 1887) |
| <i>Calanus hyperboreus</i> (Krøyer, 1838) | <i>Beroe cucumis</i> (Fabricius, 1789) |
| <i>C. glacialis</i> (Jaschnov, 1955) | Bivalvia veliger |
| <i>C. finmarchicus</i> (Gunnerus, 1756) | Cirripedia cypris |
| <i>Chiridius obtusifrons</i> (Sars, 1902) | Cladocera |
| <i>Gaidius tenuispinus</i> (Sars, 1900) | <i>Clione limacina</i> (Phipps, 1774) |
| Harpacticoida | <i>Dimophyes arctica</i> (Chun, 1897) |
| <i>Heterorhabdus norvegicus</i> (Boeck, 1872) | Echinodermata larvae |
| <i>Metridia longa</i> (Lubbock, 1854) | <i>Eukrohnia hamata</i> (Möbius, 1875) |
| <i>Microcalanus</i> spp. | Euphausiacea furcilla |
| <i>Microsetella norvegica</i> (Boeck, 1864) | <i>Frittilaria borealis</i> (Lohmann, 1896) |
| Monstrilloida | Hydromedusae ndet. |
| <i>Oithona atlantica</i> (Farran, 1908) | Isopoda |
| <i>Oithona similis</i> (Claus, 1863) | <i>Limacina helicina</i> (Phipps, 1774) |
| <i>Oncea borealis</i> (Sars 1918) | <i>Limacina retroversa</i> (Fleming, 1823) |
| <i>Pareuchaeta glacialis</i> (Hansen, 1886) | <i>Mertensia ovum</i> (Fabricius, 1780) |
| <i>Pareuchaeta norvegica</i> (Boeck, 1865) | <i>Mysis oculata</i> (Fabricius, 1780) |
| <i>Pseudocalanus</i> spp. | <i>Oikopleura dioica</i> (Fol, 1872) |
| <i>Rhincalanus nasutus</i> (Giesbrecht, 1888) | <i>Onisimus</i> spp. |
| <i>Scaphocalanus magnus</i> (Scott, 1894) | Ostracoda |
| <i>Scolecithricella minor</i> (Brady, 1883) | <i>Pandalus borealis</i> (Krøyer, 1838) |
| Nauplii copepoda | Polychaeta larvae |
| | <i>Pseudomma truncatum</i> (Smith, 1879) |
| | <i>Sagitta elegans</i> (Verrill, 1873) |
| | <i>Sarsia</i> spp. |
| | <i>Themisto abyssorum</i> (Boeck, 1870) |
| | <i>Themisto libellula</i> (Lichtenstein, 1822) |
| | <i>Thysanoessa inermis</i> (Krøyer, 1846) |
| | <i>Thysanoessa longicaudata</i> (Krøyer, 1846) |

highest in Kongsfjorden, of the order of 2700 ind·m⁻³, followed by Hinlopen, Ice station East, Billefjorden and Ice station West (approx. 1200 ind·m⁻³) (Fig. 4b).

Cluster analysis of samples collected in the WP-3 net at different stations showed two major groupings. Ice stations East and West were grouped together and differed from the shelf stations Kongsfjorden, Hinlopen, and Billefjorden (Fig. 5a). Within the shelf stations, Kongsfjorden and Billefjorden appeared the most similar and they differed from Hinlopen.

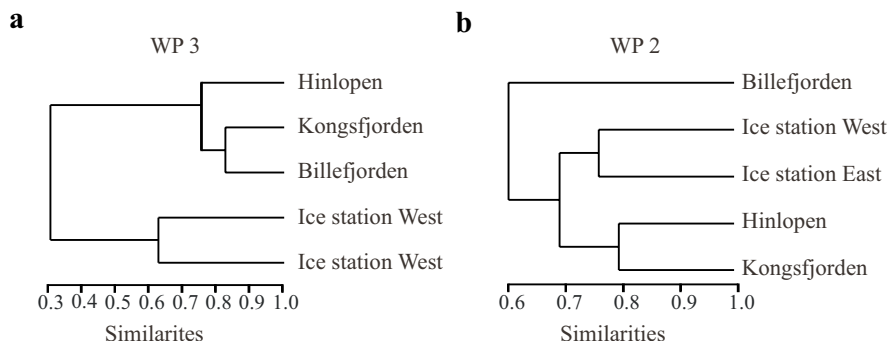


Fig. 5. Hierarchical clustering, showing similarities between stations with respect to zooplankton composition and abundance WP-3 (a) and WP-2 (b).

