

Advection of zooplankton in an Arctic fjord (Kongsfjorden, Svalbard)

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Abstract

The aim of this study was to qualify the impact advection has on local populations of planktonic organisms. The study area was Kongsfjorden, an open glacial fjord on the West Coast of Spitsbergen, divided into two basins. On a cruise in May 2001 water masses with different salinity and temperature characteristics were identified from CTD data and sampled for mesozooplankton. Water velocity was measured with a ship-mounted broad band ADCP. Flux of the calanoid copepods *Calanus finmarchicus* and *Calanus glacialis* was calculated and based on this advection of zooplankton into the fjord was determined by simulation.

The younger copepodite stages were concentrated in surface and subsurface waters and subject to high water velocities. Thus the advective impact on these copepodites was high. Older stages were located deeper in the water column and could maintain their position for a longer time. An eddy was observed in the outer basin and retained zooplankton in the fjord in simulations. The inner basin is likely to be more isolated from the shelf and residence time in this basin is thus probably longer.

Calanus finmarchicus was most abundant in the outer basin at the periphery of the eddy and the population in May in Kongsfjorden consisted presumably mainly of individuals advected into the fjord from the surrounding shelf. *Calanus glacialis* was most abundant in the inner basin and local production there is assumed to exceed advection.

Net inflow of zooplankton exceeded outflow during the study period. This impact of zooplankton is probably of high importance for higher trophic levels.

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1. Introduction

For a long time attention has been drawn to the importance of advection for ecosystems in open fjords (e.g. Matthews and Heimdal, 1980) and other open areas (e.g. Hardy and Gunther, 1935). It has been widely reported that advection influences age structure, species composition and biomass of zooplankton communities (Lindahl and Henroth, 1988; Falkenhaug et al., 1995; Durbin et al., 2000; Helle, 2000; Skreslet et al., 2000). Planktonic organisms are by definition incapable of maintaining horizontal position in a moving water

column (Hensen, 1887). Thus, the spatial component to temporal dynamics of planktonic organisms is mainly determined by the advective transport of water masses. In highly advective regions, advection (immigrants–emigrants) can exceed local production (births–deaths) of biomass by a factor of four. Little is known however about the mechanisms by which spatial and temporal variability in advection affect dynamics of local populations.

Kongsfjorden (79°N, 12°E, Fig. 1), an open fjord on the West Coast of Spitsbergen, is a study area well suited for investigating some of the advection mechanisms. Zooplankton biomass in Kongsfjorden, in comparison with other Arctic locations, is relatively high despite high predation pressure from planktivorous fish and birds (Hop et al., 2002). The abiotic environment of

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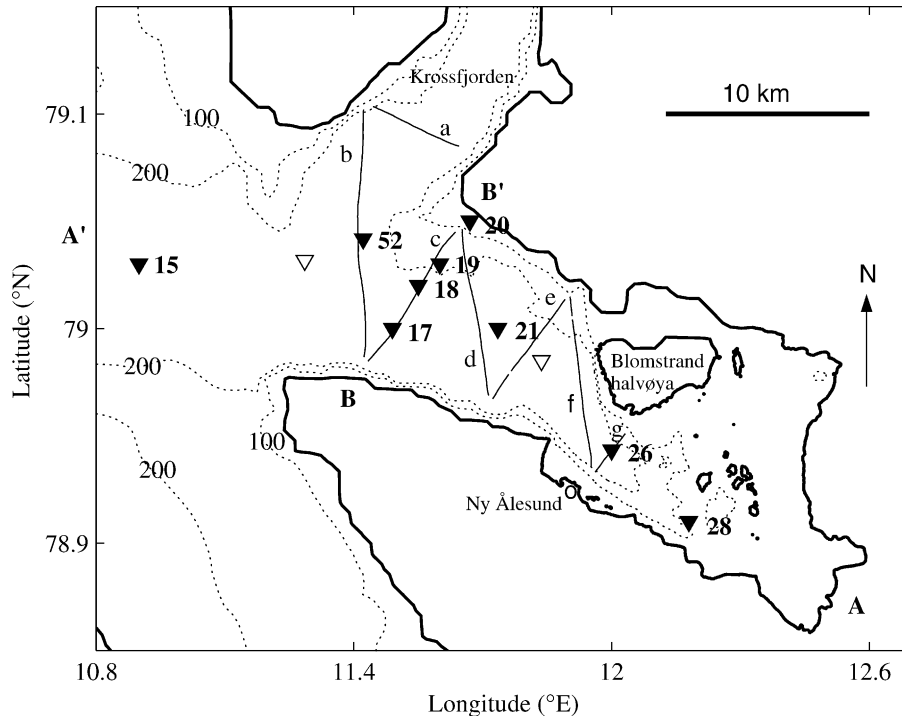


Fig. 1. Map of Kongsfjorden showing sampling stations (▼, K 15–K 52), additional CTD stations (▽) and ADCP tracks (a–g).

Kongsfjorden is not greatly different from the waters nearby and thus local production is not likely to be higher in the fjord than in surrounding waters. Advection is thus assumed to account for the high biomass found (Hop et al., 2002; Kwasniewski et al., 2003).

Exchange between Kongsfjorden and the adjacent shelf is determined by the prevailing currents and wind systems (Svendsen et al., 2002). Often instabilities in the front between the major currents of the west coast, the West Spitsbergen Current (WSC) and the Coastal Current (CC) cause filaments of Atlantic water from the WSC to approach the coast and proceed into Kongsfjorden (Saloranta and Svendsen, 2001; Svendsen et al., 2002).

The zooplankton community in Kongsfjorden reflects the mixture of water masses of Atlantic and Arctic origin. Boreal species with a center of distribution in the North Atlantic like *Calanus finmarchicus* occur together with species associated with Arctic water masses like *Calanus glacialis* (Jaschnov, 1970; Tande et al., 1985; Hassel, 1986; Koszteyn and Kwasniewski, 1989; Weslawski et al., 1991). Numerically, copepods tend to dominate the planktonic fauna in Kongsfjorden (Scott et al., 2000; Weslawski et al., 2000; Hop et al., 2002; Kwasniewski et al., 2003). Among them, the three *Calanus* species *C. hyperboreus*, *C. glacialis* and *C. finmarchicus* are by virtue of their high abundance and high lipid content of major importance in the Arctic food web (Scott et al., 1999; Falk-Petersen et al., 2002).

