Distribution of *Calanus* species in Kongsfjorden, a glacial fjord in Svalbard

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The distribution of Calanus species was investigated in Kongsfjorden in summer of 1996 and 1997. In both years Calanus finmarchicus and Calanus glacialis dominated, although the boreal C. finmarchicus was more abundant than the Arctic C. glacialis in 1997. This coincided with a 2°C higher water temperature at 50 m in 1997, indicating stronger influence of Atlantic origin water that year. Advected Calanus finmarchicus occurred in deep and subsurface layers of the outer fjord in 1996 (200 ind. m^{-3}, mainly CIII). A less abundant local population aggregated in surface layers of the inner fjord (100 ind. m^{-3}). Similarly, advected C. finmarchicus occurred in subsurface layers in 1997 (446 ind. m^{-3}, mainly CIII and CIV) and a local population in surface layers (183 ind. m^{-3}, mainly CI). Calanus glacialis in 1996 aggregated as CII and CIII in the deep layers of the outer fjord (272 ind. m^{-3}), whereas CIII–CV were abundant (216 ind. m^{-3}) in cold surface waters of the inner fjord. In 1997 C. glacialis (mostly CIII–CV) was more abundant in the outer than in the inner part of the fjord (40 and 192 ind. m^{-3}, respectively). Within Kongsfjorden, Calanus finmarchicus needs one year to complete its life cycle, whereas Calanus glacialis needs two. Calanus hyperboreus seems to be an expatriate in the fjord system.

INTRODUCTION

Copepods of the genus *Calanus* are the dominant herbivores in sub-Arctic and Arctic seas. They play a key role in pelagic food webs and thus largely influence the energy flow and functioning of productive marine ecosystems (Tande, 1991; Longhurst, 1998). Arctic copepods are rich in lipids and represent an important food source for other zooplankton species, pelagic fishes such as polar cod (*Boreogadus saida*) (Lønne and Gulliksen, 1989; Jensen *et al.*, 1991) and capelin (*Mallotus villosus*) (Hassel *et al.*, 1991; Hopkins and Nilssen, 1991), and some seabird species such as the Little Auk (*Alle alle*) (Norderhaug, 1980; Mehlum and Gabrielsen, 1993; Weslawski *et al.*, 1999; Karnovsky *et al.*, 2002).

Three *Calanus* species dominate in the sub-Arctic and Arctic seas. *Calanus finmarchicus* (Gunnerus, 1770) is a boreal species with its centre of distribution in the Norwegian Sea (Østvedt, 1955; Wiborg, 1955). It is also the most abundant calanoid copepod in the Barents Sea south of the polar front as well as along the Norwegian coast (Blindheim, 1989; Tande, 1991). However, the Norwegian Atlantic Current transports it into the Arctic Ocean (Jaschnov, 1970; Conover and Huntley, 1991; Hirche and Mumm, 1992; Thibault *et al.*, 1999) and the return Atlantic Current carries it into the Greenland Sea Gyre (Hirche *et al.*, 1994; Hirche and Kwasniewski, 1997).

Calanus glacialis Jaschnov, 1955, the only true Arctic species, is bound to shelf seas bordering the Arctic Ocean. It dominates among *Calanus* in waters north of the Polar Front in the Barents Sea (Tande, 1991; Unstad and Tande, 1991) and on the northeast Greenland shelf (Smith *et al.*, 1985; Hirche and Kwasniewski, 1997). It also occurs in Baffin Bay (Grainger, 1963; Buchanan and Sekerak, 1982), in the White Sea (Kosobokova, 1999) and in the shelf seas bordering the Arctic Ocean (Jaschnov, 1970; Hanssen, 1997; Vinogradov, 1997), but does not extend very far south of the polar front in the northeast Atlantic (Conover, 1988).

Calanus hyperboreus (Krøyer, 1838) is an Arctic/polar species with centres of its distribution in deep-water seas such as the Greenland Sea and the Nansen Basin of the Arctic Ocean (Richter, 1994; Hirche, 1997). It can be found at low abundance over most of the Nordic Seas and in the Arctic marginal seas (Conover, 1988; Hirche, 1997; Falk-Petersen *et al.*, 1999; Thibault *et al.*, 1999). In the

Barents Sea or in the Canadian Arctic, *C. hyperboreus* co-occurs with *C. glacialis*, but it is less abundant (Grainger, 1963; Conover and Huntley, 1991; Thibault *et al.*, 1999).

The presence of all three *Calanus* species in the waters of Svalbard has been documented. Nevertheless, Stott (Stott, 1936) could distinguish only two species (*C. hyperboreus* and *C. finmarchicus*), whereas Shuvalov (Shuvalov, 1966) and Koszteyn and Kwasniewski (Koszteyn and Kwasniewski, 1989) discussed the distribution of species complexes: *C. finmarchicus* including *C. glacialis*, and *C. finmarchicus* s.l., respectively. Diel considered all three species independently, but with emphasis on the species' life history at certain locations on the shelf (Diel, 1991).

Increased interest in the consequences of climate change on Svalbard fjords motivated the initiation of the 'Biodiversity and Fluxes in Arctic Glacial Fjords' research programme, with Norway, Poland and the UK as the main participating countries. Multidisciplinary research cruises were conducted with the Polish RV 'Oceania' to Kongsfjorden on Spitsbergen (Svalbard). This fjord is located in the Arctic (79°N, 12–13°E), but is influenced by sub-Arctic conditions because of influx of Atlantic water from the West Spitsbergen Current (WSC) (Svendsen *et al.*, 2002). Kongsfjorden also represents a border area between Atlantic and Arctic biogeographic zones, and the fjord contains a mixture of boreal and Arctic fauna (Hop *et al.*, 2002). An increased influx of Atlantic water into the Kongsfjorden system would alter the environment towards boreal, whereas glacial input and winter sea-ice formation would tend to make the inner part of the fjord more Arctic. The balance between Arctic and Atlantic conditions in the fjord is very probably sensitive to climate changes, with the most rapid changes occurring in the pelagic system. The *Calanus* complex in Kongsfjorden responds to variations in the distribution and dynamics of west Spitsbergen water masses. Because it contains species with different centres of distribution, modifications in the proportion of boreal and Arctic species indicate variations in the transport of water masses to the fjord. The *Calanus* complex, when monitored on a local scale (Kongsfjorden), can therefore function as an indicator for climate change and its influence on the fjordic ecosystem.

The present paper shows spatial distribution patterns of three *Calanus* species in Kongsfjorden during summer. The life history cycles of the two most abundant species, *C. finmarchicus* and *C. glacialis*, are also discussed.

METHOD

Study area

Zooplankton research was carried out during two cruises with RV 'Oceania' to Kongsfjorden in July 1996 and 1997. Kongsfjorden is an open fjord with no sill and it can be considered an extension of Kongsfjordrenna, one of the trenches cutting through the Spitsbergen shelf. There are two basins in the fjord, the outer of which is larger, which are separated by a 30-m-deep ridge and a chain of small islands and skerries (Figure 1). The depth of the fjord gradually decreases towards the end, from >300 m in the outer basin to 60–90 m in the inner basin, although there are some depressions down to 400 m depth at the entrance to the fjord. Three large glaciers are calving into Kongsfjorden: Kongsbreen and Kongsvegen at the end of the fjord, and Blomstrandbreen in the middle of its northeast coast.

Summer hydrology of Kongsfjorden

Results of hydrological studies indicate that the water column in Kongsfjorden is well stratified during summer and that distinct water masses are present (Weslawski *et al.*, 1991b; Ito and Kudoh, 1997; Svendsen *et al.*, 2002). This was also the case for 1996 and 1997, as shown by temperature and salinity distributions (Figures 2 and 3), obtained prior to zooplankton sampling from undulating profiles conducted along the fjord main axis with a Guidline 8770 probe.

The volume and spatial distribution of the water masses in Kongsfjorden result from interactions between forces governing the fjord circulation, coupled with the complex bottom topography and coastline (Svendsen *et al.*, 2002). Because Kongsfjorden is also a relatively wide fjord (cross-sectional area relative to total fjord volume in the order of 10^{-1} m^{-1}), it can be assumed that advective processes, governed by distant forcing such as tide and coastal wind, heavily influence the fjord. Inside the fjord system, the circulation is strongly influenced by the Coriolis effect because the fjord width exceeds the baroclinic (internal) Rossby radius of deformation. Strong stratification in summer due to freshwater run-off implies circulation in the layers above the pycnocline, which is governed by tide, run-off and local winds, and is relatively independent of the deeper circulation. Within this set-up, the circulation includes, schematically, a bi-directional layout of currents in intermediate/deep layers, with up-fjord flow along the southern coast and down-fjord outflow along the northern coast. Cyclonic eddies with diameters comparable to the fjord's width may appear in the outer basin. In the upper layers, the predominant situation during summer includes outflow over the entire area, forced by freshwater run-off to the inner fjord, with the brackish flow more constrained to the northern coast in the case of down-fjord wind. The water temperature drop along the glacier front is a clear evidence of the cyclonic circulation in the inner basin. Up-fjord winds,
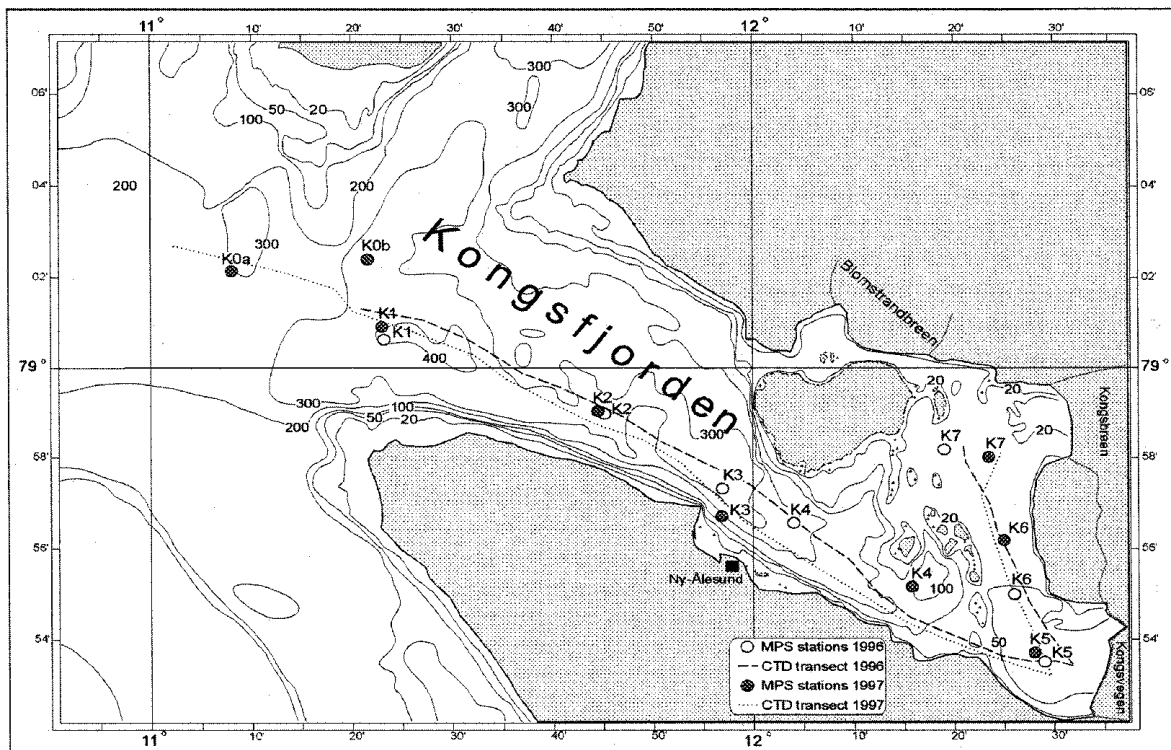
Fig. 1. Map of Kongsfjorden indicating the location of zooplankton sampling stations and CTD transects in July 1996 and 1997.