WP-2 samples were grouped into three: a cluster including the two Ice stations differed from Hinlopen and Kongsfjorden. Billefjorden was separated from all the stations in this clustering (Fig. 5b). Kongsfjorden and Hinlopen were more similar to the Ice stations than to Billefjorden.

Relative zooplankton abundance

In the WP-3 samples from Billefjorden, *C. glacialis* accounted for approximately 60% of the organisms collected. *Eukrohnia hamata* (Mobius, 1856) was barely present and *C. hyperboreus* was present in lower numbers. Only in Billefjorden were *Sagitta elegans* (Verrill, 1873), *Beröe cucumis* Fabricius, 1780, and *A. digitale* important components and together accounted for approximately 10% of the relative zooplankton abundance.

In Kongsfjorden *C. glacialis* was relatively important compared to *E. hamata*, which was present only in low numbers. *C. hyperboreus* was present in lower numbers than in Hinlopen. In Hinlopen *C. glacialis* was relatively important and *E. hamata* contributed less to the zooplankton community than at Ice station West. *C. hyperboreus* contributed approximately 35% of the sample in Hinlopen.

C. finmarchicus was present in all WP-3 samples at all stations. At Ice station West *C. finmarchicus* was the most abundant and accounted for approximately 50% of the organisms collected there (Fig. 6a). *E. hamata* contributed approximately 25%. *C. hyperboreus* was absent. At Ice station East *E. hamata* dominated the sample. *C. hyperboreus* was not present at this station. *Metridia longa* (Lubbock, 1854) was the third most abundant species at the two ice stations.

In samples collected with WP-2, *Oithona similis* was by far the most abundant species at all stations. In Kongsfjorden it constituted approximately 80%. At both Ice stations and in Hinlopen it constituted approximately 60% of the relative abundance, while in Billefjorden it contributed only 30%. Because it occurred in very large numbers, we excluded *O. similis* from further analysis in order to study the species composition in detail.

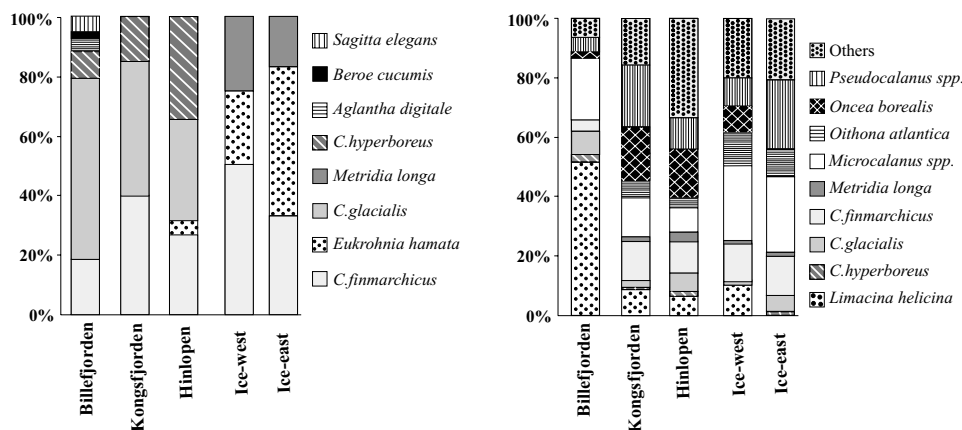


Fig. 6. Relative abundance of all species collected at five different stations investigated. a) WP-3 and b) WP-2. *O. similis* is excluded from the figure in order to look into details of species composition.

