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The distribution of juvenile benthic invertebrates in an arctic glacial fjord

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Abstract The distribution of juvenile benthic invertebrates with respect to their abiotic environment was investigated at four locations along a gradient in Kongsfjorden (79°N, 12°E), Spitsbergen, in September 1997. Heavy discharge of inorganic sediments released by the three glaciers was expected to be one of the main structuring factors of benthic communities in the fjord. Juveniles of 76 species/families are identified. Total abundance increases with distance from the fjord head due to the dominance of opportunistic polychaetes, while diversity is highest close to the glacier. Juvenile polychaetes are the most abundant taxon over all stations (92%), followed by bivalves, crustaceans and others. Polychaetes also provide most species (55%) and are the dominant taxon at every station. Their abundance is highly correlated with total organic carbon, indicating that most of them are deposit feeders. Young crustaceans rapidly decrease towards the fjord mouth, probably due to stronger bottom currents. Even though young oligochaetes are exclusively found near the glacier, no species seem to be well adapted to the high sedimentation rate close to the glacier. Juvenile suspension-feeding bivalves seem to be less disturbed by glacial discharge but appear to be more vulnerable to currents on the more exposed sites. The importance of deposit feeders and carnivores increases towards the outer stations. Non-metric multidimensional scaling confirms the distinct gradient in community composition along the fjord. Coupling the biotic data to abiotic factors (depth,

bottom-water salinity, bottom-water temperature, sediment grain size and sedimentation rate) using canonical correspondence analysis revealed that hydrographic factors are more responsible for the structuring of the benthic juvenile community at the shallow stations close to the glacier (except the station directly at the glacier). At the outer deeper stations, sediment grain size and related properties may play a more important role.

Introduction

Until now, very little has been known about the structuring effects of larval and postlarval processes on arctic macrobenthic communities. The supply of larvae and the distribution and survival of their juveniles regulate, besides abiotic factors and predation, benthic communities. These factors have often been ignored in macrobenthos studies. Arctic faunistic inventories primarily cover only megabenthic communities (Ellis 1959; Zenkevitch 1963; Dayton et al. 1994; Piepenburg et al. 1996), and diversity patterns and species distributions along physical stress gradients are usually explained simply by the presence of the adults (Włodarska et al. 1996; Kendall et al. 1997; Holte and Gulliksen 1998).

To what extent environmental factors influence the distribution and mortality of juveniles, and how far post-larval processes in soft-bottom communities are responsible for shaping the distribution of adult infauna is largely unknown (Butman 1987; Olafson et al. 1994). Mortality rates are assumed to be particularly high during the first period of juvenile life, and may exceed 30% the first day. Survivorship decreases exponentially during the first period of juvenile life, reducing all cohorts to <20% within 4 months. Thereafter mortality remains low (Gosselin and Qian 1997). It is suggested that the geographical distribution of a species often coincides with the range of larval and juvenile tolerance (Day and McEdward 1984; Burkovsky et al. 1997).

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Arctic fjords are influenced by seasonal fluctuations in light, ice cover, freshwater inflow, surface salinities and temperatures. Many fjords also have glacial discharge of water, ice and sediments (e.g. Syvitski et al. 1987). Such conditions may influence the diversity and structure of benthic communities by causing stress gradients and successional phases of community impoverishment (Gulliksen et al. 1985; Syvitski et al. 1987; Holte et al. 1996).

Görlich et al. (1987) reported that the benthos of Hornsund Fjord (Svalbard) was reduced in species richness and abundance towards the glacier front, and suggested that this phenomenon was caused by the high clastic input from the glacier. Włodarska-Kowalczyk et al. (1998) made similar observations in several fjords of East and West Spitsbergen. Włodarska et al. (1996) suggested that benthic communities influenced by strong glacial effects are less diverse compared to those in less impacted areas. Heavy sedimentation of inorganic particles dilutes the carbon available from the “organic snow” of sedimenting planktonic detritus (Görlich et al. 1987; Syvitski et al. 1987). High sedimentation rates of inorganic material may cause problems for suspension feeders and the resulting soft and unstable sediments may also create difficulties for tube-building organisms (Moore 1979). Fewer species will survive under such conditions, and opportunistic short-lived organisms

should gain an advantage (Pearson and Rosenberg 1978).

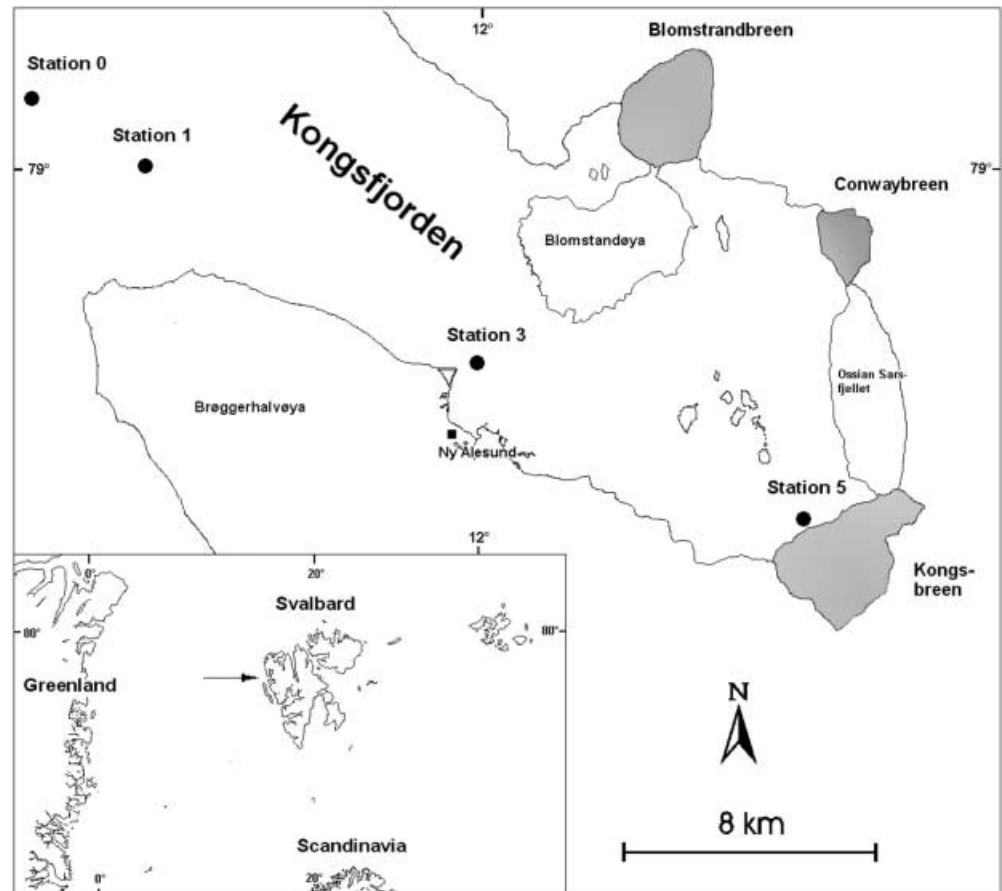
High sedimentation rates are therefore believed to be one of the major structuring factors acting on organisms within an arctic fjord. Since juveniles seem to be more sensitive to environmental factors than adults (Burkovksy et al. 1997), heavy sedimentation may drastically increase their mortality with subsequent effects on the distribution and structure of adult populations.