which are less common in summer, cause up-fjord surface currents and stacking up of water at the fjord's head that eventually turns down-fjord and flushes out when the up-fjord wind ceases or the pressure gradient becomes strong enough to overcome the wind action. The down-fjord advection of brackish water is maintained throughout the whole tidal period, although the tide modifies the strength of the flow (Ingvaldsen *et al.*, 2001; Svendsen *et al.*, 2002).

Svendsen *et al.* (Svendsen *et al.*, 2002) also summarized oceanographic measurements carried out in Kongsfjorden between 1996 and 2000, and identified five water masses (Table I). Advection from the shelf transports the most distinct and important water mass, namely Transformed Atlantic Water (TAW), which originates from Atlantic Water of the WSC. TAW obtains its properties on the way into the fjord, as a result of mixing with Arctic Water and outflow from the fjords situated further south, transported by coastal currents flowing northward around southern and western Spitsbergen. There is a significant year-to-year variability in the volume and characteristics of the TAW, which most likely affects the zooplankton composition of this water mass. Convectional processes in the fjord during autumn/winter cooling and during contact with the glacier face, and

Table I: Characteristics of water masses identified in Kongsfjorden, 1996 and 1997 (Svendsen et al., 2002)

Water mass	Acronym	Salinity (psu)	Temperature (°C)
Surface water	SW	28.0–34.4	Variable
Intermediate water	IW	33.0–34.7	Variable
Transformed atlantic water	TAW	>34.7	>1.0
Local water	LW	>34.4	<1.0
Winter cooled water	WCW	>34.4	<−0.5

input of melt water, lead to the formation of Local Water (LW). LW spreads mostly over the Atlantic origin water, but can be also found in the deep and bottom layer in the outer basin since TAW intrudes the fjord at intermediate depths. Winter Cooled Water (WCW) is produced as a result of winter cooling, sea-ice formation and sinking of dense, very cold water in deep convection processes. It can occupy the isolated bottom depressions throughout the year. Surface Water (SW), which is
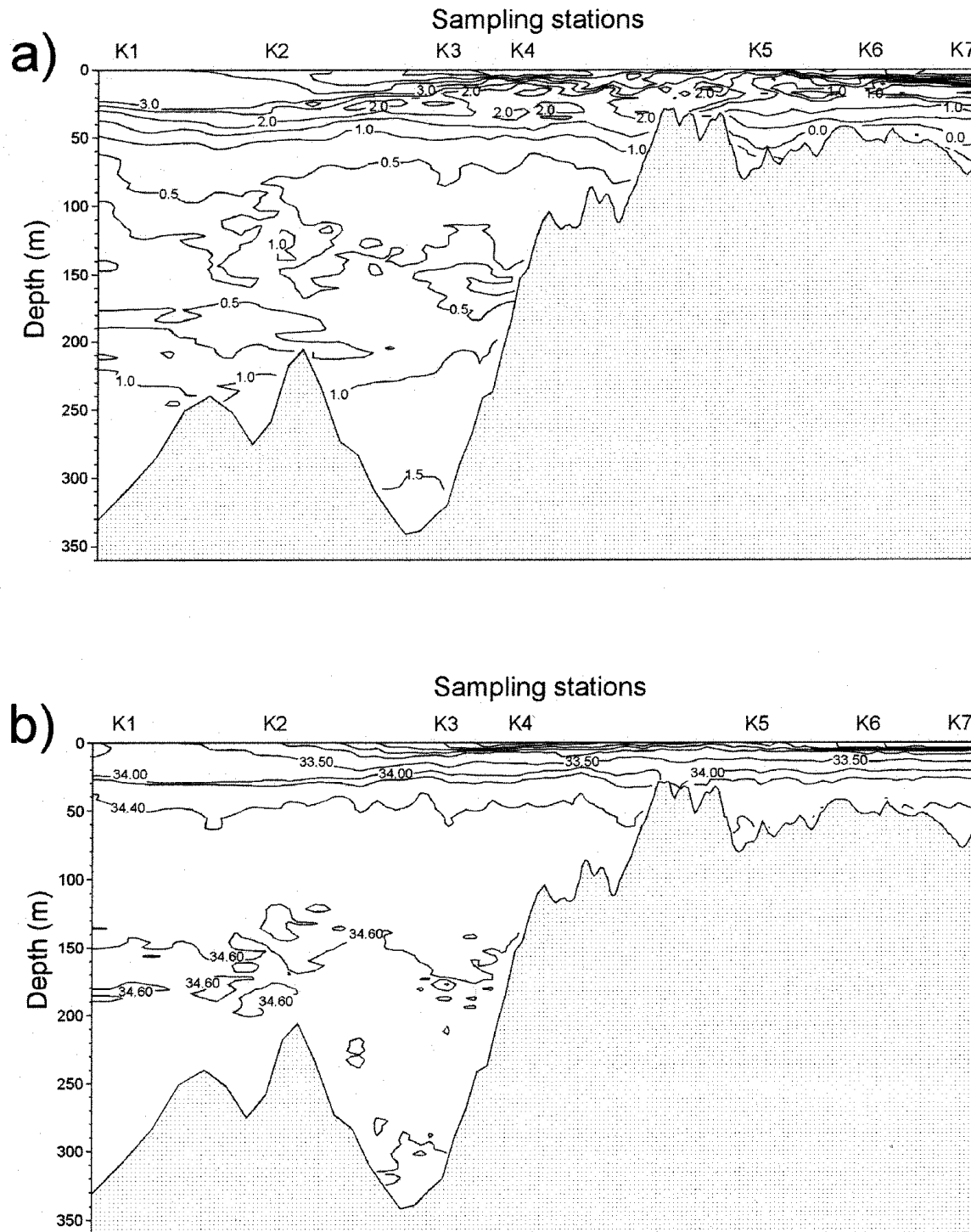
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Fig. 2. Temperature (**a**) and salinity (**b**) isopleths in Kongsfjorden on 12 July 1996. For clarity, 0.5 psu isopleths are drawn for salinity below 33 psu (Courtesy of the Marine Hydrology Laboratory, Institute of Oceanology, Polish Academy of Sciences, adjusted.)

characterized by lower salinity, occupies the upper several metres of the water column, but the layer decreases in thickness towards the fjord mouth. A transitional layer of Intermediate Water (IW) usually separates SW and TAW, and shows salinity intermediate to these two water masses. It develops through heat exchange and mixing processes between the surface waters and the underlying layers. The thickness of this
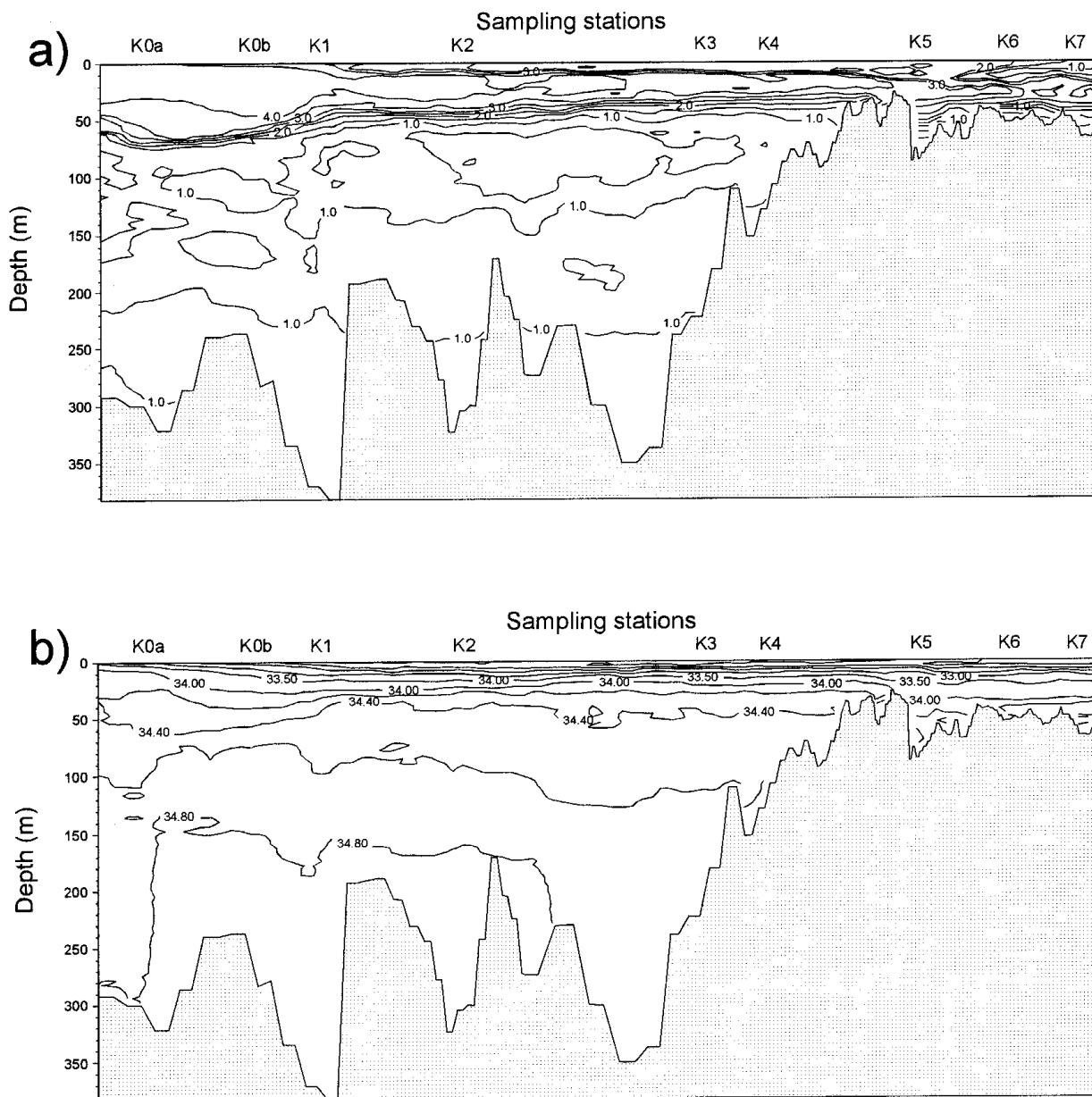
Fig. 3. Temperature (**a**) and salinity (**b**) isopleths in Kongsfjorden on 20 July 1997. See comment to Figure 2.