At all stations *Microcalanus* spp. constituted between 10–25% of the rest of the abundance, and was the second most abundant species after *O. similis*, except in Billefjorden.

In Billefjorden *L. helicina* constituted 50% of the remaining zooplankton, other than *O. similis* (Fig. 6b). *Microcalanus* spp. was the third most abundant species, constituting approximately 20% after exclusion of *O. similis*, followed by *C. glacialis*. In Kongsfjorden, the most abundant copepod species, except *O. similis*, were *Pseudocalanus* spp. and *Oncaea borealis* Sars, 1918, followed by *C. finmarchicus* and *Microcalanus* spp. The pteropod *L. helicina* constituted approximately 10%. In Hinlopen the second most abundant species were *O. borealis* and *C. finmarchicus*. *L. helicina* constituted approximately 10% at this station as well. At Ice station West no *O. borealis* were found in the WP-2 net. There was also very few *L. helicina*. Except for these two species, the relative species abundance was almost the same as at Ice station East. At Ice station East *Microcalanus* spp. was the second most abundant species, followed by *C. finmarchicus*, *Oithona atlantica* Farran, 1908, *L. helicina*, *O. borealis* and *Pseudocalanus* spp.

Copepodite age structure was analysed for the three *Calanus* species based on samples from both nets (Fig. 7). Data from the WP-3 net, which did not sample the population age structure representatively, showed basically the same copepodite age structure at all stations for *C. glacialis* and *C. finmarchicus*. The dominant stage for both species was CV, with a small proportion (maximum 15%) of CIV in Hinlopen and at the Ice stations. For *C. hyperboreus* the data from the WP-3 net showed a very similar population structure to the shelf stations, with CIV as the predominant stage. At both Ice stations CIII was the prevailing copepodite stage.

In the WP-2 samples from Hinlopen and both Ice stations *C. glacialis* and *C. finmarchicus* showed a less advanced stage structure than in the fjords, where