The aim of this study is to relate the influence of environmental factors acting along a gradient in the Kongsfjord to the structure of the juvenile fraction of the benthic community, and to contribute to the understanding of ecological processes within glacier-influenced arctic fjord systems.

Study area

The 20-km-long and 4- to 10-km-wide Kongsfjord (Svalbard) covers an area of 209 km² (Fig. 1). The maximum depth in the main outer basin is close to 350 m, while the inner fjord is 75 m deep (Ito and Kudoh 1997). There is well-marked inner fjord with a sill of about 30 m, and a 75-m-deep basin. The three glaciers (Blomsterstrandbreen, Conwaybreen, Kongsbreen), which debouch into the fjord head, have retreated

Fig. 1 Location of benthic sampling stations in the Kongsfjord in 1997



several kilometres during the recent 10–15 years and opened up extensive new areas for colonisation by benthic organisms (Lefauconnier et al. 1994; Włodarska-Kowalszuk et al. 1998).

The fjord is highly influenced by Atlantic water throughout the year. During the sampling period, the bottom temperature was 1.5°C and salinity 34.8 in the middle and outer part. In the inner basin, the near-bottom salinity was around 34.1 and the temperature around 0.3°C, which agrees well with earlier observations (Loeng 1991; Włodarska-Kowalczyk et al. 1998). There is a semidiurnal tide with a range of approximately 2 m, with tidal currents of about 0.5 m/min (Svendsen 1994; Nordlund 1995).

Glacial melt-water is estimated to transport $2 \cdot 10^6$ tons year⁻¹ of mud, sand and gravel into the fjord. The main bulk is deposited close (<0.5 km) to the glacier front (Elverhøi et al. 1980). The sedimentation rate seems to decrease exponentially along the fjord (Syvitski and Murray 1981; Gilbert 1982; Farrow et al. 1983). Ice-rafted material is released during melting, and large “drop-stones” can be found at considerable distances from the glacier front. Sedimentation rates have been estimated to be 10–15 cm year⁻¹ in the inner basin (Elverhøi et al. 1983) and 2.5 mm year⁻¹ in the deep outer basin (Skei 1994).

Materials and methods

Sampling in the Kongsfjord (Table 1) took place in September 1997 from the RV “Jan Mayen” during a cruise organised by the University Courses on Svalbard (UNIS). The four sampling stations (Fig. 1) were selected and numbered in accordance with the BIODAFF (Biodiversity and Fluxes in Glacial Arctic Fjords) Program (Weslawski 1996).

Temperature and salinity measurements were conducted in the near-bottom layer using a CTD (Neil Brown Mark III). Sediment and benthic fauna were collected with either a Midicorer (Mark II-400, Bowers & Connely, Scotland) (stations 1, 3) or a van-Veen

grab (stations 0, 5). The Midicorer delivers 4 cores (100 mm diameter, 400 mm long including 200 mm supernatant water) in each cast. The van-Veen grab was used at locations where the sediment was too fine and fluffy to activate the release mechanism of the Midicorer (station 5) or where lack of ship-time prevented the use of the corer (station 0). Sediment cores from the van-Veen grab were obtained by pressing a plastic tube (67.5 mm diameter, 200 mm long) into the sediment.

The colour and layering of the sediment, visible through the transparent plastic tubes, were recorded. The supernatant water from each core was sieved through a 125- μ m sieve, the core forced out of the tube and the upper 10 cm cut off and stored in plastic containers. Comparable studies showed that no juveniles were expected in the deeper levels (Burkovsky et al. 1997). The residue from the 125 μ m was added to the sample and preserved in 4% (borax-buffered) formaldehyde.

The samples were separated into three fractions over a cascade of 500/250/125- μ m sieves submerged in water. Each fraction was analysed separately. Sorting and identification were done under a stereomicroscope (Leica MS 5, magnification 160–400 \times). The total fractions were searched for animals. The animals were identified to the lowest taxonomic level possible and stored in 60% alcohol. The decanting method was used to reduce the amount of sediment from the 125- μ m fractions. Both fractions (decanted and bottom) were retained for further investigation. Before sorting the decanted fraction, ten petri dishes of the bottom part were examined. If more than ten animals were found, both parts were completely searched.

Whether an animal was juvenile or adult was often judged by direct comparison of small and large specimens of the same species. Distinct size groups could easily be distinguished for bivalves, polychaetes, oligochaetes and crustaceans. The smallest group was presumed to be juvenile. Since all bivalve species reach a size of up to only a few centimetres, individuals less than 1 mm were regarded as juveniles (C.P. Günther, personal communication). Newly settled animals (i.e. polychaetes) often still possessed characteristics of their planktonic origin but already had adult features, which made them easy to determine as juveniles, but difficult to identify. The number of segments was counted on larger polychaetes, and/or the body size was measured and compared to literature data (i.e. Hartmann-Schröder 1996). The same was done with many of the crustaceans, oligochaetes and others that were grouped in the category “Varia”. Species were classified into suspension feeders, deposit feeders or carnivores (Syvitski et al. 1987; Włodarska et al. 1996).

Sediment fractions were categorised as clay (<2 μ m), silt (2–63 μ m), sand (63–2,000 μ m) or pebbles (>2,000 μ m). The content of fine-grained material (<63 μ m) was determined gravimetrically after wet sieving of the sample. The particle size distribution was determined on a sedigraph following chemical dispersal and ultrasonic disintegration of aggregates. The coarser fractions were estimated after dry sieving the residue.

Sediment samples for measurement of total organic carbon (TOC) and total nitrogen (TN) (one sample/station) were pre-treated with HCL to remove inorganic carbon, followed by combustion at 1800°C, and column chromatography. The N₂ and CO₂ gases were quantified using a warm wire detector. The lower detection limit of nitrogen and organic carbon in the CHN element analyser was 1 ppt on a dry weight basis.