layer is in the order of tens of metres, although variable along the fjord axis.

Zooplankton sampling and processing

Sampling was carried out between 13 and 14 July 1996, and 21 and 24 July 1997, with a Multi Plankton Sampler (MPS; square opening of 0.25 m²) equipped with five nets (0.180 mm mesh) that could be closed in sequence. The filtered water volume was calculated in 1996 from wire length and the net mouth area, assuming 100% filtration

efficiency at 0.5 m s⁻¹ hauling velocity, whereas in 1997 it was calculated from flow meter readings.

The horizontal arrangement of the sampling stations was related to the bottom profile, along the length axes of the main fjord and the inner basin (Figure 1). This included seven stations in 1996 and nine in 1997. The sampling locations were similar in 1996 and 1997, except for stations K0a and K0b, which were further out in the fjord deeper waters in 1997. Taking into account the circulation pattern described by Svendsen *et al.*

Table II: Location, time and collection method of Calanus individuals measured for construction of length–frequency histograms

Location	Coordinates	Date	Net, mesh size, depth
Atl.	70.00°N 13.00°E	25 July 1987	WP2, 0.18 mm, 200–0 m
	71.00°N 15.00°E	16 July 1988, 20 July 1989	
	72.00°N 13.00°E	7 July 1987	
Mix	73.50°N 17.00°E	25 July 1989	WP2, 0.18 mm, 200–0 m
	73.50°N 15.00°E	24 July 1989	
	74.00°N 17.00°E	25 July 1989	
	74.00°N 15.00°E	25 July 1989	
	75.00°N 15.00°E	27 July 1989	
	75.00°N 13.00°E	27 July 1989	
	75.50°N 17.00°E	30 July 1988, 29 July 1989	
	76.00°N 13.00°E	31 July 1987	
	76.00°N 17.00°E	1 August 1987, 30 July 1988, 28 July 1989	
	76.50°N 15.00°E	1 August 1987, 30 July 1988, 29 July 1989	
FJL	82.33°N 52.50°E	22 August 1991	WP2, 0.2 mm, 50–0 m
K94	78.93°N 11.93°E	10 Jun, 14 July, 4 August, 11 August 1994	Conical net, 0.1 mm, 20–0 m
K96	78.97°N 11.79°E	13 July 1996	MPS, 0.180 mm, 240–0 m
	78.95°N 11.90°E	13 July 1996	MPS, 0.180 mm, 340–0 m

Regions or water masses are Atlantic water (Atl.), mixed Atlantic/Arctic water (Mix), Franz Josef Land (FJL), Kongsfjorden 1994 (K94) and 1996 (K96).

(Svendsen *et al.*, 2002), the location of sampling stations closer to the southern side of the fjord suggests that we surveyed the main incoming water masses, and the respective plankton, the water masses of the middle fjord and the inner basin, as well as the outgoing surface water.

In 1996, after preliminary examination of the temperature and salinity distributions, fixed sampling depth strata were chosen. Because of greater variation in vertical stratification between locations in 1997, sampling strata were demarcated individually at each station, as indicated in figures for distribution patterns. Sampling strata can be seen in figures illustrating distribution patterns. A total of 64 zooplankton samples were collected (28 in 1996 and 36 in 1997). All samples were preserved in 4% formaldehyde in sea water buffered with hexamine.

Sorting and identification of the zooplankton were carried out according to the procedure in Falk-Petersen *et al.* (Falk-Petersen *et al.*, 1999). Representatives of *Calanus* were identified to species based on morphology and prosome lengths of individual copepodid stages, which is similar to identification methods applied in other studies (Eilertsen *et al.*, 1989b; Tande, 1991; Unstad and Tande, 1991; Hirche *et al.*, 1994).

Bimodal prosome length distributions for copepodid stages CI–CIV from Kongsfjorden and other high-latitude locations (Table II) were used to separate *C. finmarchicus* (smaller modes) from *C. glacialis* (larger modes) (Figure 4). The prosome length distributions for populations of the two species were non-overlapping from Atlantic (southern WSC) and Arctic (Franz Josef Land) locations. Two modes could also be identified for CI–CIV from Kongsfjorden (July 1994 and 1996), although the larger modes (*C. glacialis*) were shifted towards smaller values, resulting in some degree of overlap in distributions. This was also the case for populations from mixed Atlantic/Arctic water masses near the polar front south of Spitsbergen. We assume that the negative shift for the Arctic *C. glacialis* occurs because
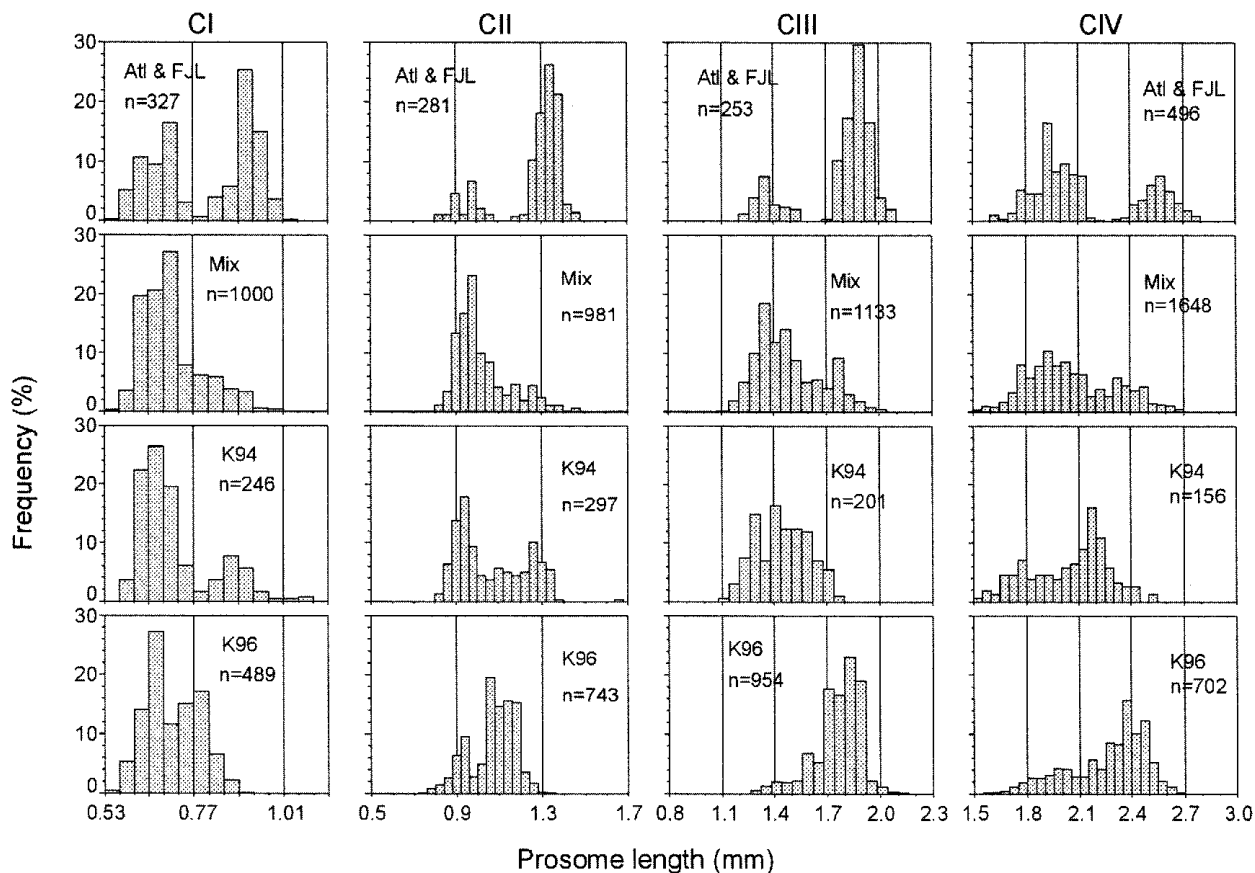
Fig. 4. Prosome length distributions of *Calanus* CI–CIV from various north latitude locations.

water temperature in marginal areas influenced by relatively warm Atlantic water ($T > 3°C$) is higher than the temperature in its core distribution area ($T < 0°C$ in Arctic Water) (Jaschnov, 1970; Conover, 1988; Loeng, 1991; Tande, 1991). Negative relationships between body length of *Calanus* and temperature over geographical ranges were found by Grainger (Grainger, 1961) and Frost (Frost, 1974), and for *Pseudocalanus* by Corkett and McLaren (Corkett and McLaren, 1978). The range of temperature in areas of convergence is probably less influential for the boreal *C. finmarchicus*, since the length mode for this species was consistent among the locations compared. The length modes for populations from Kongsfjorden differed between 1994 and 1996, but this is probably a result of sampling mainly the surface layers during spring and summer in 1994 versus the entire water column during midsummer in 1996. We suppose that *C. glacialis* abandons surface layers when the temperature increases above 3–4°C, similarly to what has been observed in the White Sea (Kosobokova, 1999). Large CI and CII were collected on 10 June 1994, before the seasonal warming of the surface water to 3°C,

whereas most of CIII and CIV were collected later in the summer. The late occurrence of these stages is probably also coupled with reduced growth in *C. glacialis* because of suboptimal, higher temperatures. The population sampled in 1996 included individuals from deeper and colder water, at conditions closer to optimal for growth.