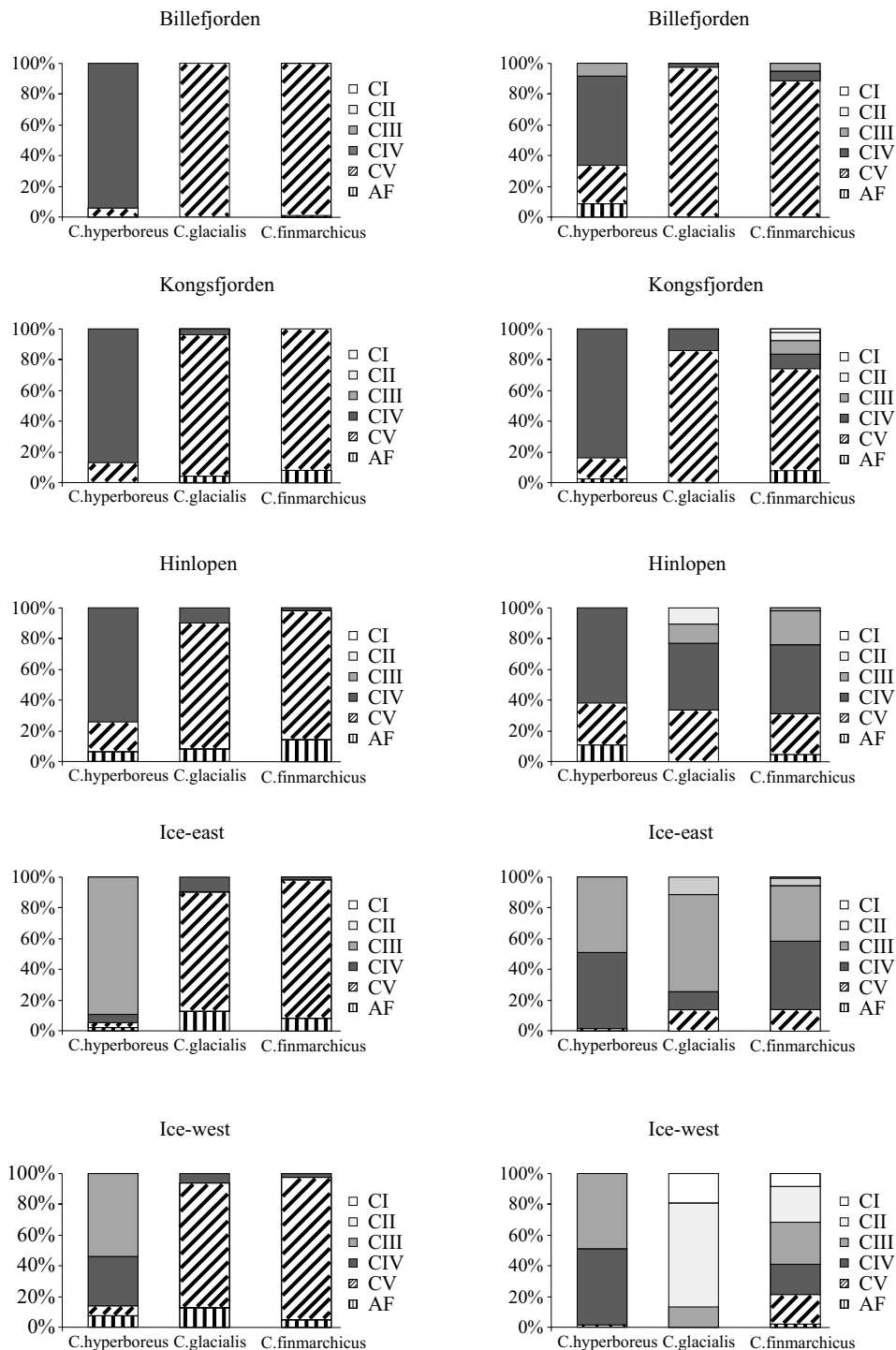


Fig. 7. Developmental stages of *Calanus* species at different stations. a) WP-3 and b) WP-2.

older overwintering stages were dominant. *C. glacialis* had a large fraction (80%) of stage CII at the Ice station West, and all stages of *C. finmarchicus* were present. At both Ice stations *C. hyperboreus* was split between stage CIII and CIV, while CIII dominated at the shelf stations Billefjorden, Kongsfjorden and Hinlopen. Adult females of *C. hyperboreus* were present both in Billefjorden and Hinlopen.

Discussion

Four of our five sampling stations were influenced by Atlantic origin water related to the direct presence of the WSC, or inflow of this water to the fjords. In Kongsfjorden, which is an open fjord without a sill, water from the WSC is mixed with Arctic-derived water and locally produced fjord water. This results in a relatively high temperature but lower salinity than Atlantic water (Svendsen *et al.* 2002). At Ice station West, Polar Water was found only in the upper 100 m layer. Beneath the Polar Water, Atlantic Water was observed. The core of Polar Water flowing out through the Fram Strait was probably located further to the west than our sampling position. At Ice station East we also expected to find Polar Water. The CTD-data showed, however, that this station was influenced by the WSC. The water in the upper 50 meters was cold and less saline and could be characterised as a typical melt water, present in ice-covered areas in the summer. Water masses in Hinlopen were influenced by Atlantic Water, a branch of the WSC penetrating from the north, as well as by Arctic Water from the Barents Sea (Loeng 1991), entering from the south. The water masses we found in this area have the temperature-salinity characteristics of Arctic Surface Water, typical for the Greenland and Iceland Sea (Smith 1990). We assume though, that the water masses in Hinlopen originate from the two main sources mentioned (i.e. AW, WSC and Ar W from the Barents Sea), but gained very similar TS characteristics, being exposed to similar processes that influence water mass formation in the Greenland and Island Seas. The CTD-data from Billefjorden suggest that this station has no Atlantic inflow. We assume from the two-layered water structure the presence of a surface layer (warmer and less saline) and deep layer (very cold and more saline), and that Billefjorden has limited exchange with surrounding waters, and then probably only through the surface layer.