This study had the rare opportunity to combine information about the distribution of zooplankton with near simultaneous oceanographic data. Data are presented on how advection affected local populations of *Calanus finmarchicus* and *Calanus glacialis* in Kongsfjorden.

2. Material and methods

2.1. Field sampling

Kongsfjorden (79°N, 12°E) consists of two basins separated by a 30-m-deep sill and a chain of small islands. In the shallow (<80 m) inner basin three large glaciers (Kongsbreen, Kongsvegen and Blomstrandbreen) calve into the fjord. The outer larger basin is deeper (<400 m) and relatively open towards the Fram Strait. Detailed information about the physical environment of Kongsfjorden can be found in Svendsen et al. (2002).

During a cruise with R/V “Lance” from 18th to 25th of May 2001, sampling was conducted along two transects: transect AA’ from the inner part of the fjord towards the shelf (five stations: K 28, K 26, K 21, K 52, K 15) and transect BB’ across the mouth of the fjord (four stations: K 17, K 18, K 19, K 20) (Fig. 1).

At each station a depth-related salinity and temperature profile was obtained by a Seabird CTD. From the CTD data water bodies with different characteristics

Table 1
Stations sampled during the cruise

Station	Date	Time	Net	Sampling intervals (m)
K 28	22 May	01:30	WP2	90–0
K 26	21 May	22:00	WP2	275–100–0
K 21	21 May	16:00	WP2	250–100–0
K 52	21 May	14:00	WP2	200–100–0
K 15	20 May	23:00	WP2	300–100–0
K 17	24 May	02:00	Multinet	270–210–100–50–0
	24 May	18:25	Multinet	270–210–100–50–0
	25 May	02:45	Multinet	270–210–100–50–0
K 18	24 May	02:30	Multinet	170–100–60–0
	24 May	18:45	Multinet	170–100–60–0
	25 May	02:00	Multinet	170–100–60–0
K 19	24 May	03:00	Multinet	210–175–100–35–0
	24 May	19:00	Multinet	210–175–100–35–0
	25 May	01:35	Multinet	210–175–100–35–0
K 20	24 May	03:30	Multinet	55–25–0
	24 May	19:35	Multinet	65–25–0
	25 May	01:25	Multinet	65–25–0

(salinity and temperature) were identified and sampled for mesozooplankton by vertical hauls carried out either with a multiple opening closing net (Multinet, Hydrobios Kiel, 180 μm mesh size, 0.25 m^2 mouth opening) or with a WP2 net (180 μm mesh size, 0.255 m^2 mouth opening) (Table 1). Hauling velocity was $\sim 0.5 \text{ m s}^{-1}$. Net type influences the catch obtained mainly by differential catch efficiency as a result of different mesh size and mouth opening (McGowan and Franusdorf, 1966). Multinet and WP2 net used had the same mesh size and approximately the same mouth opening, thus samples obtained by both nets should be comparable. Limited ship time and the need to perform ADCP transects at a predetermined time did not permit replicates of samples to be taken across transect BB'; along transect AA' three replicates were taken at each station. The obtained abundance from stations K 17, K 18, K 19 and K 20 is therefore more likely to be biased due to patchily distributed zooplankton. Net samples were preserved in a 4% formaldehyde in seawater solution after removal of gelatinous zooplankton.

The spatial distribution of *Calanus* spp. along transect AA' was examined by Bray–Curtis similarity index between sample pairs based on relative copepodite stage abundance and applying afterwards non-metric multidimensional scaling (MDS) (Field et al., 1982; Clarke and Warwick, 1994). For all computations the PRIMER 5 (version 5.2.0, ©PML 2001) software package was used.

Water velocity in the study area was measured with a ship-board mounted broad band Acoustic Doppler Current Profiler (ADCP, RD Instruments BB 150 WM) along a zigzag transect inside Kongsfjorden and along a triangle transect connecting the mouth openings of Kongsfjorden and Krossfjorden (Fig. 1). ADCP transects were taken in two series: series 1 starting on the 22nd and series 2 starting on 24th of May (Table 2).

Table 2
Date and time of ADCP measurements along specified tracks and the according water level in Kongsfjorden

ADCP series	Track	Date	Time of ADCP measurements	Time of high and low tide, respectively	Level over normal null (cm)
1	a	22 May	00:09–00:40		
	b	22 May	01:05–02:21	01:11	141
	c	22 May	02:47–04:16		
2	d	22 May	04:22–06:30	07:12	33
	e	24 May	19:15–21:34	20:43	16
	f	24 May	21:42–22:59		
	b	25 May	01:14–02:57	02:18	151
	g	25 May	03:01–04:08		
	a	25 May	04:12–05:51		
	a	25 May	05:56–06:25		

Wind speed and direction were obtained from the Koldewey station of the Alfred-Wegener Institute in Ny Ålesund.

2.2. Analysis of samples in the laboratory

From sub-samples (1/2 to 1/128ths, containing approximately 500 copepods) organisms were identified to the lowest possible taxonomic level and counted. If nauplii were abundant, 5-ml sub-samples were taken with a pipette from well-mixed samples with known volume and from these nauplii were counted. This was repeated until ~ 200 nauplii (not determined to species) were counted. The abundance of organisms was computed, based on filtered volumes calculated by multiplying vertical hauling distance with mouth opening area assuming 100% filtration efficiency. At stations where the WP2 net was used, zooplankton abundance of the lower water bodies was calculated by subtracting the abundance of the upper layer(s) from the abundance of the total water column.

Since anatomical differences between the three co-occurring *Calanus* species (*C. hyperboreus*, *C. glacialis* and *C. finmarchicus*) are only easily observable on late copepodites of *C. hyperboreus* (developmental stage CIV onwards; Jaschnov, 1955; Grainger, 1961) separation into species was done according to size distribution (e.g. Grainger, 1963; Jaschnov, 1970; Unstad and Tande, 1991; Madsen et al., 2001). The cephalothorax length of all *Calanus* copepodites counted was measured under a stereomicroscope equipped with a calibrated eyepiece reticule. For each developmental stage size groups were separated by use of the program MIX version 3.0 (MacDonald and Green, 1988) (Table 3). This program is designed for separating age groups of shrimps by size (e.g. Penaflores and Virtanem, 1996; Ragonese and Biachini, 1996) and can be used in the same way to separate species of *Calanus* by size.