Prosome length limits were determined after comparing values used in the studies conducted previously with our length–frequency diagrams. Because of the consistently smaller copepodid sizes for *C. glacialis*, but not for *C. finmarchicus*, in areas influenced by Atlantic water, we have set the prosome length limits for *C. glacialis* CI–CIV lower than those determined previously for this species in Arctic waters (Table III). Prosome lengths for older copepodid stages (CV, CIV) separated well for all regions investigated and generally concurred with prosome lengths used in other studies.

Statistical analysis

Two statistical methods were applied to reveal the spatial distribution patterns of the *Calanus* species: hierarchical

Table III: Prosome length (mm) of copepodid stages used for separation of Calanus species

Stage	C. finmarchicus	C. glacialis	C. hyperboreus
CI	<0.75	0.75–1.0	>1.0
CII	<1.1	1.1–1.4	>1.4
CIII	≤1.6	1.6–2.1	>2.1
CIV	<2.2	2.2–3.0	>3.0, 5th metasome segment with acute process
CV	<2.9	≥2.9	5th metasome segment with acute process
CVI female	<3.2	≥3.2	5th metasome segment with acute process

agglomerative clustering and non-metric multidimensional scaling (Field *et al.*, 1982; Clarke and Warwick, 1994). The resulting representations of the similarities between samples with regard to copepodid stage composition offered suggestions about patterns of the species distribution in space. The PRIMER version 4.0 (Plymouth Marine Laboratory, UK) software package was used for all the calculations. Both methods were applied separately for each of the two species (*C. finmarchicus* and *C. glacialis*) and for each year on data matrices of 28 or 35 samples and six copepodid stages (CI–CVI females). One sample from 1997 (K4_3) was excluded from the calculations because of very low abundance of copepods (i.e. outlier). All eight analyses (methods × species × years) were based on Bray–Curtis similarities between sample pairs computed from relative copepodid stage abundances. The complete link option was applied in clustering, whereas the package-recommended options of Kruskal's non-metric MDS procedure were followed in ordination.

RESULTS

The zooplankton community in Kongsfjorden included 38 species/genera, 8 higher taxa of holoplankton and 12 higher taxa of meroplankton (Table IV). For both years, the most abundant zooplankton elements were two *Calanus* species (*C. finmarchicus* and *C. glacialis*) plus other copepod species *Oithona similis* Claus, 1866, *Pseudocalanus* [including both *P. minutus* (Krøyer, 1845) and *P. acuspes* (Giesbrecht, 1881)], *Microcalanus* spp., *Metridia longa* (Lubbock, 1854), *Oncaea borealis* Sars, 1918, as well as copepod nauplii. However, they ranked differently each year (Table V).

Distribution patterns of *Calanus*

Calanus finmarchicus was one of the two abundant *Calanus* species in Kongsfjorden. Copepodid stages CI–CV and females were almost ubiquitous in the fjord, and males were rare in both years. However, the concentration as well as the proportion of copepodid stages of the species varied greatly between sections of the fjord. Based on the similarity of the samples with respect to copepodid stage composition (Figure 5), five aggregations of *C. finmarchicus* were determined in 1996 (CF96-1 to CF96-5; Figure 6).

Aggregation CF96-1 consisted mostly of CI–CIII, and was present in surface and intermediate layers (down to 100 m) in the middle and outer part of the fjord (Figure 6). CF96-2, dominated by CIII, was located in the water volume below CF96-1 (100–200 m). CF96-3 consisted of mainly CV and adult females, and was found as a distinct aggregation in the deepest parts of the fjord. CF96-4 consisted almost exclusively of adult females and was located in surface layers (<50 m) in the middle and inner parts of the fjord. CF96-5 was comprised mostly of CV and adult females, and was limited in its distribution to the bottom layers of the inner basin. The aggregations of *C. finmarchicus* differed in abundance (Table VI). The most abundant aggregations were in the surface and intermediate layers down to 200 m in the outer fjord (CF96-1, CF96-2) with mean concentrations of all copepodid stages of 193 and 200 individuals (ind.) m^{-3}, respectively. There were fewer *C. finmarchicus* copepodids in the bottom layers over depressions in the outer fjord (CF96-3, 127 ind. m^{-3}). The abundance decreased further towards the inner fjord basin (CF96-4, 100 ind. m^{-3}), where it was the lowest in the bottom layers (CF96-5, 35 ind. m^{-3}).

Exercising the two statistical methods in order to reveal the similarity between the samples from 1997 yielded a more apparent separation into four groupings (Figure 7). We postulate that this pattern reflects the presence of four aggregations of *C. finmarchicus* in Kongsfjorden in 1997 (CF97-1 to CF97-4; Figure 8).

Aggregation CF97-1 was located in the surface layers in the outer basin and comprised mostly younger copepodid stages (CI–CIV), predominantly CI. CF97-2 was composed of the same range of younger copepodid stages, with CIII and CIV being the most abundant. This aggregation resided below CF97-1 in the intermediate layers along the whole fjord, except at the outermost station. On shallow stations in the inner fjord, however, CF97-2 occupied nearly the entire water column, except for a thin subsurface layer in which CF97-3 occurred. The aggregation CF97-3, dominated by CIV, was otherwise

Table IV: List of taxa identified in the samples from Kongsfjorden, 1996 and 1997

Taxon	1996	1997	Taxon	1996	1997
Holoplankton			**Holoplankton** (continued)		
Calanus hyperboreus	+	+	Polychaeta		+
Calanus glacialis	+	+	Ostracoda	+	+
Calanus finmarchicus	+	+	*Boreomysis arctica*	+	
Pareuchaeta norvegica	+	+	*Thysanoessa inermis*	+	+
Pseudocalanus minutus	+	+	*Thysanoessa raschii*	+	+
Pseudocalanus acuspes	+	+	*Thysanoessa longicaudata*		+
Microcalanus spp.	+	+	*Themisto libellula*	+	+
Scolecithricella minor	+	+	*Themisto abyssorum*	+	+
Acartia longiremis	+	+	*Limacina helicina*	+	+
Metridia longa	+	+	*Clione limacina*	+	+
Metridia lucens		+	*Sagitta elegans*	+	+
Bradyidius similis	+	+	*Eukrohnia hamata*	+	+
Neoscolecithrix farrani	+	+	*Oikopleura* sp.	+	+
Heterorhabdus norvegicus		+	*Fritillaria borealis*	+	+
Gaidius tenuispinus		+			
Calanoida Tharybidae sp.	+	+			
Calanoida Phaennidae sp.	+		**Meroplankton**		
Calanoida Platycopioidae sp.	+				
Oithona similis	+	+	Cirripedia nauplii	+	+
Oithona atlantica	+	+	*Sabinea septemcarinata*	+	+
Oncaea borealis	+	+	Decapoda larvae	+	+
Cyclopoida		+	Cumacea	+	+
Microsetella norvegica	+	+	Isopoda	+	+
Harpacticoida	+	+	Nematoda	+	+
Monstrilloida	+	+	Polychaeta larvae	+	+
Aglantha digitale		+	Gastropoda veliger	+	+
Hydromedusae	+	+	Bivalvia veliger	+	+
Dimophyes arctica		+	Echinodermata larvae	+	+
Mertensia ovum	+	+	Bryozoa larvae		+
Beroe cucumis	+	+	Pisces larvae	+	
Rotatoria		+			
Turbellaria		+			

Table V: Proportions of the 10 most abundant zooplankton taxa in Kongsfjorden, 1996 and 1997 (as regional means based on abundance in the entire water column)