Data from the three fractions were combined and normalised (m⁻²). The number of individuals per station is given as the arithmetic mean m⁻². Faunal diversity was calculated using species richness (*S*) (Warwick and Clarke 1995), the Shannon-Wiener index (*H'*, log₁₀) (Shannon and Weaver 1963) and Pielou's Evenness (equitability) index (*J*) (Peet 1974). Non-metric multidimensional scaling (MDS) was used to explore the resemblance pattern among the sites (Clarke 1993). The analysis was based on the Bray-Curtis similarity coefficient calculated from the double square-root transformed faunal data. Canonical correspondence analysis (CCA) (Ter Braak 1986) was used to relate community composition information to ten selected environmental parameters (i.e. distance to the glacier front, TOC, TN, the amount of clay, silt, sand, pebbles in percent within the sediments, depth, salinity and

Table 1 Station number, date, position and physical parameters determined in the Kongsfjord, Svalbard 1997

Station no.	0	1	3	5
Date	02 Sep.	01 Sep.	02 Sep.	31 Aug.
Latitude	79°02'	79°01'	78°56'	78°54'
Longitude	11°08'	11°23'	11°57'	12°27'
Distance from the glacier (km)	31.1	25.2	11.8	0.3
Depth (m)	301	283	285	77
Bottom temp. (°C)	1.7	1.1	1.3	0.3
Bottom salinity (psu)	34.8	34.8	34.8	34.1
No. of samples	8	7	8	10
Area sampled (cm ²)	286	550	628	443
TOC (%)	1.6	1.8	0.7	0.2
TN (%)	0.3	0.3	0.1	0.1
C/N	6.2	6.0	5.8	3.8
Clay (%)	25.6	42.6	48.0	50.0
Silt (%)	64.5	53.7	45.6	44.5
Sand (%)	9.8	3.7	6.2	3.9
Pebbles (%)	0.2	0.0	0.1	1.6

temperature close to the bottom). The PRIMER package (Warwick and Clarke 1995) was used for the calculation of MDS, Shannon-Wiener and Evenness indices, and the CANOCO package (Ter Braak 1992) for the CCA analysis.

Results

Environmental setting

The near-bottom salinity at the three outer stations were close to Atlantic water conditions and somewhat less saline at the station close to the fjord head. The bottom-water temperature decreased from outside the fjord (1.7°C) to close to the glacier (0.3°C) (Table 1).

The surface sediment (1–3 cm) consisted of very fine and light material. Deeper down it became more consolidated. An upper light-brown to ochre oxic layer and a deeper black anoxic layer were clearly visible in all sediment cores, except at station 5 close to the glacier front where the sediment consisted only of the ochre part. The transition between the upper and the lower layer was not clear-cut, but rather a smooth change from light to dark. In the middle part of the transect, the light layer was 10–20 cm thick, whilst at the outer station the darker anoxic layer appeared 0.1–2 cm below the surface.

Silt and clay fractions dominated the sediment in the fjord. The sand fractions increased from the inner to the outer parts. Significant proportions of pebbles were found only at station 5 (Table 1).

The amount of TOC and TN in the sediment increased with distance down the fjord head, with a small decrease at the station located outside the mouth (Table 1).

Faunal composition

A total of 76 taxa were identified, with polychaetes (42), bivalves (12) and crustaceans (11) being the most abundant taxa. In terms of specimens, 92% of all juveniles identified were polychaetes. The remaining 8% were bivalves (3%), crustaceans (2%), oligochaetes (1%), and *Priapulida*, *Echiurida*, *Sipunculoida*, *Phoronoida* and *Cnidaria* (2%). No juveniles of the phylum *Echinodermata* were recorded.

Abundances

The mean abundance increased from the head (5,924 ind. m⁻²) to the mouth (31,522 ind. m⁻²) of the fjord (Fig. 2a). At the outermost station, the abundance decreased slightly (21,238 ind. m⁻²). The mean abundance of polychaetes exceeded that of the other groups by 10–30 times (Fig. 2c). Because the polychaetes were the most abundant group at all stations, their density distribution followed the same pattern as the mean total

abundance. While the densities of “Varia” decreased gradually towards the mouth of the fjord (Fig. 2b), there was a sharp drop in the abundance of the oligochaetes between stations 5 and 3. No oligochaetes were found at the outer station. Crustaceans and bivalves had their highest abundance at stations 3 and 1. Less than 100 ind. m⁻² of the crustaceans were found close to the glacier. Their numbers rose to about 800 ind. m⁻² at station 3 and dropped to 0 ind. m⁻² at station 0. Bivalves were found in relatively high numbers at the two innermost stations. The highest densities of 900 ind. m⁻² were found at station 1. There was a sharp drop to about 70 ind. m⁻² at the outermost station.

Species diversity

The highest mean number of species (*S*) was found at station 3 (55 species) and station 1 (51 species) and the lowest number at the outermost station 0 (23 species) (Fig. 3a). The glacier-influenced station 5 had only a moderate value (30 species), but the highest variability. The mean values of the Shannon diversity (*H'*) decreased only slightly with distance from the glacier head (Fig. 3b) and showed no clear difference between the stations. The evenness showed no significant change along the transect (Fig. 3b).

Deposit feeders are most common at all sampling sites and their relative amount increased from 57% at the inner station to 78% towards the outer (Fig. 4). The proportion of suspension feeders decreased from 39% at the innermost station to 13% at the station outside the fjord. The number of carnivores was a little higher at the outer than at the inner stations.

Twelve of the 67 identified taxa were found on all 4 stations, while 30 taxa were found at one station only. Eighteen taxa were among the most abundant species (further referred to as “top-ten” list) present on all stations. Eleven of the top-ten species were polychaetes. Five taxa, all polychaetes, were common top-ten species on all stations (Table 2). These were *Cossura longocirrata*, which accounted for 37% (27,809 ind. m⁻²), *Nereis* sp. (8.3%), *Scoloplos* sp. (8.0%), *Levensenia* sp. (7.7%) and *Euchone papillosa* (7.0%). These five species represented 68.7% of all specimens found. While the relative abundance of *C. longocirrata* was very low at station 5 (9.4%), it became dominant at station 0 (52%). *Nereis* sp. was most important at the innermost station (24.5%), but its relative abundance decreased to 2% at the outermost station. *Scoloplos* sp. increased in numbers towards the entrance of the fjord. *E. papillosa* was most abundant at the two middle stations, with 5.1% (station 3) and 11.6% (station 1). *Levensenia* sp. was present at all stations, with relative abundance between 4.7% and 9.2%. The relative abundance of the other juveniles decreased from 54.7% at station 5 to 18.9% at station 0.