Table 3

Size limits set to separate the three *Calanus* species according to the MIX-analyses

Stage	Cephalothorax length (mm)		
	<i>C. finmarchicus</i>	<i>C. glacialis</i>	<i>C. hyperboreus</i>
CI	<0.86	0.86–1.13	>1.13
CII	<1.22	1.22–1.61	>1.61
CIII	<1.74	1.74–2.30	>2.30
CIV	<2.34	2.34–3.18	>3.18
CV	<3.09	3.09–4.02	>4.02
Female	<3.37	3.37–4.51	>4.51

2.3. Computing and simulating advection of zooplankton

To calculate exchange of organisms through transect BB' this transect was divided into 115 grid points. For each grid point (x, y) at all depths (d) current velocity with its eastern (u) and northern (v) component and zooplankton abundance (Z , mean of the three zooplankton samples) were multiplied and the direction of the current normal to the latitude/longitude grid identified (Eq. (1)):

$$\text{Flux}(d, x, y) = Z(d, x, y)[\cos(-33^\circ)u(d, x, y) + \sin(-33^\circ)v(d, x, y)] \quad (1)$$

Inflow was then $\sum \text{Flux}(d, x, y) > 0$ and outflow $\sum \text{Flux}(d, x, y) < 0$. The computations were done for both ADCP series. Abundance of zooplankton between the southern- and northernmost station and south and north coast, respectively, was interpolated linearly. The same was done for current velocity. Current velocity and zooplankton abundance were assumed to be zero at the coast. Surface currents are depending on local winds and usually stronger than currents in deeper layers. As no current data exist above 14 m (due to limitations of the ADCP used), current was assumed to flow with the same strength and direction in the surface layer as at 14 m. This assumption involves the least speculations, and is thus the most reasonable estimation of the real profile we can get, although it may bias results towards an underestimation of the flow.

To obtain the current pattern in Kongsfjorden, currents were interpolated between the ADCP transects using the Delaunay triangulation integrated in matlab (version 6.5, MathWorks).

The tidal component of the water flow was estimated by multiplying the surface area of Kongsfjorden (200 km², Chart 522, Norwegian Polar Institute) with the difference in water level at low and high tide (Table 2) and then dividing the obtained volume with the time period between tidal minima and maxima.

Advection of zooplankton for both ADCP series was simulated with a Lagrangian model starting at the

zooplankton sampling stations. Copepods were considered as particles that were additionally to the currents influenced by some random movement (rand) in the horizontal plane (Eqs. (2) and (3)):

$$x(t + \Delta t) = x(t) + \Delta t u(x(t), y(t)) + \text{rand} \quad (2)$$

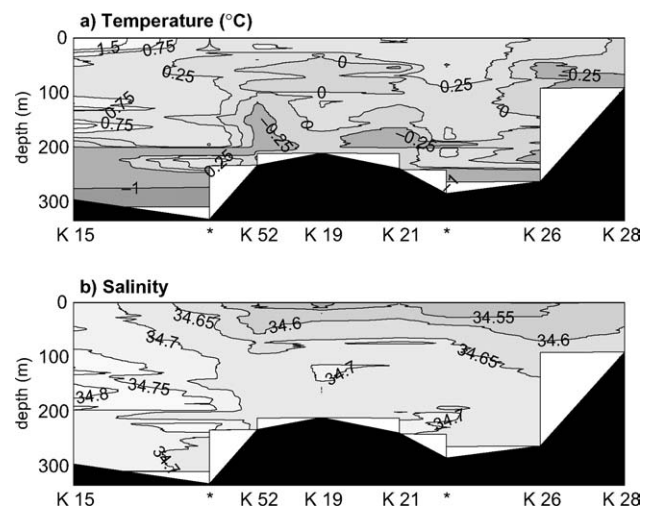
$$y(t + \Delta t) = y(t) + \Delta t v(x(t), y(t)) + \text{rand} \quad (3)$$

To evaluate the influence of tidal variability of currents on zooplankton advection a simulation with shifting between the two flow regimes (tidal outflow at ADCP series 1 and tidal inflow at ADCP series 2) every 6 h was set up.

3. Results

3.1. Water masses

During sampling Kongsfjorden was ice-free outside of station K 28. Melt water (SW) characterized by low salinity and still relatively low temperature ($S < 34.6$, $T > 0.25$ °C) formed a layer of less than 50 m thickness at the surface of the fjord (Fig. 2). Three water bodies could be distinguished below the melt water layer. Winter cooled water (WCW, $T < 0$ °C, $34.6 < S < 34.7$) had formed above the inner basin and extended there throughout the entire water column. Vertical extension of this water mass decreased further outward in the fjord; WCW could be traced on the shelf (between K 52 and K 15) only at 150 and 200 m depth (Fig. 2). From the shelf Transformed Atlantic Water (TAW, $T > 0.75$ °C, $S > 34.7$) entered the fjord. It protruded up to K 52 and further before it was transformed (mixed with fjord water) to a water mass of lower temperature and salinity (Fig. 2). Water of intermediate temperature and salinity (0 °C $< T < 0.75$ °C, $34.6 < S < 34.7$)