| Abundant taxa, 1996	Abundance (%)	Abundant taxa, 1997	Abundance (%)
Calanus glacialis	25.2	Oithona similis	28.8
Calanus finmarchicus	25.0	*Calanus finmarchicus*	22.8
Pseudocalanus spp.	21.6	*Pseudocalanus* spp.	13.3
Oithona similis	15.3	Calanoida nauplii	10.3
Calanoida nauplii	5.7	*Metridia longa*	6.9
Microcalanus spp.	2.1	*Calanus glacialis*	6.3
Metridia longa	1.0	*Microcalanus* spp.	3.8
Bradyidius/Neoscolecithrix	0.9	*Oncaea borealis*	2.4
Calanus hyperboreus	0.6	*Fritillaria borealis*	2.1
Oncaea borealis	0.6	*Calanus hyperboreus*	1.4
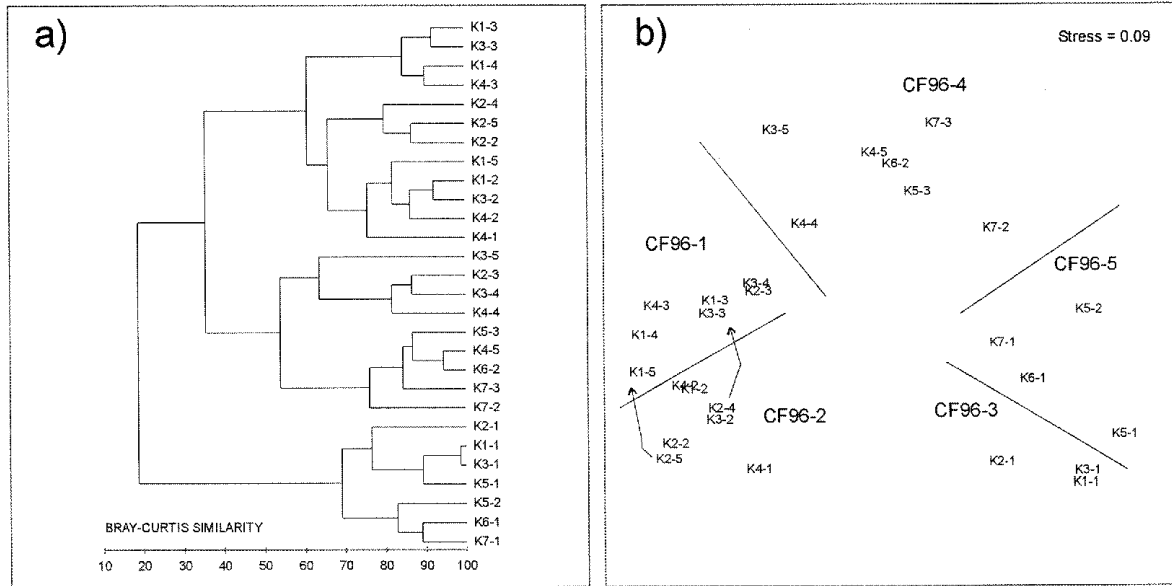
Fig. 5. Clustering dendrogram (**a**) and ordination plot (**b**) illustrating similarity between samples from 1996 in terms of copepodid stage composition of *C. finmarchicus*. Lines on the ordination plot indicate ultimate separation of samples into aggregation groups.
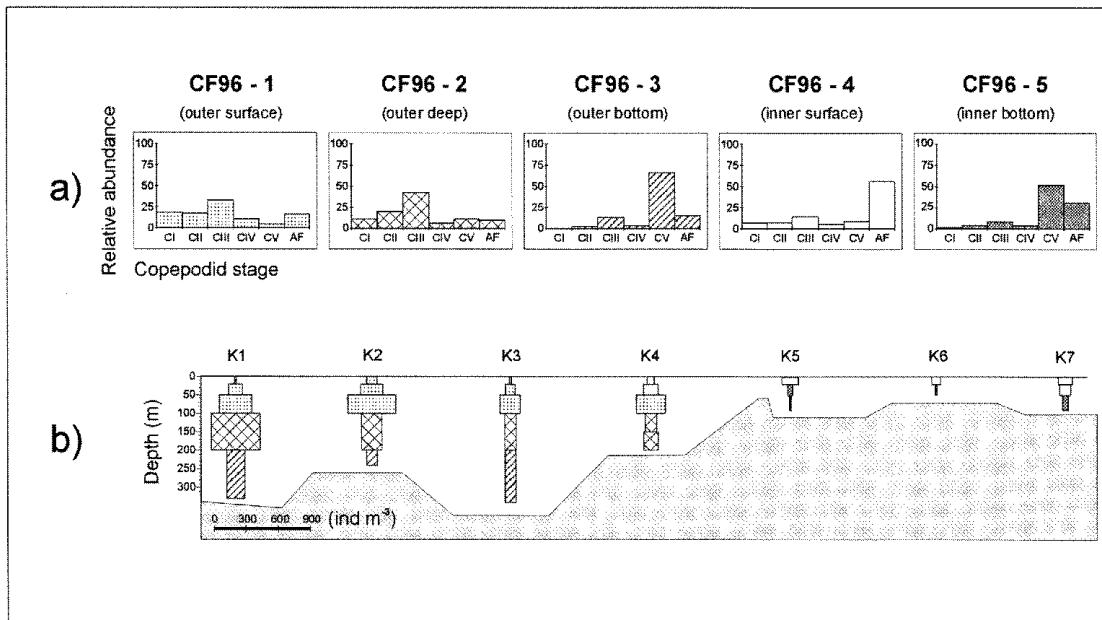

Fig. 6. Histograms of copepodid stage composition (**a**) and scheme of distribution of aggregations (**b**) of *C. finmarchicus* in Kongsfjorden, 1996. The distribution of the aggregations is depicted by the patterns in horizontal bars for the copepod abundance at particular locations; these correspond to patterns in individual histograms. Bar size is proportional to copepod abundance.

present in the deep and the bottom layers of the middle fjord, as well as the bottom layers of the inner fjord. CF97-4 comprised exclusively older copepodid stages, predominantly CV and adult females. This aggregation was limited to the bottom layers over depressions at the mouth of the fjord. In 1997, the highest abundance was in the intermediate layers (CF97-2, 446 ind. m^{-3}), where CIII and CIV prevailed. The abundance of aggregations of both surface (CF97-1, 183 ind. m^{-3}) and deep layers (CF97-3, 214 ind. m^{-3}) was each about half of that. The lowest abundance was in the bottom layers over depressions in the outer basin (CF97-4, 103 ind. m^{-3}).
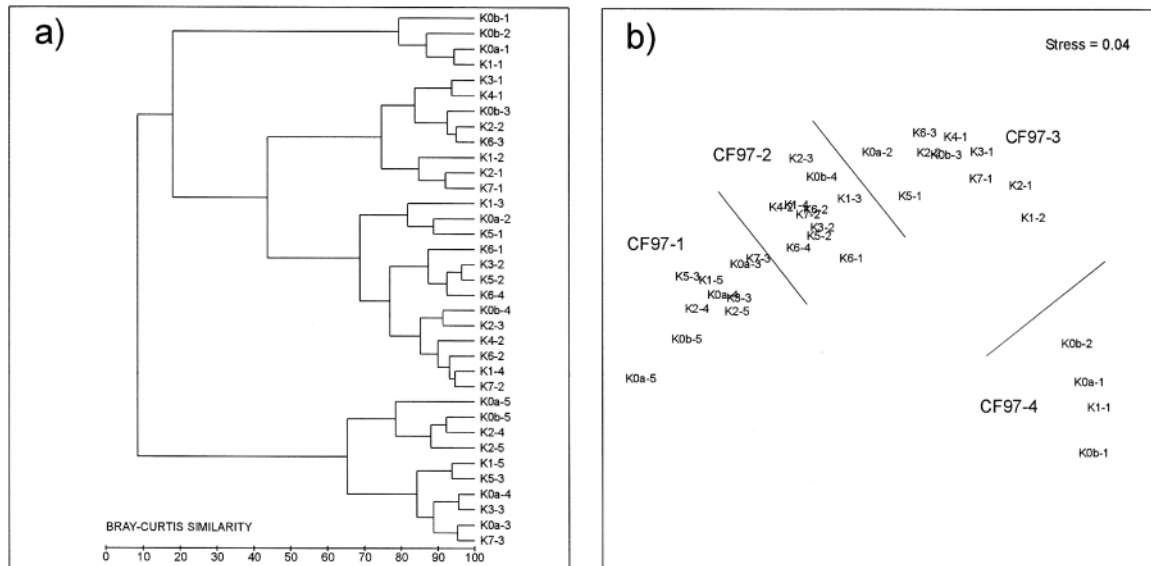
Fig. 7. Clustering dendrogram (**a**) and ordination plot (**b**) illustrating similarity between samples from 1997 in terms of copepodid stage composition of *C. finmarchicus*. See comment to Figure 5.
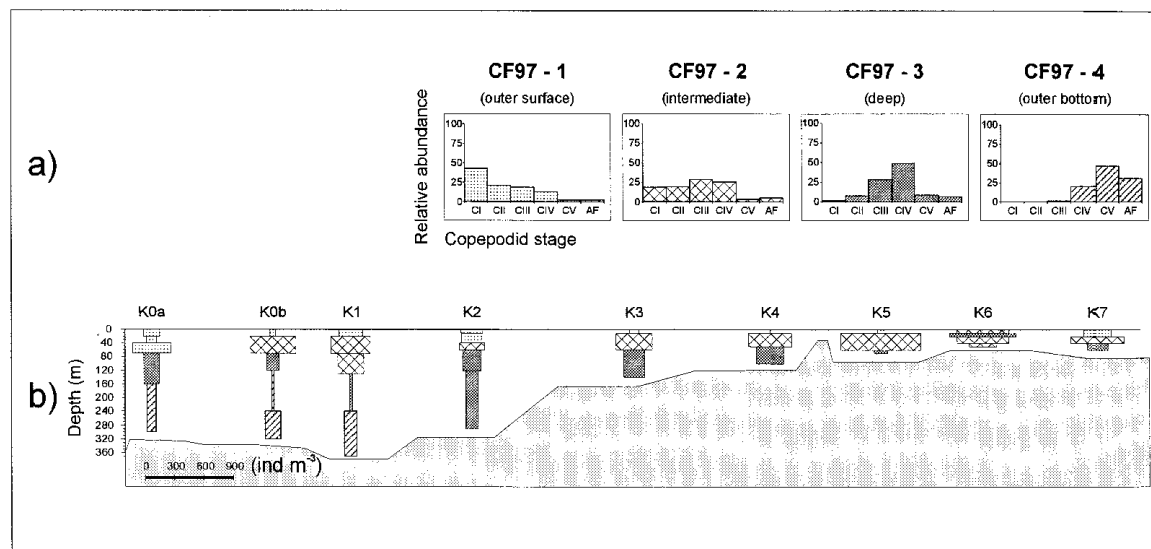

Fig. 8. Histograms of copepodid stage composition (**a**) and distribution scheme of aggregations (**b**) of *C. finmarchicus* in Kongsfjorden, 1997. See comment to Figure 6.

Calanus glacialis was the second-most abundant *Calanus* species in Kongsfjorden. As for *C. finmarchicus*, CI–CV and females were widespread throughout the fjord, and males were rare. Based on statistical analyses of the samples from 1996 (Figure 9), the presence of five distinct aggregations of the species was confirmed in 1996 (CG96-1 to CG96-5; Figure 10).