As expected, differences in the number of zooplankton collected in WP-2 and WP-3 were found, which can be attributed to the different sampling performances of the two nets. The WP-3 net collected mostly animals larger than 1mm, which usually occur in lower numbers than smaller zooplankters (Koszteyn and Kwaśniewski 1989, Richter 1994, Auel and Hagen 2002, Hop *et al.* 2002). The number of organisms collected in the WP-3 net is therefore almost two orders of magnitude lower than in the WP-2 net, which collected both small and larger individuals.

Samples collected with WP-3 at shelf localities (Billefjorden, Kongsfjorden and Hinlopen) showed higher total abundance than samples from the Ice stations.

We assume that this difference could be related to the seasonal migration of many zooplankton organisms to greater depths for overwintering (Scott *et al.* 2000). In both Ice stations (open sea) we sampled only the upper water layer and missed the zooplankton that had migrated down. In shelf stations the depth limited the zooplankton migration, and we sampled the entire water column. The highest abundance of zooplankton collected with the WP-2 net was recorded in Kongsfjorden. This fjord is known as a site with strong advection from the WSC and the SC (Svendsen *et al.* 2002). This process obviously causes favourable conditions for some zooplankton species, since we observed the highest total abundance of zooplankton there (2700 ind·m⁻³). The zooplankton abundance was higher than described by Hop *et al.* (2002), where only about 1000 ind·m⁻³ were observed, indicating a dynamic system. Another explanation for the high abundance in Kongsfjorden could be the trapping of zooplankton by the eddy formation in the mouth of the fjord (Ingvaldsen *et al.* 2001, Svendsen *et al.* 2002). High numbers of total zooplankton was also observed in Hinlopen (2200 ind·m⁻³). Like Kongsfjorden, Hinlopen seems to be a very dynamic area, with a lot of mixing of different water masses, creating favourable conditions for several zooplankton species. Lower numbers of total zooplankton were observed in the other three locations. The lowest number (1150 ind·m⁻³) was recorded at Ice station West, probably due to strong vertical stratification, migration, and generally lower zooplankton abundance in Polar waters (Richter 1994). At this station, as well as at Ice station East (1500 ind·m⁻³), a part of the zooplankton community most likely migrated deeper in the water column (overwintering stages) (Conover 1988) and abundance there was similar to mean abundances recorded in the Greenland Sea Gyre (1200 ind·m⁻³) (Richter 1994).

Although Billefjorden is situated on the shelf, total zooplankton abundance was low compared to Kongsfjorden and Hinlopen. This is probably caused by lack of exchange with the surrounding waters. We assume that limited exchange with surrounding waters and specific hydrological conditions (strong runoff from surrounding glaciers and the presence of dense winter-cooled water) may favour only selected components of the zooplankton community, namely cold water Arctic species like *C. glacialis* and *L. helicina*.

Billefjorden and Kongsfjorden were most similar with respect to community composition and abundance in WP-3 samples (Fig. 5a). The zooplankton communities in these two fjords had large proportions of *C. glacialis*, *C. finmarchicus*, and low proportions of *C. hyperboreus*. Hinlopen was different from the two fjord stations, probably because of its high abundance of *C. hyperboreus*. In addition, the copepodite stage structure of *C. hyperboreus* was more similar in Kongsfjorden and Billefjorden than in Hinlopen, where there were more CV and females present. An interesting feature of the zooplankton community in Billefjorden was the high percentage of *Microcalanus* spp. Most likely the presence of this species accounts for the similarities between Billefjorden and the Ice stations. The high