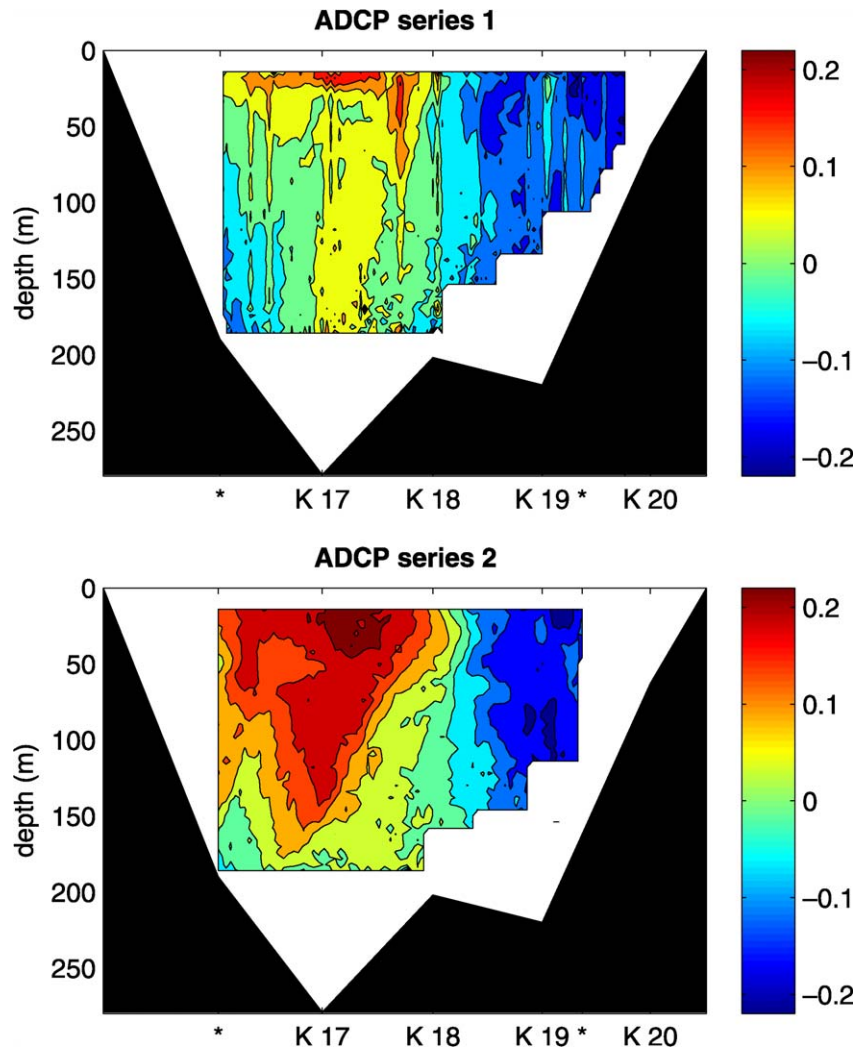


Fig. 3. East–west component (m s^{-1}) of current along transect BB' at the mouth of Kongsfjorden. Positive values indicate eastward-directed flow. Asterisks mark beginning and end of the ADCP measurements.

occupied the layer between SW and WCW in the outer basin (from K 52 inwards to nearly K 26).

3.2. Currents

Both ADCP data series showed an overall current pattern with an inflow along the southern shore of Kongsfjorden and an outflow along the northern shore (Figs. 3–8). During ADCP series 1, inflowing water formed a cyclonic eddy, persisting down to at least 90 m (Fig. 8, left). At depths below 100 m an outflow (presumably of WCW) at the south was detected

(Fig. 3). During ADCP series 2 the observed eddy occurred further out in the fjord, in the area between Krossfjorden and Kongsfjorden (Fig. 8, right). In the inner basin current velocities were very low. Current velocity was strongest close to the surface and decreased gradually with depth (Fig. 8).

3.3. Water exchange

Water exchange through transect BB' varied between ADCP series (Table 4). Tide was receding while performing measurements at the mouth of Kongsfjorden

Table 4

Water exchange through transect BB' (ADCP track c) at the mouth of Kongsfjorden for both ADCP time series (positive numbers denote flow into Kongsfjorden)

	Inflow ($10^6 \text{ m}^3 \text{ s}^{-1}$)	Outflow ($10^6 \text{ m}^3 \text{ s}^{-1}$)	Net flow ($10^6 \text{ m}^3 \text{ s}^{-1}$)	Tidal component (T) ($10^6 \text{ m}^3 \text{ s}^{-1}$)	Ratio $T/\text{net flow}$
Series 1	0.06934	-0.05386	0.01547	-0.01200	0.7755
Series 2	0.10288	-0.05335	0.49535	0.01392	0.2810

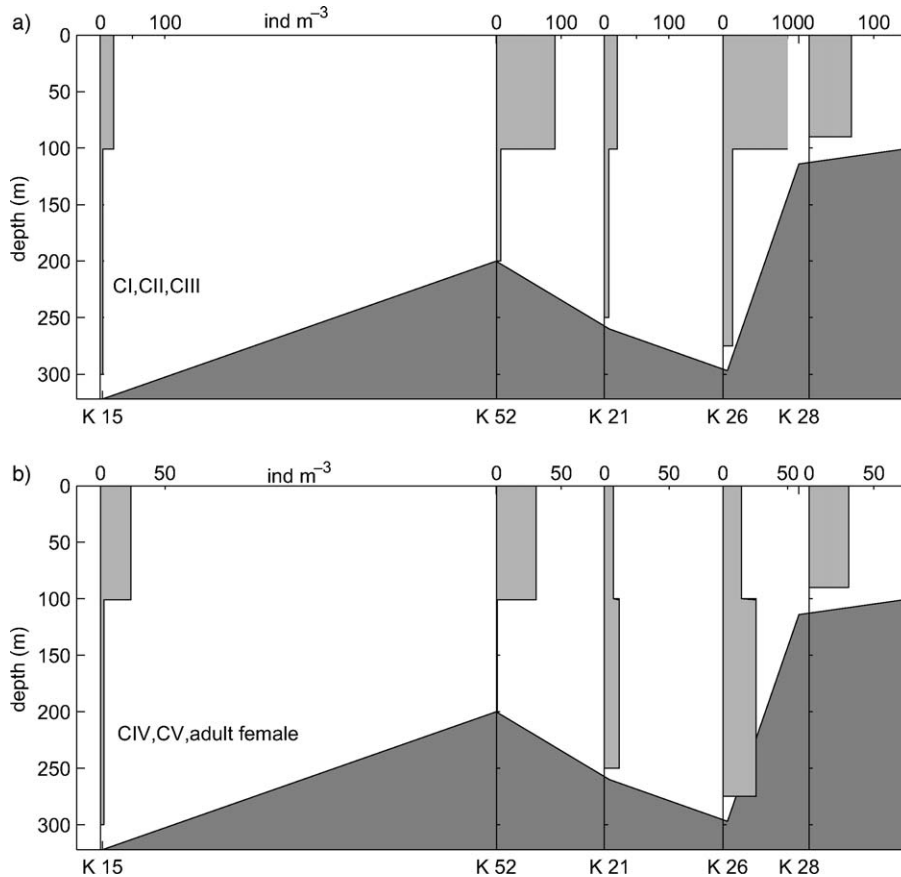


Fig. 4. Abundance of *Calanus finmarchicus* along transect AA' from the shelf towards the inner basin of Kongsfjorden. (a) Copepodite stages CI, CII and CIII, (b) copepodite stages CIV and CV and adult females. The distance between stations pictured is relative to the real distance between stations.

during ADCP series 1 (Table 2) and a strong wind directed out of the fjord was present. In this situation the inflow at the southern side of the fjord decreased and the net water flow was weak but directed into the fjord (Table 4). While measuring current at the mouth of the fjord during ADCP series 2 the tide was rising (Table 2) and only a weak outwards directed wind was observed, resulting in a larger net water flow into the fjord.