Two bivalve species were represented on the top-ten list. *Macoma calcarea* was only found at the innermost

station, while *Yoldiella* sp. occurred most frequently at the middle stations. Two species of Crustacea were also among the top-ten species. The amphipod, *Onisimus* sp., was found in the inner part of the fjord and the tanaid, *Thyphlotanais pulcher*, was only found on the two middle stations.

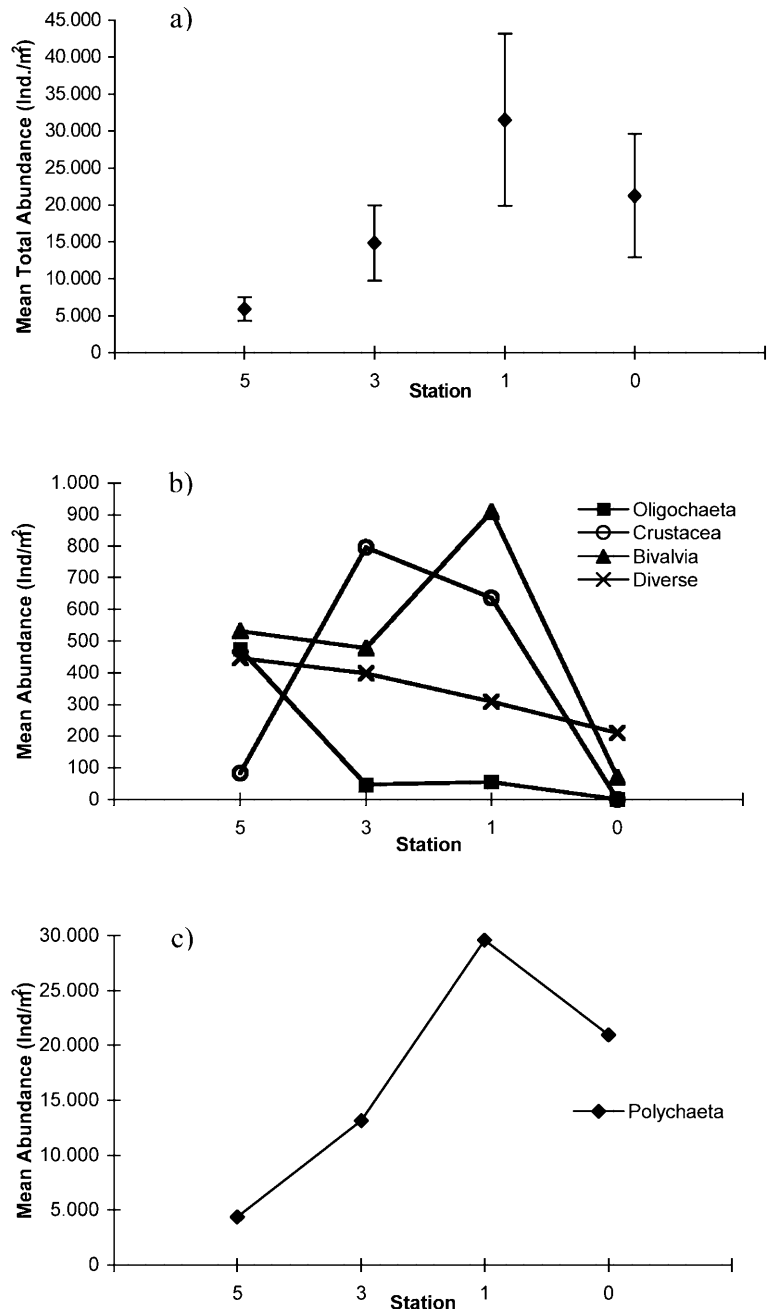
The MDS analysis of single samples shows a clear gradient from station 5 to station 0 (Fig. 5).

The correlation matrix of the CCA shows that the first species axis is highly negatively correlated with distance, depth, bottom temperature and bottom salinity and positively correlated with the amount of pebbles (Table 3). The second species axis shows a high correlation to TN and silt. The environmental vectors, bot-

tom temperature, bottom salinity and pebbles are highly correlated to depth. The environmental factors of distance, TOC, TN, clay, silt and sand are highly associated to each other. The position of these last vectors fell about equidistant between the first and second axis (Fig. 6).

A comparison of the length of the vectors in the plot reveals that all variables that were included, except sand, have about the same influence on structuring the juvenile fauna within the fjord. The vector of sand is relative short, which implies that it has only a weak influence. The order of the ten variables, in terms of decreasing influence, is depth, bottom salinity, distance, TN, pebbles, silt, TOC, bottom temperature, clay and sand.

Fig. 2 Juvenile (a) mean total abundance, b mean abundance of the groups Oligochaeta, Crustacea, Bivalvia, "Varia" and c Polychaeta found along the fjordic transect in the Kongsfjord in 1997



The sampling sites are distributed in the CCA ordination plot in accordance with the environmental situation expressed by the position of the vectors (Fig. 6). The relative influence of each vector on a station becomes apparent by drawing a perpendicular line from it to the vector. At stations 5 and 3, for example, clay seems to have a great importance, while it has only little influence at station 0. The first axis has strong negative

correlations with depth (-0.98), distance from the glacier face (-0.88), bottom temperature (-0.84) and salinity (-0.95) and has a strong positive correlation with pebbles (0.91). It, therefore, represents a gradient from station 0 at the fjord entrance to station 5 near the glacier face. Axis 2 has relatively weak negative correlations with total nitrogen (-0.68) and silt (-0.66) and a weak positive correlation with clay (0.59). All other

Fig. 3 **a** Mean number of species; **b** Shannon-Wiener and Evenness Indices (with standard deviation) of the four investigated stations for the juvenile fauna of the Kongsfjord in 1997