proportion of *Microcalanus* spp. in Billefjorden could be due to the presence of cold water, since these species seem to prefer colder, deeper environments and are very abundant e.g. in the Greenland/ Iceland Sea (qstved 1955, Kwaśniewski 1994). The two ice stations were grouped together, and both had much lower total zooplankton abundance than the other stations. The species composition was similar, with high abundance of the open water chaetognath *E. hamata*. *Metridia longa* also contributed to the similarity by showing higher abundance at the two ice stations than at the shelf stations. At the same time, all *Calanus* species had a higher proportion of younger developmental stages at the Ice stations compared to the shelf stations. As regards the development of *C. glacialis* and *C. finmarchicus*, Ice station West is the most delayed station, compared to Billefjorden and Kongsfjorden. The overall trend seems to be a gradient of late development at the ice stations, through Hinlopen, Kongsfjorden and to the most advanced age structure in Billefjorden. The reason for the higher proportion of *C. hyperboreus* copepodite stage CIII at the ice stations can be that the population development was delayed by later phytoplankton bloom (Mann and Lazier 1996). Prolonged primary production over the shelf, in comparison to open sea, possibly allows *C. hyperboreus* populations on the shelf to achieve an older developmental stage by the same time of the year than what is possible for the two open sea populations. Another possible explanation is that CIV already migrated deeper to overwintering depths, which we did not sample. *C. finmarchicus* was most abundant at Ice station West, suggesting a strong influence of Atlantic water, supported by the CTD profile. The zooplankton community structure in Billefjorden, sampled with WP-2, was very different from all other stations (Fig. 5). Surprisingly, Billefjorden had a much lower total abundance of zooplankton than Hinlopen and Kongsfjorden, nearly of the same order as the Ice stations. Compared to Kongsfjorden, which is described as very dynamic due to the strong mixing of water masses, the low abundance in Billefjorden might be explained by its shallow sill, which restricts advection to the upper 50 meters. Low abundances of *O. similis* and *C. finmarchicus* and high abundances of the Arctic species *L. helicina* and *C. glacialis* in Billefjorden is different from all other stations. The special features of the Billefjorden zooplankton community can be attributed to its outstanding hydrological conditions, namely the pronounced stratification with cold water below 50 meters. Ice stations and Billefjorden differ from the shelf stations by having a higher proportion of the open water copepods *Microcalanus* spp., which can be explained by the cold-water masses at these stations. Kongsfjorden and Hinlopen had higher relative abundances of *O. borealis* than Ice station East, and *O. borealis* did not significantly appear either in Ice station West or in Billefjorden. These similarities could contribute to the grouping of Kongsfjorden and Hinlopen. The high percentage of the youngest stages of *C. glacialis* and *C. finmarchicus* found in WP-2 samples in Ice station West and Ice station East could contribute to classifying the two ice stations as similar. More important was probably both the low total zooplankton abun-

dance and the similar species composition, including *Microcalanus* spp. and *O. atlantica*, which were present in lower numbers at the shelf stations. Similar among all stations was the high dominance of the small omnivorous copepod *O. similis*, suggesting that phytoplankton production decreased and that the zooplankton communities had shifted from being dominated by herbivores to being dominated by omnivores feeding on decaying phytoplankton.

Conclusions

We conclude from our study that the zooplankton community structure is clearly different between stations in respect to community composition and abundance, as well as with respect to the seasonal development of zooplankton, in this study illustrated by *Calanus* spp. It is likely that the most important factors structuring the zooplankton communities are the different water masses (Atlantic vs. Polar or Arctic waters) they inhabit, as well as different timing of seasonal phenomena like ice melting and the onset of the phytoplankton bloom. Dynamic processes, including the mixing of different water masses, seem to create favourable conditions for many species, which results in their higher abundance over the shelf where these conditions occur. Local bathymetry can cause entrapment of cold water, thereby including Arctic species or open water species to shelf communities by the process of advection.