3.4. Zooplankton

Nauplii of *Calanus* spp. (46.5% of all individuals) and nauplii of calanoid copepods (34.2%) were by far the most abundant zooplankton organisms. Larvae of polychaetes and echinoderms were also abundant but varied between locations. Apart from nauplii and larvae, copepods dominated, the most abundant being *Calanus glacialis* (7.3%) followed by *Calanus finmarchicus* (4.9%), *Oithona similis* (3.1%), *Calanus hyperboreus* (1.2%) and *Pseudocalanus* spp. (0.9%).

From the inner lagoon (K 28) towards the outermost station at the shelf (K 15) the abundance of *Calanus glacialis* and *Calanus finmarchicus* generally decreased (Figs. 4 and 5). K 26 and K 52, both situated at the periphery of the observed eddy, were however similar in

species composition and abundance while K 21, located close to the center of the eddy had lower abundance than K 52 and K 26. Abundance of *C. finmarchicus* was highest at K 26 and K 52 (120 ind m^{-3}). Younger copepodite stages were located in the upper 100 m while a large part of the older copepodites and adult females stayed in lower layers in the central fjord (Fig. 4). The MDS analysis of samples revealed the similarity between the upper 100 m of K 26 and K 52 and their dissimilarity with the upper 100 m of K 21 as well as the difference between the deeper layer of the shelf station K 15 and the deeper layers of the fjord stations K 26, K 21 and K 52 (Fig. 6a). Maximum abundance of *C. glacialis* was found at the station closest to the ice edge (K 28) (Fig. 5). At K 26 and K 52, of the younger stages about one third of the individuals were located in the waters below 100 m compared to a negligible amount at K 21 and K 15. MDS analysis showed the similarity of the deeper waters of the outer “eddy stations” K 52 and K 26 with the upper 100 m of the central “eddy station” K 21 (Fig. 6b). Older stages and adults stayed in the deeper layers at K 21 and K 15 but were located in the upper 100 m at K 26 and K 52 (Fig. 5).

Absolute numbers of the copepodite stages of *Calanus* spp. varied between the three zooplankton sampling

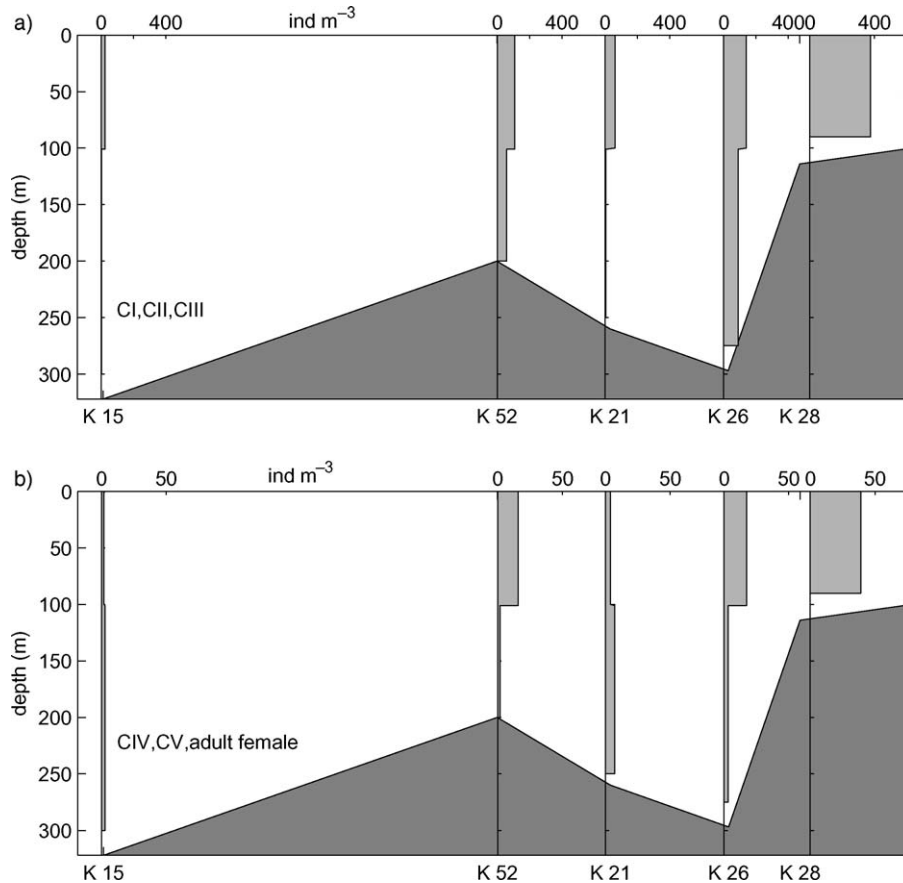


Fig. 5. Abundance of *Calanus glacialis* along transect AA' from the shelf towards the inner basin of Kongsfjorden. (a) Copepodite stages CI, CII and CIII, (b) copepodite stages CIV and CV and adult females. The distance between stations pictured is relative to the real distance between stations.

series taken at the mouth of Kongsfjorden (transect BB'). Relative abundance of copepodites between the different stations was however similar in all series (Table 5).

3.5. Advection of zooplankton

There was no big advective effect on either of the copepodite stages or on females of *Calanus* spp. during

the net outflow situation (ADCP series 1) (Fig. 7, left). In contrast at the net inflow situation (ADCP series 2) large quantities of young copepodites of both species were advected into Kongsfjorden (Fig. 7, right).