Aggregation CG96-1 consisted mainly of CII–CIV, with CIII being dominant, and was located in the upper 100 m of the outer fjord and in the intermediate layers of the middle fjord. CG96-2, which consisted mainly of CII and CIII, was below CG96-1 at 100–200 m depth in the outer basin. CG96-3 consisted of a larger range of copepodid stages, CII–CV, and was detected in the bottom layers over the depressions at the fjord's entrance and in the intermediate and the bottom layers of the inner basin. CG96-4, consisting predominantly of CIII–CV, inhabited surface layers in the middle to inner fjord. CG96-5 was comprised almost exclusively of CV, and was limited in distribution to the intermediate and
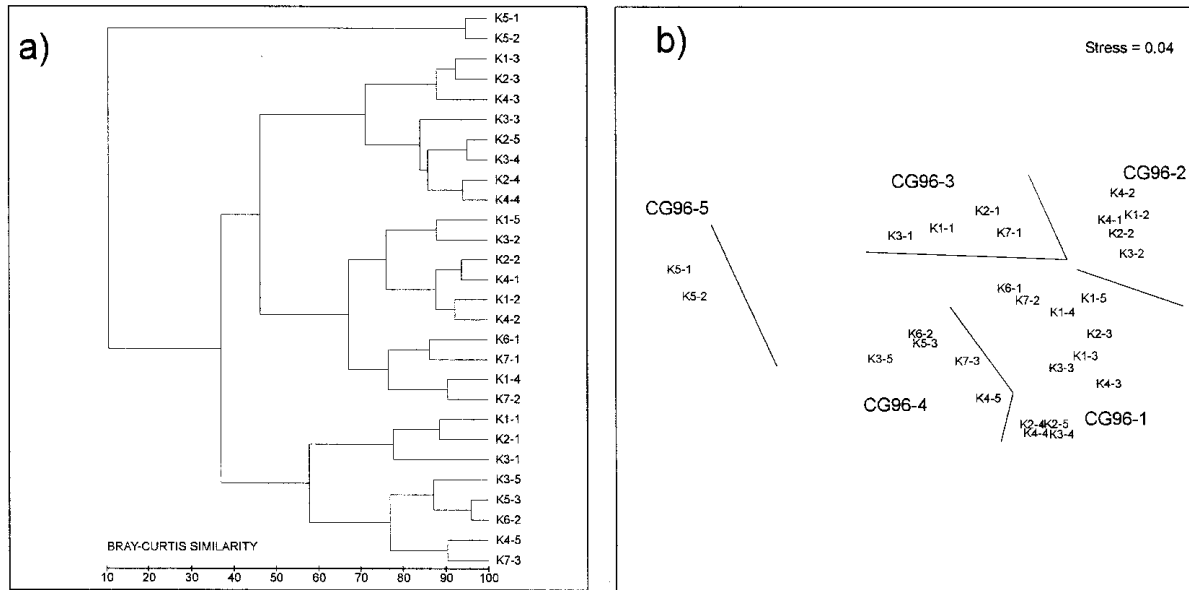
Fig. 9. Clustering dendrogram (**a**) and ordination plot (**b**) illustrating similarity between samples from 1996 in terms of copepodid stage composition of *C. glacialis*. See comment to Figure 5.
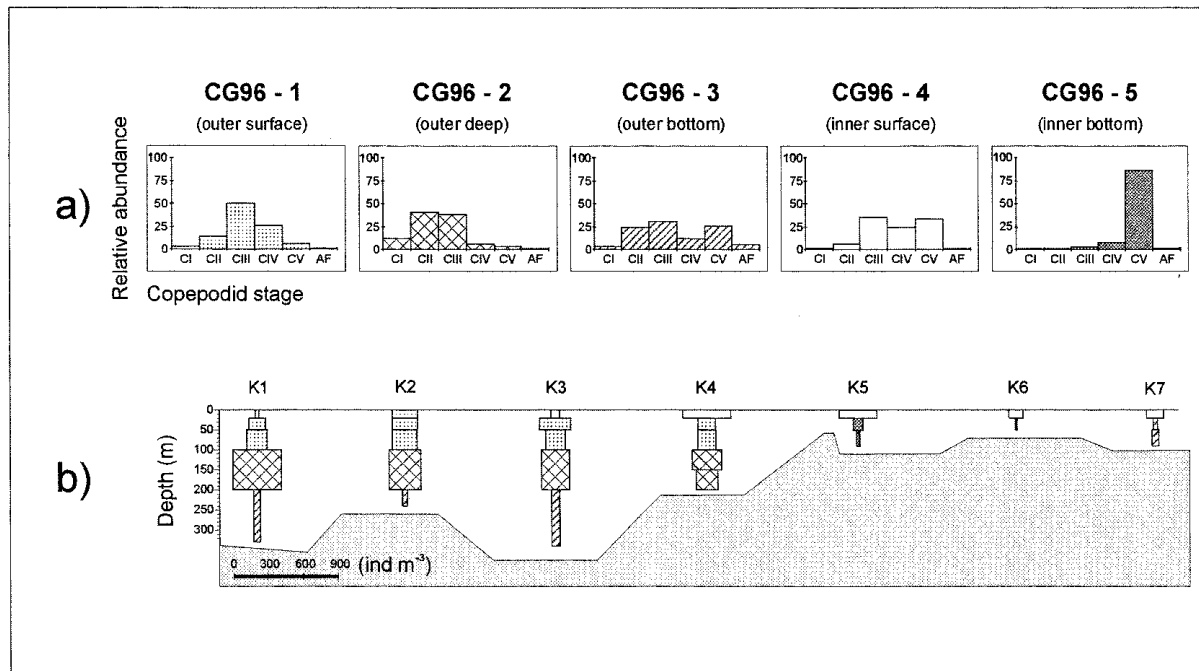

Fig. 10. Histograms of copepodid stage composition (**a**) and distribution scheme of aggregations (**b**) of *C. glacialis* in Kongsfjorden, 1996. See comment to Figure 6.

bottom layers in the southern part of the inner basin. Concentrations of copepodid stages of *C. glacialis* in individual aggregations in 1996 differed substantially (Table VI). The highest mean total abundance was in the deep layers of the outer fjord (CG96-2, 272 ind. m^{-3}). It was not much lower in the surface layers (CG96-1, 174

ind. m^{-3}; CG96-4, 216 ind. m^{-3}), but diminished towards the bottom in both the outer and inner fjord (CG96-3 and CG96-5 with 46 and 56 ind. m^{-3}, respectively).

The examination of similarity in copepodid stage composition of *C. glacialis* between individual samples from 1997 yielded a dendrogram with three groupings of

Table VI: Mean abundance (ind. m^{-3}) of Calanus *copepodid stages in aggregations, Kongsfjorden 1996 and 1997*

Species	Aggregation	CI	CII	CIII	CIV	CV	CIVF	All stages
1996								
C. finmarchicus	CF96-1	35	36	55	21	9	37	193
	CF96-2	22	40	87	12	19	20	200
	CF96-3		3	16	4	85	19	127
	CF96-4	11	7	15	5	8	54	100
	CF96-5	1	2	3	1	16	12	35
C. glacialis	CG96-1	4	22	89	47	11	1	174
	CG96-2	35	108	104	16	7	2	272
	CG96-3	1	11	13	5	13	3	46
	CG96-4	3	12	81	54	65	1	216
	CG96-5	1	1	1	5	47	1	56
C. hyperboreus	CH96		0.5	1.0	3.2	0.6	0.3	5.6
1997								
C. finmarchicus	CF97-1	78	38	34	24	5	4	183
	CF97-2	83	86	127	113	15	22	446
	CF97-3	2	17	60	105	17	13	214
	CF97-4	1	1	1	21	48	31	103
C. glacialis	CG97-1	1	1	8	17	12	1	40
	CG97-2	1		1	2	10	1	15
	CG97-3	2	4	63	86	35	2	192
C. hyperboreus	CH97		0.2	0.7	9.9	1.5	1.0	13.4

samples, but a more obscure MDS plot (Figure 11). After discussing the results, the presence of three aggregations of *C. glacialis* in Kongsfjorden in 1997 was suggested (CG97-1 to CG97-3; Figure 12).

In aggregations CG97-1 and CG97-3, CIII–CV were abundant, with CIV dominating. CG97-1 was located in the surface and middle layers (<120 m) of the outer basin, whereas CG97-3 was located at all depths in the inner basin and at mid-depths at the head end of the outer basin. In CG97-2, located in the bottom layers of the outer basin, the same copepodid stages were present, although the older CV was the most abundant. The density of *C. glacialis* was low in the outer fjord, both in the upper part of the water column (CG97-1, 40 ind. m^{-3}) and close to the bottom (CG97-2, 15 ind. m^{-3}). It was highest in the inner part of the fjord (CG97-3, 192 ind. m^{-3}).

Calanus hyperboreus was the least abundant of the three *Calanus* species in Kongsfjorden. CI was absent and CII, when present, was negligible. The majority of the population (on average 57% in 1996 and 74% in 1997) consisted of CIV. No significant differences in copepodid stage composition of this species between stations of the fjord could be detected, which suggested that one age group inhabited the entire fjord each year (i.e. CH96 and CH97; Figure 13).

In 1996, *C. hyperboreus* aggregated in the upper water layers, except at the mouth of the fjord were it was found in the deeper part of the water column (Figure 13a). The highest abundance (maximum 18 ind. m^{-3}) was in the middle to inner fjord, where CIV was, generally, the dominating copepodid stage. CV was most abundant in the bottom layers at stations K1–K3. The mean density for 1996 was 6 ind. m^{-3} (Table VI).