Acknowledgements. — We wish to thank our supervisor of this project, the ever-patient Sławek Kwaśniewski, for his accurate explanations, thoroughness, and enormous taxonomical knowledge. Further we wish to thank those who made the course AB-310 possible: Bjørn Gulliksen, Ole Jørgen Lønne, Stig Falk-Petersen and Ketil Eiane. We also thank the crew on R/V *Jan Mayen*, the University Centre on Svalbard for use of their laboratory, and our fellow students for good company.

References

- ASKNES D.L., AURE J., KAARTVEDT S., MAGNESEN T. and RICHARD, J. 1989. Significance of advection for the carrying capacities of fjord populations. *Marine Ecology Progress Series* 50: 263–274.
- AUEL H. and HAGEN W. 2002. Mesozooplankton community structure, abundance and biomass in the central Arctic Ocean. *Marine Biology* 140: 1013–1021.
- BARNES R.S.K. and HUGES R.N. 1999. *An Introduction to Marine Ecology*. 3rd ed. Blackwell Science, London, 362 pp.
- CLARK D.R., AAZEM K.V. and HAYS G.C. 2001. Zooplankton abundance and community structure over a 4000 km transect in the north-east Atlantic. *Journal of Plankton Research* 23: 365–372.
- CONOVER R.J. 1988. Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the Northern Hemisphere. *Hydrobiologia* 167/168: 127–142.

- CONOVER R.J. and HUNTLEY M. 1991. Copepods in ice-covered seas – Distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. *Journal of Marine System* 2: 1–41.
- EILERTSEN H.C., TANDE K.S. and TAASEN J.P. 1989. Vertical Distributions of Primary Production and Grazing by *Calanus glacialis* Jaschnov and *C. hyperboreus* Kroyer in Arctic Waters (Barents Sea). *Polar Biology* 9: 253–260.
- FALK-PETERSEN S., SARGENT J.R., HOPKINS C.C.E and VAJA B. 1982. Ecological investigations on the zooplankton community in Balsfjorden, northern Norway: lipids in the euphausiids *Thysanoessa raschii* and *T. inermis* during spring. *Marine Biology* 68: 97–102.
- FALK-PETERSEN S., PEDERSEN G., KWAŚNIEWSKI S., HEGSETH E.N. and HOP H. 1999. Spatial distribution and life-cycle timing of zooplankton in the marginal ice zone of the Barents Sea during the summer melt season in 1995. *Journal of Plankton Research* 21: 1249–1264.
- FIELD J.G., CLARKE K.R. and WARWICK R.M. 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series* 8: 37–52.
- HARRIS R., WIEBE P., LENZ J., SKJOLDAL H.R. and HUNTLEY M. (ed.). 2000. *Zooplankton Methodology Manual*. Academic Press, London.
- HIRCHE H.-J. 1997. Life cycle of the copepod *Calanus hyperboreus* in the Greenland Sea. *Marine Biology* 128: 607 – 618.
- HOP H., PEARSON T., HEGSETH E.N., KOVACS K.M., WIENCKE C., KWAŚNIEWSKI S., EIANE K., MEHLUM F., GULLIKSEN B., WIODARSKA-KOWALCZUK M., LYDERSEN C., WEŚLAWSKI J.M., COCHRANE S., GABRIELSEN G.W., LEAKEY R.J.G., LONNE O.J., ZAJĄCZKOWSKI M., FALK-PETERSEN S., KENDALL M., WANGBERG S.A., BISCHOF K., VORONKOV A.Y., KOVALTCHOUK N.A., WIKTOR J., POLTERMANN M., DI PRISCO G., PAPUCCI C. and GERLAND S. 2002. The marine ecosystem of Kongsfjorden, Svalbard. *Polar Research* 21: 167–208.
- INGVALDSEN R., REITAN B.M., SVEDSEN H. and ASPLIN L. 2001. The upper layer circulation in Kongsfjorden and Krossfjorden – A complex fjord system on the west coast of Spitsbergen. *Memoirs of National Institute of Polar Research, Special Issue* 54: 393–407.
- KARNOVSKY N.J., WEŚLAWSKI J.M., KWAŚNIEWSKI S., WALKUSZ W. and BESZCZYŃSKA-MOELLER A. 2003. The foraging behaviour of Little Auks in a heterogeneous environment. *Marine Ecology Progress Series* 253: 289–303.
- KOSZTEYN J. and KWAŚNIEWSKI S. 1989. Comparison of fjord and shelf mesozooplankton communities of the southern Spitsbergen region. *Rapp. P.-v. Réun. Cons. Int. Explor. Mer.* 188: 164–169.
- KWAŚNIEWSKI S. 1994. Distribution of zooplankton in epipelagic zone on the border of Norwegian and Barents Seas in summer. Gdansk University, Ph.D. thesis.
- KWAŚNIEWSKI S., HOP H., FALK-PETERSEN S. and PEDERSEN G. 2003. Distribution of *Calanus* species in Kongsfjorden, a glacial fjord in Svalbard. *Journal of Plankton Research* 25: 1–20.
- LOENG H. 1991. Features of the physical oceanographic conditions in the Barents Sea. *Polar Research* 10: 5–18.
- MANN K.H. and LAZIER J.R.N. 1996. *Dynamics of Marine Ecosystems*. 2nd ed. Blackwell Science. London, 475 pp.
- OSTVED O.J. 1955. Zooplankton investigations from weather ship M in the Norwegian Sea, 1948–49. *Hvalradets Skrifter, Scientific Results of Marine Biological Research* 40: 1–93. 40.
- PIECHURA J., BESZCZYŃSKA-MOELLER A. and OSIŃSKI R. 2001. Volume, heat and salt transport by the West Spitsbergen Current. *Polar Research* 20: 233–240.
- PFIRMAN S.L., BAUCH D. and GAMMELSDOT T. 1994. The Northern Barents Sea: Water Mass distribution and Modification. *The Polar Oceans and their Role in shaping the Environment. Geophysical Monograph* 85: 77–94.
- RICHTER C. 1994. Regional and seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea. *Berichte zur Polarforschung* 154: 1–86.