Simulations based on the current regime obtained from ADCP series 1 indicated retention of zooplankton in the fjord system. Zooplankton was 'collected' in the center of the eddy (at 18 m), circled around in the eddy

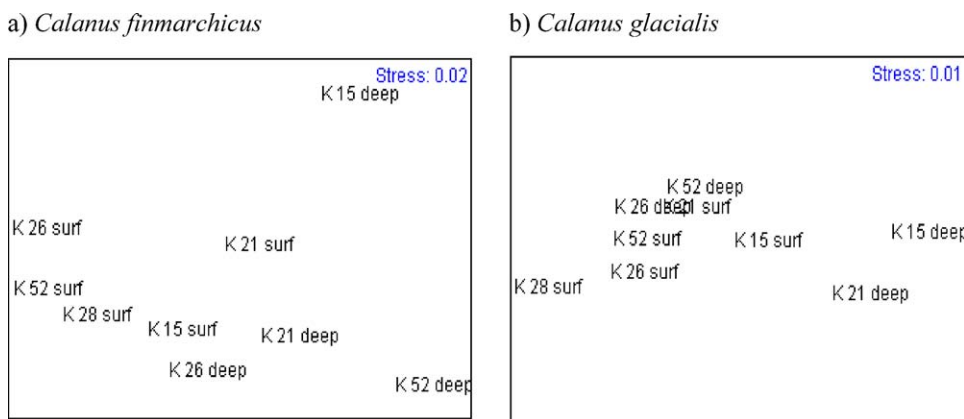


Fig. 6. Multidimensional scaling of samples of transect AA' from the shelf towards the inner basin of Kongsfjorden. Surf are samples from the upper 100 m while deep are samples from the layer below.

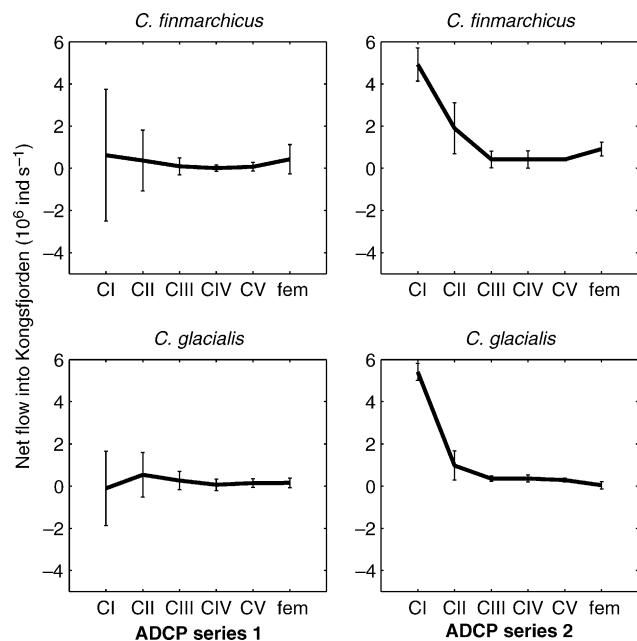


Fig. 7. Flux of all copepodite stages of *Calanus* spp. into Kongsfjorden. Left a net water outflow situation (ADCP series 1), right a net water inflow situation (ADCP series 2). Error bars specify the 95% confidence interval.

(at 50 m) or drifted slowly inwards (at 94 m) (Fig. 8, left). In the very south, however, the simulations showed an outwards drift at 94 m after approximately 12 h. With simulations based on data from ADCP series 2, when no eddy was present, the situation changed and zooplankton tended to be advected out of the fjord (Fig. 8, right) even though the net water flow into the fjord increased during this series (Table 4). Residence time in the fjord in the upper layers was dependent on the starting point of the simulations; it was longest starting at the southernmost station K 17 (18 h at 18 m, 12 h at 50 m). Particles starting at the northern stations K 19 and K 20 drifted out of the fjord immediately. Simulated drift at 94 m was slow and directed outwards. Shifting of the flow regime every 6 h to simulate tidal influence on advection resulted in a zooplankton drift, which lay between tidal outflow (ADCP series 1) and inflow (ADCP series 2). The zooplankton remained a shorter time in the system than at the tidal inflow but was still 'trapped' in the eddy during tidal outflow (Fig. 9).

4. Discussion

The impact of advection on zooplankton communities in fjords can be assessed by the ratio between cross-sectional area at the fjord mouth and the total fjord volume (A/V , Aksnes et al., 1989). In open fjords with deep sills and hence a large A/V ratio, the advective impact on zooplankton populations is large (Aksnes

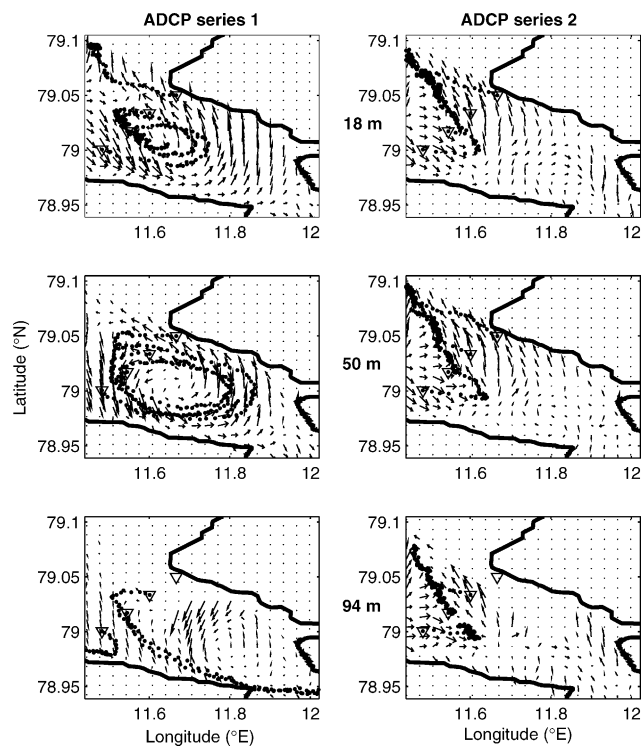


Fig. 8. Simulated zooplankton drift for three depths (18, 50 and 94 m) and the two different flow regimes (left ADCP series 1, right ADCP series 2). ∇ depict stations sampled for zooplankton and/or hydrography. Simulations were stopped after 60 h. Dots denote movement after 1 h, asterisk movement after 12 h. Starting points were for 18 and 50 m at the four zooplankton sampling stations along transect BB' (∇) and for 94 m at the three southern stations along this transect. The northernmost station K 20 is only 65 m deep.