In 1997, the distribution of *C. hyperboreus* was more uniform with higher concentrations close to the bottom in the outer basin and in the intermediate layers of the inner basin, whereas surface waters were generally avoided (Figure 13b). The concentration of the species was highest in the inner fjord (maximum 59 ind. m^{-3}), although it was also high in the bottom layers at the outermost stations. The copepodid stage composition was almost exclusively CIV, and the mean abundance was more than twice that of 1996 (13 ind. m^{-3}).
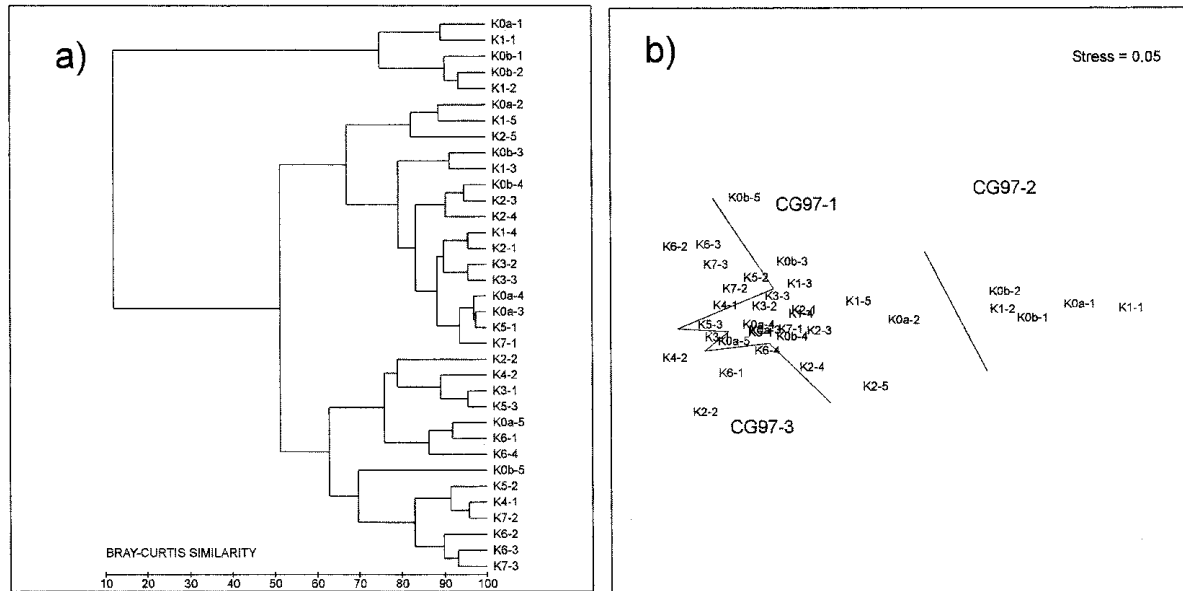
Fig. 11. Clustering dendrogram (**a**) and ordination plot (**b**) illustrating similarity between samples from 1997 in terms of copepodid stage composition of *C. glacialis*. See comment to Figure 5.
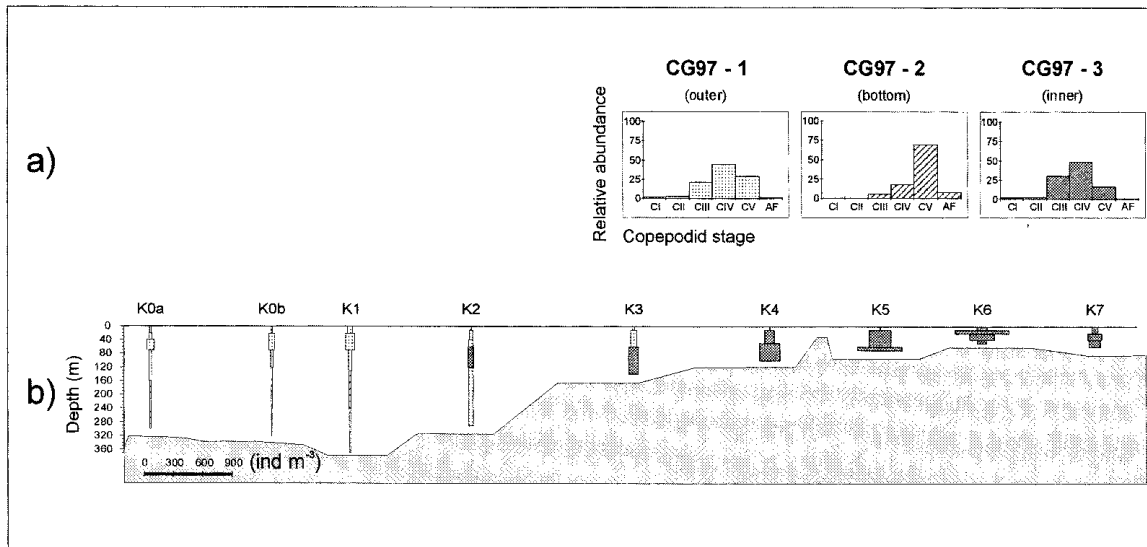

Fig. 12. Histograms of copepodid stage composition (**a**) and distribution scheme of aggregations (**b**) of *C. glacialis* in Kongsfjorden, 1997. See comment to Figure 6.

DISCUSSION

Kongsfjorden has relatively rich zooplankton fauna, comparable with that of other fjords within the area of the Nordic Seas. This study confirmed the presence in Kongsfjorden of all zooplankton taxa found previously in Spitsbergen fjords (Stott, 1936; Digby, 1961; Koszteyn and Kwasniewski, 1989; Kwasniewski, 1990; Weslawski *et al.*, 1990, 1991a,b; Sywula *et al.*, 1993). It supplemented the list of taxa with five species known from the surrounding waters (Nosova, 1964; Shuvalov, 1966; Dalpadado and Skjoldal, 1991), namely *Metridia lucens* Boeck, 1864, *Gaidius tenuispinus* (Sars, 1900), *Thysanoessa raschii* (M. Sars, 1864), *Thysanoessa longicaudata* (Krøyer, 1846) and *Boreomysis arctica* Krøyer, 1861, plus first time recorded copepods *Bradyidius similis* (Sars, 1902), a species of Tharybidae, a species of
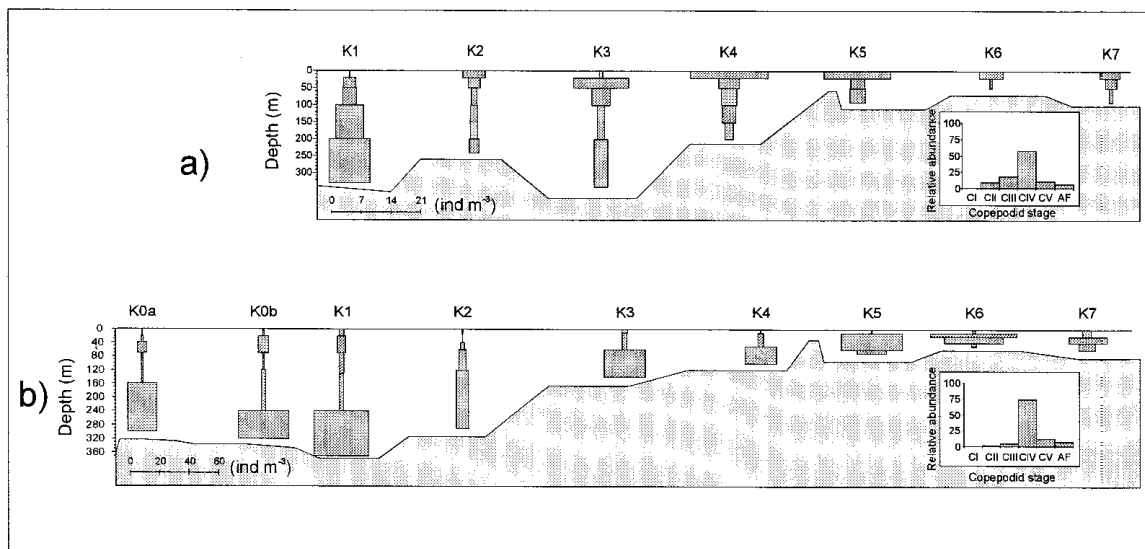
Fig. 13. Distribution of *C. hyperboreus* (all copepodid stages) in Kongsfjorden in 1996 (**a**) and in 1997 (**b**). Histograms illustrate fjord mean copepodid stage composition in particular years.

Phaennidae, a species of Platycopioidae and a species of Monstrilloida. The last five taxa had not been reported in the area before, most likely because their habitat, deep and bottom waters, had not been sampled extensively enough.

The sympatric occurrence of *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*, as well as some other species such as *M. lucens*, *Oithona atlantica* Farran, 1908 and *Limacina helicina* Phipps, 1774, indicates that the zooplankton fauna in Kongsfjorden originates from different biogeographic zones. The scheme of circulation in the area supports this hypothesis (Loeng, 1989; Hopkins, 1991). The WSC, which flows northward along the west coast of the island, carries warm Norwegian Atlantic Water with Atlantic fauna. *Calanus finmarchicus* is the primary copepod representative for this water mass (Hirche and Mumm, 1992). This current also accommodates *C. hyperboreus*, but in low abundance (Smith *et al.*, 1985; Hirche *et al.*, 1991). The South Cape Current, which flows around the southern tip of Spitsbergen, brings cold water originating from the northern Barents Sea, referred to as Barents Sea Polar Water (Hopkins, 1991) or Arctic Water (Loeng, 1989). It transports cold-water fauna, including *C. glacialis* and *C. hyperboreus*, which dominate the area where this water originates (Conover, 1988; Eilertsen *et al.*, 1989b; Vinogradov, 1997). The open entrance to Kongsfjorden facilitates the unobstructed transport of offshore and shelf waters along with their associated fauna, and this transport is controlled by regional water dynamics and tides (Svendsen *et al.*, 2002).

The species composition suggests the unique position of the zooplankton from Kongsfjorden in relation to zooplankton of other fjords in the Nordic Seas region.

The presence of *C. glacialis* and the lack of several warm water species make the zooplankton from Kongsfjorden different from that of the fjords of northern Norway (Hopkins, 1981; Barthel, 1995) or Iceland (Astthorsson and Gislason, 1992). The lack of warm water species also makes it different from the zooplankton of the White Sea (Prygunkova, 1974). On the other hand, the presence of Atlantic components constitutes the main difference between the zooplankton in Kongsfjorden and the zooplankton in the fjords of east Greenland (Ussing, 1938; Digby, 1954; Hirche and Kwasniewski, 1997; Weslawski *et al.*, 1997; Rysgaard *et al.*, 1999). Thus, this special position of Kongsfjorden on the border of different climatic and biogeographic zones makes it well suited for studying how the zooplankton communities face the consequences of climate change.