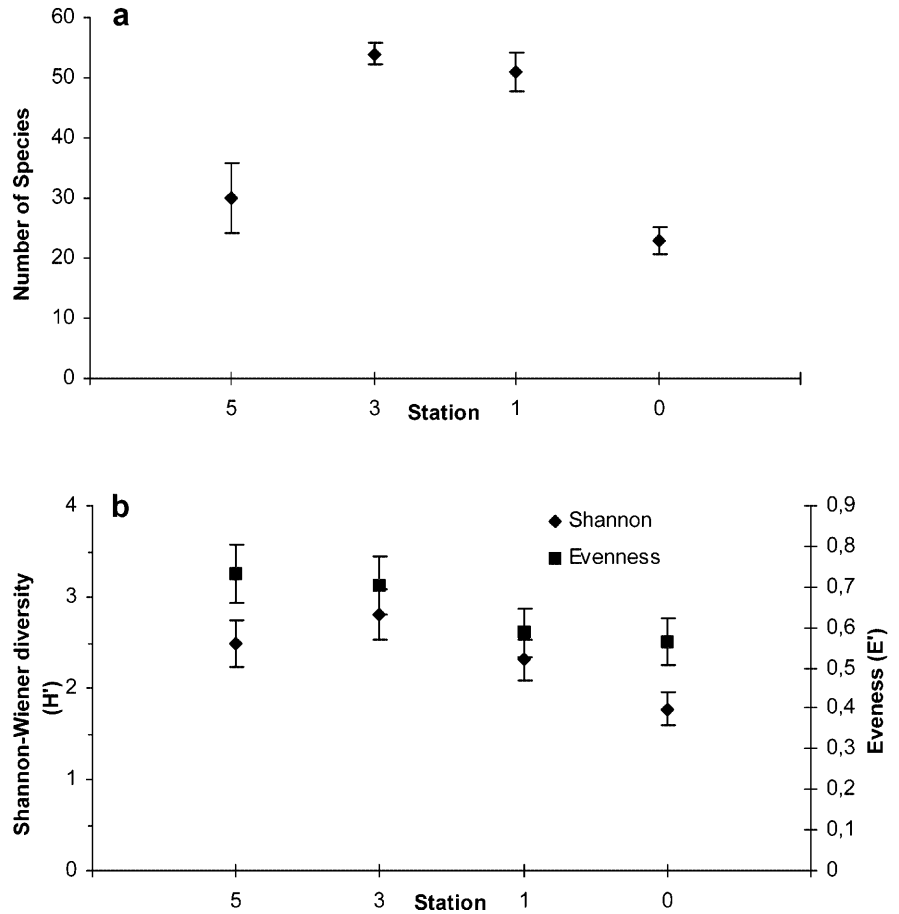
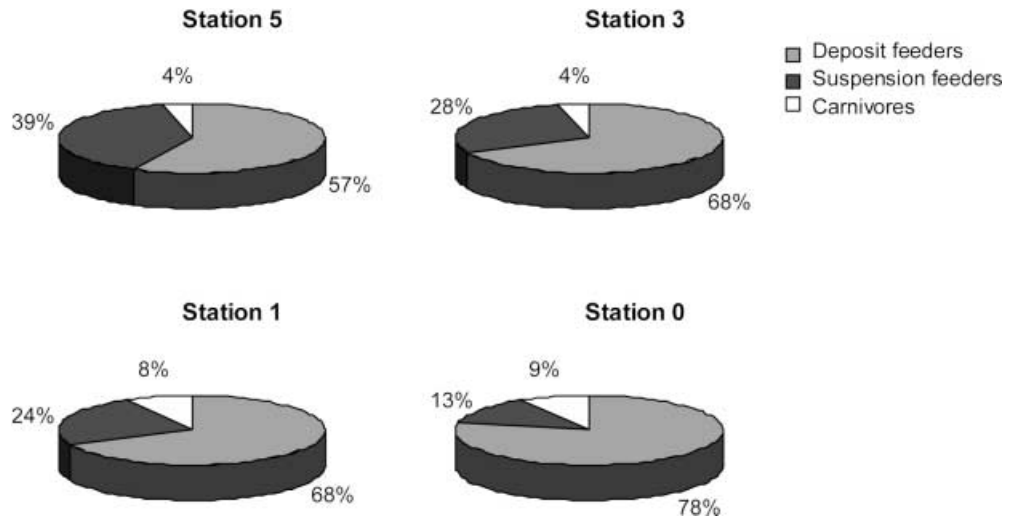


Fig. 4 The relative abundance of juvenile deposit feeders, suspension feeders and carnivores of all species at the sampling sites in the Kongsfjord in 1997



variables have low correlations with this axis. Thus it represents a sedimentary gradient of decreasing silt and increasing clay as distance from the glacier face increases. The species with high scores on axis 1, i.e. those tolerant of the lower temperatures and salinities at the shallower inner fjord stations, are the oligochaete species, the amphipod *Onisimus* sp., the bivalve *Mya* sp., Spionid larvae and the echiurid, *Hamingia arctica*. The species with negative scores on this axis, and thus associated with the deeper outer areas influenced by more oceanic conditions, include the bivalve *Nuculana* sp., the priapulid *Halycryptus* sp. and the polychaetes *C. longocirrata*, *Eteone* sp., *Scoloplos* sp., *E. papilosa* and *Maldane sarsi*. Species with high positive scores on axis 2 include two species of tanaids and opheliid, capitellid and sphaerodorid polychaetes. These are particularly

associated with stations 1 and 3 in the central area of the fjord, which suggests that this axis defines a gradient between the inner and outer fjord conditions and those of the central fjord. Thus, both stations 0 at the entrance and 5 near the glacier face have negative scores on this axis. Axes 1 and 2 account in total for more than 83% of the species variability.

Discussion

The gear

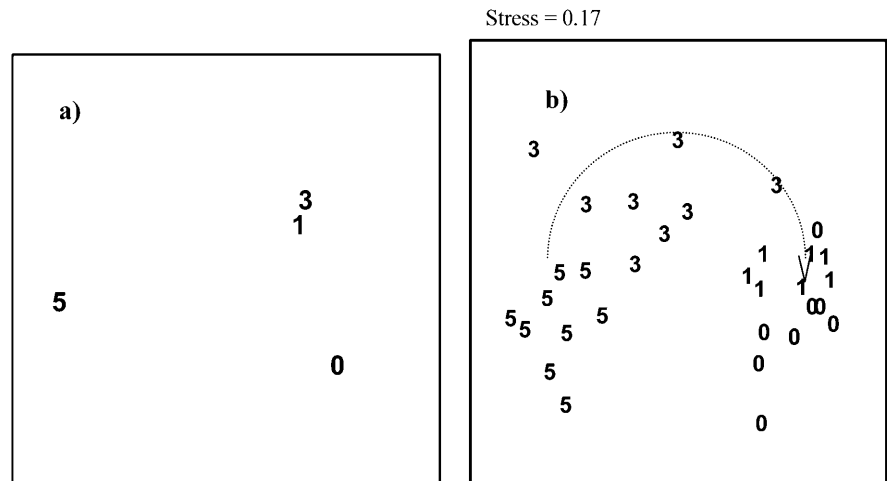
One of the biggest drawbacks in this study was the use of different sampling gear for the sampling. One might argue that sampling by Midicorer is much more effective