et al., 1989). Kongsfjorden is such an open fjord and compared to Krossfjorden (A/V ratio 10^{-4}) and Malangen (A/V ratio 10^{-5}) in mainland Norway, where the zooplankton community has been shown to be largely influenced by advection (Matthews and Heimdal, 1980; Falkenhaug et al., 1995), Kongsfjorden has a large A/V ratio (7×10^{-2} ; fjord volume from Ito and Kudoh, 1997). Thus an important advective impact can be expected. To our knowledge no data exist on the fjord volume of the inner basin of Kongsfjorden, this basin might however be more isolated from the shelf than the outer basin since a more prominent shallow sill separates it. Thus the impact of advection on populations located in the inner basin might be smaller.

The advective impact on the zooplankton was largely dependent on their position at the fjord entrance. Younger copepodite stages in surface waters were largely influenced by the high current speeds and drifted freely into and out of the fjord. It has to be kept in mind that zooplankton exchange above 14 m was calculated based on current values from 14 m. Due to strong wind during the first part of the study period current speed and thus exchange of copepodites was probably even higher. Older copepodite stages located deeper in the water

Table 5

Abundance (ind m⁻³) of *Calanus finmarchicus* and *Calanus glacialis* along transect BB' at the three zooplankton sampling series (see Table 1 for the sampled depths at the different stations)

Series	1	2	3	1	2	3	1	2	3	1	2	3			
<i>C. finmarchicus</i>	CI, CII, CIII			K 17			K 18			K 19			K 20		
Depth 1	224.71	137.96	133.69	75.85	156.44	369.78	113.78	109.71	174.73	227.56	204.80	420.98			
Depth 2	120.89	170.67	128.00	37.33	17.78	120.89	4.92	18.60	57.98	66.37	88.89	109.40			
Depth 3	15.80	90.07	36.35	3.05	33.19	28.44	14.22	6.64	19.91						
Depth 4	6.52	24.89	6.52				4.06	47.24	10.16						
	CIV, CV, female														
Depth 1	22.76	44.09	44.09	42.67	29.63	71.11	60.95	34.54	73.14	62.58	99.56	85.33			
Depth 2	27.02	25.60	36.98	21.33	3.56	56.89	6.56	7.66	6.56	18.96	39.11	21.88			
Depth 3	20.54	46.62	22.12	17.27	21.33	18.96	3.79	5.21	5.69						
Depth 4	4.44	4.74	5.33				5.59	3.05	9.65						
<i>C. glacialis</i>	CI, CII, CIII														
Depth 1	115.20	79.36	115.20	106.67	59.73	134.40	197.49	60.34	98.74	465.92	225.28	122.88			
Depth 2	233.60	244.48	276.48	310.40	141.60	188.80	79.26	101.42	174.28	209.07	428.80	368.00			
Depth 3	90.31	271.64	174.93	89.60	187.73	129.07	118.61	55.47	126.29						
Depth 4	27.20	82.13	67.20				52.57	0.46	53.49						
	CIV, CV, female														
Depth 1	5.12	19.20	14.08	29.87	3.20	36.27	14.63	16.46	45.71	30.72	35.84	25.60			
Depth 2	10.24	11.52	15.36	9.60	3.20	14.40	7.38	2.95	5.91	0.00	3.20	11.20			
Depth 3	3.56	17.78	7.11	2.74	14.93	8.53	1.71	2.13	5.12						
Depth 4	1.60	4.27	1.07				6.86	2.29	3.20						

column were subject to lower current velocities and could thus maintain their position in the fjord for a longer time. Females, which presumably had ascended to spawn in spring (Conover, 1988), were also subject to a substantial advective influence. *Calanus glacialis* females were mainly restricted to the surface waters at K 20 and K 18, where simulations postulated they were advected out of the fjord within 3 h. Females of *Calanus finmarchicus* were more widespread over depth and were relatively more common in the south. Although these vertical and horizontal position differences were only minor they accounted for the net outflow of *C. glacialis* females even at the net water inflow situation (ADCP series 2) and for the net inflow of *C. finmarchicus* females.

Calanus finmarchicus is probably close to its northern reproduction limit in Kongsfjorden and overwinters here as CIV and CV (Scott et al., 2000). Prior to reproducing, these CIV and CV copepodites need a food uptake to fulfil the energy demand for developing to adult females (Runge and Plourde, 1996; Rey et al., 1999). It is likely that CIV, CV and females in the deep layer in the inner fjord basin had overwintered there. The results may indicate a spring ascent in small (K 26) to moderate (K 28) numbers to the upper 100 m to feed on the phytoplankton bloom, which in Kongsfjorden usually culminates during the end of May in ice-free waters (Eilertsen et al., 1989a). High numbers of *Phaeocystis pouchetti*, which in these waters predominate during the phytoplankton bloom (Eilertsen et al., 1989a, 1989b), were observed at nearly all stations. CV and adult females occurred primarily on the northern side of Kongsfjorden with mainly outflowing water. The

few CV and adult females in the upper 100 m at the shelf probably have their origin in the TAW. If *C. finmarchicus* CII and CIII copepodites were locally produced at prevailing water temperatures (0 °C), the spawning time of the females had to be in early March (Table 6). Since a feeding period is likely to be needed before spawning and *C. finmarchicus* predominately spawns in late April in the Polar front region (Melle and Skjoldal, 1998; Niehoff et al., 2002) this is unlikely and the cause of presence of organisms must be sought elsewhere. Copepodite stages CI, CII and CIII occurred primarily in the south, where inward flowing water prevailed. It is likely that these copepodites were produced in the warmer (2–3 °C) TAW at the shelf where they could develop more rapidly (Table 6) and were advected into Kongsfjorden. In May 2001 *C. finmarchicus* was the most abundant copepod at the shelf (Daase, pers. comm.). The source of CI copepodites could, however, be twofold: partly locally produced (early spawning of some ascended females in beginning of April) and mainly advected into the fjord (spawning time end of April) (Table 6).