- SAKSHAUGG E., BJORGE A., GULLIKSEN B., LOENG H. and Mehlum F. 1994. Økosystemet Barentshavet, Universitetsforlaget AS, 28–30.
- SCOTT C.L., KWAŚNIEWSKI S., FALK-PETERSEN S. and SARGENT J.R. 2000. Lipids and life strategies of *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* in late autumn, Kongsfjorden, Svalbard. *Polar Biology* 23: 510–516.
- SMITH W.O. (ed.) 1990. *Polar Oceanography*. Academic Press, Inc. San Diego, California USA, 406 pp.
- SVENDSEN H., BESZCZYŃSKA-MOELLER A., HAGEN J.O., LEFAUCONNIER B., TVERBERG V., GERLAND S., ORBAEK J.B., BISCHOF K., PAPUCCI C., ZAJACZKOWSKI M., AZZOLINI R., BRULAND O., WIENCKE C., WINTHER J.G. and DALLMANN W. 2002. The physical environment of Kongsfjorden-Krossfjorden, an Arctic fjord system in Svalbard. *Polar Research* 21: 133–166.
- SYVITSKY J.P.M., BURELL D.C. and SKEI J.M. 1984. *Fjords; processes and products*. Springer Verlag, New York, 319 pp.
- TANDE K.S. 1991. *Calanus* in North Norwegian fjords and in Barents Sea. *Polar Research* 10, 389–407.
- UNSTAD K.H. and TANDE K.S. 1991. Depth distribution of *Calanus finmarchicus* and *Calanus glacialis* in relation to environmental conditions in the Barents Sea. *Polar Research* 10: 409–420.
- VALIELA I. 1995. *Marine Ecological Processes*. 2nd ed., Springer Verlag, 686 pp.
- WIBORG K.F. 1955. Zooplankton in relation to hydrography in the Norwegian Sea. *Fiskeridir. Skr. Ser. Havunders* 11: 1–66.

Received 15 February 2003

Accepted 11 July 2003