Table 2 Number of individuals per square metre and assumed feeding strategies (*D* deposit feeder, *S* suspension feeder, *C* carnivore) for the ten most frequent taxa at each sampling station. The taxa are sorted relative to their abundance (>1%) on each station

from the mouth to the head of the fjord (*left to right* in the table). The “top-ten” selected abundances are shown in **bold numbers** and **bold names** indicate “top-ten” species common to all four stations

Group	Taxon	Type	Station			
			0	1	3	5
Polychaeta	<i>Cossura longacirrata</i>	D	11,073	12,787	3,390	559
Polychaeta	<i>Nereis</i> sp.	D	419	2,092	2,117	1,453
Polychaeta	<i>Levensenia</i> sp.(<i>gracilis</i>)	D	1,956	2,528	700	447
Polychaeta	<i>Chaetozone setosa</i>	D	838	1,655	525	1,286
Polychaeta	<i>Scoloplos</i> sp.	D	3,144	1,364	1,226	140
Polychaeta	<i>Euchone papilosa</i>	S	629	3,656	764	84
Polychaeta	<i>Spio filicornis</i>	D	943	1,601	1,448	28
Varia	<i>Planula</i> spp.	S	70	109	287	419
Polychaeta	<i>Lumbrinereis</i> sp.	C	524	1,037	987	0
Bivalvia	<i>Yoldiella</i> sp.	D	0	473	223	84
Polychaeta	<i>Parougia</i> sp.	D	279	1,037	366	0
Polychaeta	<i>Nerillidae</i> sp.	S	245	109	143	28
Crustacea	<i>Thyphlotanais pulcher</i>	D	0	73	398	0
Polychaeta	<i>Eulalia hansonii</i>	D	0	73	0	168
Crustacea	<i>Onisimus</i> sp.	D	0	0	48	84
Oligochaeta	Oligo II	D	0	55	0	391
Polychaeta	<i>Ophelina</i> sp.	D	419	18	0	0
Bivalvia	<i>Macoma calcarea</i>	D	0	0	0	112
	Total		20,540	28,666	12,621	5,281
	No. of species		12	16	14	14

Fig. 5 MDS plot for **a** mean abundance, **b** the single samples (the *arrow* showing the fjordic direction) of the juvenile fauna in Kongsfjorden 1997



than a grab, especially since stations where the grab was used are characterised by low species numbers. Bearing this in mind, only those grab samples where the supernatant water was still present in the grab were taken. Since the grab had two hatches on top, water exchange during the haul can be excluded. Somerfield and Clarke (1997) compared four typical methods used for sediment collection and their associated meiofauna. They found no differences between the methods when analysing the data by univariate indices. Only the very sensitive MDS revealed minute differences although they were within the intra-sample variability. Since in this study the single samples were compared by MDS (Fig. 5), this should not result in a gradient but rather in a separation of

stations 0 and 5. Also, a one-way ANOSIM test (999 permutations, Global $R=0.157$, $\alpha=0.5\%$) shows that between-stations and within-stations similarities are equal. Therefore the hypothesis that all samples can be treated as equal cannot be rejected. However, the influence of the sampling gear on the data cannot be removed and should be borne in mind during the further discussion.

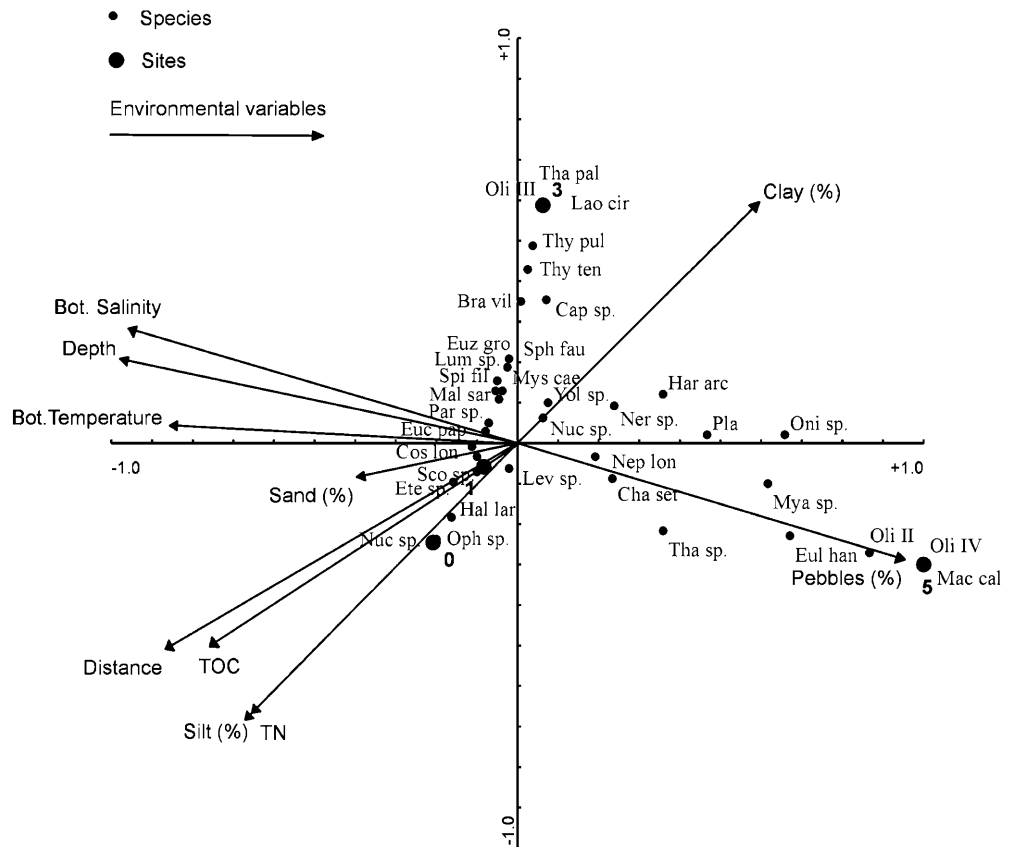
The environment

The near-bottom temperatures measured during this study (1997) correspond well with those of Weslawski

Table 3 Correlation matrix for axes and environmental factors from the CCA run (high correlations with $r \geq \pm 0.80$ are in **bold**)