Calanus glacialis is a true Arctic shelf species and is usually absent from Atlantic waters (Jaschnov, 1970; Tande et al., 1985; Hirche and Kwasniewski, 1997; Kosobokova, 1999). In Kongsfjorden *C. glacialis* is likely to have a two-year life cycle with CIV and CV as the first and the second year overwintering stage (Scott et al., 2000; Kwasniewski et al., 2003). The high abundance of all stages in the inner basin compared to the low abundance at the shelf mirrors the presence of local WCW and TAW, respectively. *Calanus glacialis* was found in deeper waters than *Calanus finmarchicus* in

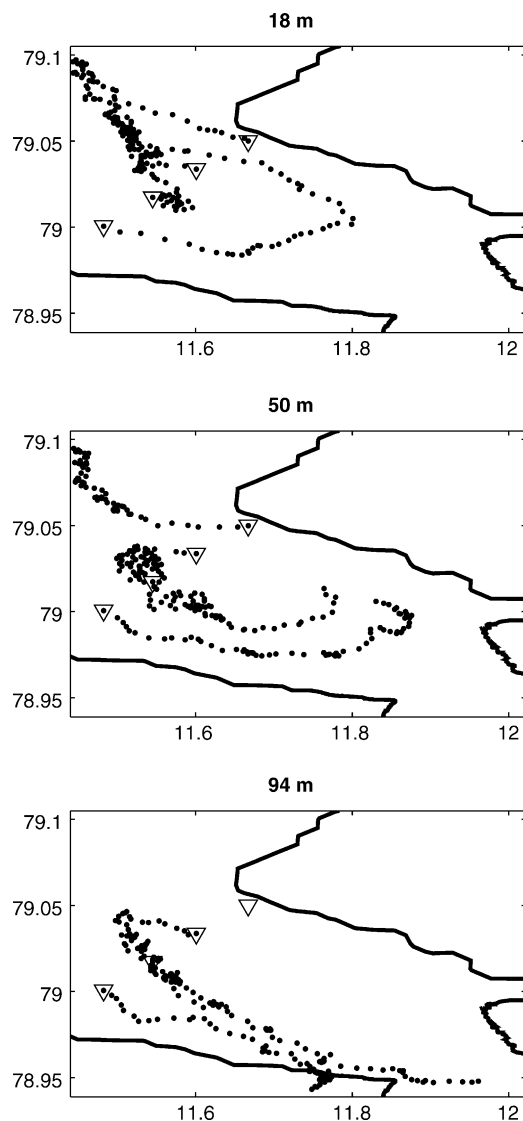


Fig. 9. Simulated zooplankton drift with every 6 h altering flow regime. Simulations lasted for 60 h. Starting points were the same as in Fig. 8.

Kongsfjorden, which might be understood as a preference for colder temperature (Kosobokova, 1999), as well as lower current velocity (Hirche and Kwasniewski, 1997). Unstad and Tande (1991) also found *C. glacialis* in deeper waters than *C. finmarchicus* in the Polar Front

Table 6

Hatching time (days) from egg to CI, CII and CIII, respectively (Campbell et al., 2001), and the appropriate backcalculated spawning time of females at different temperatures

Temperature (°C)	0	2	3
CI	51	36	31
CII	63	45	38
CIII	78	55	47
Spawning time	Beginning of March—beginning of April	Beginning—mid of April	Mid—end of April

region of the Barents Sea. *Calanus glacialis* spawns before and during the phytoplankton bloom (Smith, 1990; Hirche and Kwasniewski, 1997; Kosobokova, 1999; Falk-Petersen et al., 1999; Niehoff et al., 2002). From there it is possible that CI, CII as well as CIII have developed inside the fjord. During the present study virtually all CV and females had already ascended and stayed in the surface layer, which indicates an early spawning, and all stages were most abundant at the north of the fjord where outflow prevails. This makes local production of the young stages very likely. A considerable proportion of CI, CIV, CV and adult females were however observed in surface and subsurface layer in the south as well. This indicates advection into the fjord and since Kongsfjorden is an open fjord it is unlikely that the *C. glacialis* community in the fjord is completely isolated from the shelf and it can be conjectured that the *C. glacialis* community in Kongsfjorden also may be fed from two main sources: partly advected in from the outside shelf and partly locally produced. The latter presumably contributing relatively more to the *C. glacialis* community than to the *C. finmarchicus* community.

Smaller estimates of advective loss than gain of *Calanus* spp. indicate that the eddy, observed at the net water outflow situation, kept zooplankton inside the fjord. The simulated tidal shift in flow regime showed that residence time of organisms inside Kongsfjorden increased even if the eddy was not persisting continuously but altered with another circulation pattern. It is not unlikely that the observed eddy is the main circulation system in the mouth area of Kongsfjorden and Krossfjorden (Svendsen et al., 2002). From model runs, Ingvaldsen et al. (2001) also report eddies to form in this area after a period of strong wind forcing. Eddies in the mouth area could thus act as an efficient retention mechanism for zooplankton in Kongsfjorden.

Wind generated internal Kelvin waves can propagate into wide (compared to the internal Rossby radius) open fjords like Kongsfjorden (Ingvaldsen et al., 2001) and bring large amounts of shelf waters rapidly into the fjord (Svendsen, 1995). Offspring of spawning copepod females at the shelf, mainly *Calanus finmarchicus* (Daase, pers. comm.), could be brought into Kongsfjorden with this shelf water (TAW) and under a flow regime like the observed eddy, circulate several times inside the fjord during which time further development would occur. If a similar flow regime as the eddy persisting during summer is presumed, during circulation in the eddy the advected young copepodites from the shelf would develop to older copepodite stages. In the case of *C. finmarchicus* older copepodites descend as early as in early summer (Scott et al., 2000; Madsen et al., 2001). They thereby would reach a zone of lower water velocity, which would increase retention time for these lipid-rich copepodites in the fjord system.

For the ecosystem in Kongsfjorden this advective gain of *Calanus* spp. is of major importance. The additional supply of *Calanus* spp., mainly *C. finmarchicus*, could support large populations of the higher trophic levels, like polar cod (*Boreogadus saida*) and little auks (*Alle alle*). On the other hand it represents a high grazing pressure on the prolonged phytoplankton bloom in Kongsfjorden (Eilertsen et al., 1989a).

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