Aggregation is a well-known feature of pelagic invertebrates, including social aggregations as discussed in a recent review by Ritz (Ritz, 1994). Swarms and schools in polar pelagic animals have been studied mostly for krill in the Northern Hemisphere [e.g. (Falk-Petersen and Kristensen, 1985)] and even more often in the Southern Hemisphere [e.g. (Hamner *et al.*, 1983)]. Krill aggregations often consist of uniform size/age groups (Hamner *et al.*, 1989). There are few examples of size/age-specific or social groupings in copepods (Omori and Hamner, 1982; Hamner, 1988; Kaartvedt, 1996). This is probably because little effort has been put into sampling copepod communities on scales fitted to the species ambits (Haury *et al.*, 1978). The examination of copepodid stage compositions and distribution in this study suggests that there were distinct aggregations of *Calanus* present in

Kongsfjorden, for both *C. glacialis* and *C. finmarchicus*. These distinct aggregations had different copepodid stage composition, generally consisting of young copepodids (CI–CIV) in surface and intermediate layers, probably actively feeding, and the older copepodids (mainly CV and females) in the bottom waters, most likely assembled for overwintering.

The distribution of *Calanus* species in Kongsfjorden can be interpreted based on species biology and life history characteristics, and the circulation and mixing of water masses in Kongsfjorden (Svendsen *et al.*, 2002). Some discrepancies can be attributed to the resolution of sampling and to the location of stations relative to the circulation pattern. In fjords of northern Norway and northwards, the boreal *C. finmarchicus* has a 1 year life cycle (Tande, 1982; Tande *et al.*, 1985), and this has also been suggested for Kongsfjorden (Scott *et al.*, 2000). The spawning time of the species coincides with the period of maximum phytoplankton spring bloom (Tande, 1982; Tande *et al.*, 1985). In Balsfjorden (70°N, Northern Norway), *C. finmarchicus* starts to develop gonads by mobilizing lipids in January–February (Falk-Petersen *et al.*, 1987). Yet, to complete spawning, the species is dependent on energy input from the phytoplankton bloom in mid-April. The new generation develops to CIV by June (Østvedt, 1955; Tande, 1982). Conover (Conover, 1988) and Hirche (Hirche, 1991) considered CV as the over-wintering copepodid stage, whereas Pedersen *et al.* (Pedersen *et al.*, 1995) documented the presence of both CIV and CV as overwintering stages in the Barents Sea.

We hypothesize that in 1996 the stock of *C. finmarchicus* in Kongsfjorden included two populations: the local population in the inner basin and the advected population in the outer part of the fjord. The local population consisted mainly of females and CV. A relatively high number of females in the surface layers in the inner basin suggests that the local population was still in the reproductive phase. The few CV in the inner bottom layers were probably a non-spawning part of the local population. The part of the local population of *C. finmarchicus* in the surface layers was subjected to outgoing transport with surface waters, related to the complex estuarine circulation (Svendsen *et al.*, 2002), but at the same time as the WCW in depressions could protect some of the stock from advection. We suggest that the population dominated by young CII and CIII of *C. finmarchicus* in the outer fjord originated on the shelf and had been advected in. The vertical distribution of this population in intermediate layers matched the depth of suggested incoming flow from the shelf (Svendsen *et al.*, 2002). The progressive decrease in concentration of the advected population towards the inner fjord further substantiates this postulate. We propose that *C. finmarchicus* in the deepest part of the

fjord resided below the incoming/outgoing flow and could have been building a residual stock, although this situation could have been temporary. With respect to the *C. finmarchicus* life cycle, our findings concur with Scott *et al.* (Scott *et al.*, 2000), who proposed that CIV and CV could both overwinter successfully in Kongsfjorden, and that CIV completes its development to CV, and then to females, the following spring. Such development, which depends on food intake, must occur during or after the spring bloom. With respect to the advected population of *C. finmarchicus*, it is assumed that at a water temperature of 2°C it needs 54 days to reach CIII (Corkett *et al.*, 1986). Hatching time is back-calculated to the beginning of May, the time when it is likely that the phytoplankton bloom in ice-free waters outside the fjord would occur (Weslawski *et al.*, 1988; Eilertsen *et al.*, 1989a). The period with ice cover in the middle and inner Kongsfjorden extends to between April and June (Svendsen *et al.*, 2002), but generally causes a delayed bloom in May (Hop *et al.*, 2002.) This may cause a subsequent delay in the development of the local population of *C. finmarchicus*.

In 1997, the uppermost layers accommodated younger copepodid stages of *C. finmarchicus*, with CI dominating. We assume that they were that year's offspring from the local population in Kongsfjorden. Intermediate layers at the fjord's entrance having the temperature/salinity characteristics of TAW were occupied by a much more developed population, with CIII and CIV dominating. We suggest that these copepodids were advected from coastal waters and represented a shelf population that may have hatched at the beginning of May. The CIV, CV and females in deep and bottom waters probably represented an initial overwintering stock of *C. finmarchicus* in Kongsfjorden. Hydrological observations indicate a different situation in 1997 compared with 1996 [Figures 2 and 3; (Hop *et al.*, 2002; Svendsen *et al.*, 2002)]. The expanse of LW in the inner basin of the fjord was much less in 1997 and TAW occupied most of this area. The salinity of TAW was significantly higher and water temperature increased by 1°C and by >2°C at 100 and 50 m, respectively, in 1997 compared with 1996. The stronger contribution of the Atlantic component could account for the enlargement of the area occupied by the shelf population and, thus, its higher abundance in the fjord. Unlike in 1996, the temperature isopleths clearly suggest penetration of outer basin water into the inner one in 1997. The regular advective inflow becomes disturbed over shallow locations (illustrated by the distribution of temperature and salinity near station K6 in the inner basin; Figure 3), where an envelope of cold water intruded in the subsurface layer. In such locations, the distribution of *Calanus* aggregations also showed irregularities, which were in accordance with the temperature

and salinity anomalies. There the aggregation of older stages predominated by CIV, regularly found close to the bottom and in the deep layers, was found in the subsurface layer. The higher temperature and later sampling, by 10 days in 1997, could explain the predominance of younger copepodids and lack of females of *C. finmarchicus* in the local population of this year. These factors could also have accounted for a higher proportion of CIV in the shelf population in 1997 compared with 1996.

Within its original Arctic range, *C. glacialis* has a 2 year life cycle (Tande *et al.*, 1985; Eilertsen *et al.*, 1989b), with spawning taking place before or during the algal bloom (Smith, 1990; Hirche and Kwasniewski, 1997; Falk-Petersen *et al.*, 1999; Kosobokova, 1999), although a 1 year life cycle has also been observed (Maclellan, 1967). In the Barents Sea, this species spawns in March–April (Pedersen *et al.*, 1995) and develops into CIII by the end of the plankton production period (Tande *et al.*, 1985). Most likely, it develops from eggs to CIV within a single year (Scott *et al.*, 2000). However, further development from CIV to CV is unlikely to be achieved in a single year and must, therefore, be postponed to the second year of life.

In Kongsfjorden during mid-July, all copepodid stages of *C. glacialis* from CI to CV and females existed both in 1996 and 1997. CII–CIV were the most abundant in subsurface and deep layers, and avoided warm surface waters. CV was located near the bottom, although it was also found in surface layer in the inner fjord when surface water was cold (<2°C). At the time of sampling in 1996, the bulk of the population that was concentrated in the subsurface to deep layers was CII–CIV; these were most likely actively feeding, as inferred from observations of copepods with pigmented gut content, and plenty of faecal pellets on the sieves during processing of the samples. Lower abundance near the surface in the outer fjord could have been caused by relatively high temperature (>3°C). The descent of *C. glacialis* as a result of the heating of surface layers was observed in the White Sea population (Kosobokova, 1999). The smaller fraction of CV, located close to the bottom, had possibly descended to deeper layers to overwinter. The weaker advection from the WSC or more contribution of Arctic Water and water from other fjords in the water advected from the shelf in 1996 may explain the relatively high abundance of *C. glacialis* also in the outer fjord. Another possibility is aggregation of the descending stock, escaping higher water temperature in the outer fjord. The temperature influence on CV was apparent because this stage was most abundant in the cold WCW and in the surface layer of the inner basin.

In July 1997, the bulk of *C. glacialis* was CIII and CIV in the inner basin. A less numerous aggregation with the same copepodid stage structure was located in the upper part of the water column in the outer fjord, whereas copepodid stage V was found in the depressions. Scott *et al.* (Scott *et al.*, 2000) showed that, by September 1997, the *C. glacialis* stock present above 200 m in Kongsfjorden had developed into CV as the most abundant copepodid stage. Taking this into account, we support their conclusion that *C. glacialis* has a 2 year life cycle in Kongsfjorden, with CIV as the first overwintering copepodid stage and CV as the second. As in other locations (Kosobokova, 1999), spawning most likely takes place early in the year in order to allow time for development and avoid exposure of the offspring to the seasonal increase in temperature. The lack of ice cover or its earlier break-up in the outer fjord allows the phytoplankton bloom to occur as early as April (Hop *et al.*, 2002). Advected phytoplankton would supply the food, until the bloom in the fjord commenced. It is also possible that *C. glacialis* begins to spawn in the absence of phytoplankton, as observed in other Arctic locations (Smith, 1990; Hirche and Kwasniewski, 1997). The lower *C. glacialis* abundance in 1997 relative to 1996 may have been caused by higher advection of WSC derived water [Figures 2 and 3; (Hop *et al.*, 2002; Svendsen *et al.*, 2002)], which generally has low abundance of this species. In the outer fjord where TAW dominated, the stock of *C. glacialis* was low. The highest abundance of *C. glacialis* was observed towards the fjord's head where LW and WCW prevailed. The scarcity of *C. glacialis* CII in 1997 may have been attributed to later sampling.

Calanus hyperboreus is an Arctic/polar species that spawns during the winter (Vinogradov, 1977; Hirche and Niehoff, 1996). After the onset of the spring bloom, offspring develop rapidly into CIII. This species has a 3- to 4-year life cycle, depending on the food availability, and it overwinters mainly as CIII–CV (Hirche, 1997; Scott *et al.*, 2000). In Kongsfjorden, the occasional presence of CI, CII and very few CIII of *C. hyperboreus* was noted in the period from May until September (Scott *et al.*, 2000; personal observations). Females were always present in very low numbers. We assume that *C. hyperboreus* does not maintain a fjord population based on local spawning and that the majority of its copepodids are advected into the fjord. Thus, *C. hyperboreus* is probably an expatriate in the fjord system. The pattern of spatial distribution of *C. hyperboreus* in Kongsfjorden may reflect the species' preference for lower temperature and/or its ontogenetic migratory pattern, which includes movements into deep water for overwintering.

ACKNOWLEDGEMENTS

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