	Species axis 1	Species axis 2	Species axis 3	Environ. axis 1	Environ. axis 2	Environ. axis 3	Distance	Depth	Bottom temp.	Bottom sal.	TOC	TN	Clay (%)	Silt (%)	Sand (%)
Distance	-0.88	-0.48	-0.01	-0.88	-0.48	-0.01									
Depth	-0.98	0.21	0.02	-0.98	0.21	0.02	0.75								
Bottom temp.	-0.84	0.01	0.55	-0.84	0.01	0.55	0.72	0.83							
Bottom sal.	-0.95	0.28	-0.09	-0.95	0.28	-0.09	0.70	0.99	0.75						
TOC	-0.78	-0.47	-0.42	-0.78	-0.47	-0.42	0.91	0.65	0.42	0.65					
TN	-0.67	-0.68	-0.30	-0.67	-0.68	-0.30	0.92	0.50	0.39	0.47	0.96				
Clay (%)	0.59	0.59	-0.55	0.59	0.59	-0.55	-0.80	-0.46	-0.79	-0.34	-0.50	-0.63			
Silt (%)	-0.66	-0.67	0.36	-0.66	-0.67	0.36	0.89	0.50	0.74	0.40	0.67	0.79	-0.98		
Sand (%)	-0.39	-0.17	0.91	-0.39	-0.17	0.91	0.41	0.36	0.82	0.24	0.00	0.11	-0.83	0.69	
Pebbles (%)	0.91	-0.31	0.29	0.91	-0.31	0.29	-0.65	-0.95	-0.60	-0.98	-0.68	-0.48	0.19	-0.28	-0.04

Fig. 6 CCA plot with species, environmental vectors and sampling sites (note: not all species are included in the plot)



(1996) from 1996, but were slightly higher than those of Gromisz et al. (1996) from 1995. The near-bottom salinity measurements agree well with those found by Weslawski (1996) and Ito and Kudoh (1997) for the same period of the year. In general, there is a slight tendency for lower salinities in the shallower parts. Although the inner station lies quite close to the glacier, no detectable reduction in salinity due to melting was observed. Single measurements give only a momentary picture of the situation in the fjord. The correlation of such data with the biotic data should, therefore, be treated with care. In addition, the rapidity of changes constrains the presence of a species. It is known that marine species are able to survive in less saline water (e.g. Baltic Sea, estuaries) or vice versa when only minor and/or long-term changes occur (Schmidt-Nielsen 1994).

Scouring is not likely to influence the benthos at the selected stations since they are located deeper than the depth (≈ 40 m) at which icebergs can have an effect in this fjord (Dowdeswell and Forsberg 1992).

Tidal mixing of water masses in the inner, shallower parts can be excluded in the Kongsfjord. Ito and Kudoh (1997) concluded that the tidal currents are weak and exceeded by wind-driven water movements.

In the deeper outer areas, tidal currents might be an effective mixing agent (Syvitski 1989; Ito and Kudoh 1997). Annual mixing of water layers and storm events may also have effects on the salinity in these areas of the fjord.

During the melting season, station 5 is highly impacted by sedimentation. Keck and Tatur (unpublished work) found sedimentation rates in 1994 of $107.5 \text{ g m}^{-2} \text{ day}^{-1}$ at a depth of 150 m in the inner part, which decreased rapidly to $12.2 \text{ g m}^{-2} \text{ day}^{-1}$ at a depth of 328 m towards the outer parts. The sampling sites of Keck and Tatur do not coincide with those in this study. Their results can thus be considered only qualitatively. Sedimentation is expected to increase exponentially with decreasing distance from the glacier. The sedimentation rate close to station 5 is therefore considered to be high compared to the other stations. Little is known about sedimentation rates in winter, but they are probably greatly reduced compared to the summer situation (Syvitski et al. 1987; Syvitski 1989; Ito and Kudoh 1997). Sedimentation rates may also differ greatly between years.

The highest fractions of both coarse and fine particles were found close to the glacier (Table 1). The deposition of larger and heavier particles is self-explanatory. The retention of fine particles in this area needs further explanation: Two effects may account for the observed pattern. The gradual sedimentation of particles that have been transported away from the glacier front in the outgoing surface layer may be enhanced due to flocculation processes when entering the more saline and deeper water (Syvitski et al. 1987; Syvitski 1989). Here the finer material may be captured by the in-flowing compensation current and transported back to the gla-

cial front, where it accumulates. The outgoing current transports slightly coarser material, which is not subjected to such flocculation processes. Further out in the fjord, deposited particles may be re-suspended and transported away by coastal currents (Syvitski et al. 1987). In general, the distance a particle is carried out of the fjord depends on the surface plume velocity and particle-removal processes (Syvitski 1989). Sediment transport by tidal and/or coastal currents may explain the higher amounts of sand and pebbles at the outer station.

Görlich et al. (1987) found an average of less than 2% TOC for Hornsund Fjord, which is comparable to our findings in the Kongsfjord ($\sim 1\%$ TOC). The accumulation of organic carbon is probably a result of sedimentation from phytoplankton blooms within the fjord. Many fjords are very productive areas, sustaining primary production from early spring to late autumn (Apollonio 1973; Syvitski et al. 1987). In-situ biomass production within the sediments may also contribute significantly to the organic input (Syvitski et al. 1987). Another source might be macrozooplankton that gets entrapped by the estuarine circulation, caused by the freshwater discharge of the glaciers, and that die due to osmotic shock, as described by Weslawski and Legezynska (1998) and Weslawski et al. (2000) for Kongsfjord. The small amount of organic carbon in the sediments at the innermost station may be a dilution effect caused by the heavy sedimentation of inorganic matter (Hoskin and Burrell 1972; Farrow et al. 1983; Elverhøi 1984; Syvitski et al. 1987). However, Zajaczkowski and Legezynska (2001) found that all dead plankton sinking to the bottom is instantly taken up by the highly mobile amphipod, *Onisimus caricus*, which is found near the glacier in very high densities. Low carbon in the sediment may constrain the presence of deposit feeders at this station, for whom organic carbon is an important food source (Piepenburg et al. 1996). The higher amount of TOC found within the sediments at the outer stations agrees well with the observation that the redox front lies almost directly below the surface, which points to anoxic conditions caused by the bacterial breakdown of organic carbon.

Biological data

The juvenile species found correspond well with the adult macrofauna within the fjord (Wlodarska-Kowalczyk et al. 1998). The number of species was reduced both towards the head and mouth of the fjord. In two other West Spitsbergen fjords (van Mijen and Raudfjord), there is a reduction in species richness towards the inner parts only (Gulliksen et al. 1985; Wlodarska-Kowalczyk et al. 1998). Gulliksen et al. (1985) found the highest number of species outside the fjord and therefore concluded that low water exchange caused by the sill and heavy sedimentation in the inner parts have the

greatest effect on the species composition. The lack of a sill at the entrance of the Kongsfjord may account for this difference.

The mean abundance is directly influenced by the high abundance of polychaetes at all stations. This extreme dominance may be the result of several factors. Many polychaete species are referred to as "opportunists" with a cosmopolitan distribution (Wlodarska et al. 1996; Wlodarska-Kowalczyk et al. 1998). One of the characteristics of opportunists is to produce many offspring at a time to quickly exploit new territories (Begon et al. 1996). A high proportion of the Kongsfjord juvenile species are opportunists (55%). The same pattern is reported for the adult macrofauna in other arctic fjords (Görlich et al. 1987; Wlodarska-Kowalczyk et al. 1998). *Cossura longocirrata* (38%) and *Nereis* sp. (31%) contributed to more than two-thirds of the total abundance in their study. *C. longocirrata* and *Chaetozone setosa* are among the most common adult species in the Kongsfjord (Wlodarska-Kowalczyk et al. 1998). In this study, juvenile *C. setosa* were only found in moderate numbers, and nothing is known about the presence of adults of *Nereis* sp. in the fjord. Piepenburg et al. (1996) found *Nereis zonata* in the other fjordic parts around Svalbard.

The low number of bivalve species may partly be due to their small size, which makes them too small to be identified properly. However, a lot of bivalve larvae were still present in the water column and had not yet settled (I. Fetzer, personal observation). The number of juvenile bivalves decreased strongly towards the outer station where currents and turbulence may cause early juvenile mortality (Gosselin and Qian 1997).

Currents and turbulence may also be responsible for the decline in juvenile crustaceans in the outer parts of the fjord. The crustacean species found belonged to the epifauna, which are vulnerable to near-bottom currents. Their low presence close to the glacier might be due to the high levels of fine material, which can lead to malfunction and clogging of the gills. It is also reported that moulting is difficult in high-sedimentation areas. These species may become entangled in their old carapaces (Moore 1979). The only juvenile crustacean found close to the glacier was the rather large and highly mobile amphipod, *Onisimus* sp.

Oligochaetes were mainly found in the vicinity of the glacier. Three of the four species identified were found at station 5 only.

No juvenile echinoderms were detected, although brittle stars are reported to be one of the common groups of megabenthic communities around Svalbard (Zenkevitch 1963; Gulliksen et al. 1985). Piepenburg et al. (1996) reported that brittle stars were the most important group in terms of constancy and relative abundance in their study. Juvenile echinoderms may not tolerate the highly variable salinities found in glacier-influenced fjords (Schmidt-Nielsen 1994). The presence of adult ophiuroids may indicate that they enter the inner parts of the fjord via migration only.

Multivariate analysis of the data

The gradual change in species composition and abundance along the fjordic gradient is reflected and summarised in the MDS plot (Fig. 5). Samples taken at one site are plotted in distinct groups, indicating that they are more similar to each other than to samples from other sites. As averages, sites 3 and 1 are quite similar in species composition while stations 0 and 5 differ markedly. This specific distribution pattern probably reflects the pattern of environmental factors the juveniles are confronted with at the single stations. Both the outer and the inner station are probably more impacted by major disturbance forces (Table 4).

The CCA plot (Fig. 6) indicates that, apart from sand, the abiotic variables included in this study are of similar importance. Temperature, salinity, depth and distance show a strong negative correlation with axis 1, indicating a hydrographic gradient of decreasing temperature, salinity and depth from the outer to the inner parts of the fjord. Pebbles show a strong positive correlation with this axis, indicating that the deposition of the larger sedimentary fractions increases with decreasing distance from the glacier face. The sedimentation rate decreases with distance and depth (A. Keck and A. Tatur, unpublished work) and it is thought that the sedimentation rate and grain size composition are strongly correlated (Syvitski et al. 1987; Syvitski 1989). The annual sedimentation rate and environmental regime (e.g. stratification of water and currents) will therefore control the grain size composition at any given site.

The sampling sites (5, 3, 1, 0) are distributed along, but at varying distance from, axis 1, which represents the fjordic gradient. Station 5 is at the one extreme of the first axis, reflecting the low salinities and temperatures in the shallower inner fjord, compared to the central and outer areas. The CCA results showed that a few taxa, e.g. *Onisimus* sp. and oligochaetes II and IV, had high positive values on axis 1 and were associated with the variable temperatures and salinities of the inner basin. *Nuculana* sp. and *Halycryptus* sp. are associated with the siltier sediments at the outer station. Those with high

Table 4 Assumed environmental situation present at the sample sites (++ very high; + high; o medium; - little; - very little)

Station	5	3	1	0
Sedimentation	++ ^a	+	o	-
Depth	-	+	+	+
Grain size	-	o	o	o
TOC	-	o	++	+
TN	-	o	+	+
Salinity	- ^a	o	o	o ^b
Sal. variation	+ ^a	-	-	o
Temperature	- ^a	o	o	o ^b
Temp. variation	+ ^a	-	-	o

^aSeasonal variations

^bInfluenced by open sea

positive values on axis 2 are associated with the high clay levels of the central stations. The majority of the taxa, including those with the highest densities (e.g. *Cossura longocirrata*, *Scoloplos* sp. and *Levensenia* sp.), are clustered closely around the centre of the plot. This suggests that the majority of the juveniles were not strongly influenced by either the sedimentary or the hydrographic gradients in the fjord.

Effects of sedimentation

It is not possible to distinguish between the effects of accumulation of fine sediments (unstable bottom) and sedimentation rates (burrowing and dilution of TOC) on the survival and distribution of benthic juveniles. But it can be assumed, especially for sessile species less than a millimetre in size, that a sedimentation rate of a few millimetres per day will increase its energy expenses drastically. The energy costs of constantly removing sediment from the tubes may lower their survival rate, especially in the food-impooverished inner parts of the fjord.

Those larvae that are released at the end of the year or during winter may be able to settle and grow to a size at which burrowing is no longer a problem, when sedimentation increases during the summer months. This kind of reproduction is reported for several bivalve and polychaete species (e.g. Hartmann-Schröder 1996). Species with larvae that do not depend on primary production (e.g. with lecithotroph, pelagic larvae) may gain an advantage because they can release their larvae in winter (at times of low sedimentation).

Melt-water discharge from the nearby glaciers strongly influences both temperature and salinity near the bottom (Ito and Kudoh 1997). Thermal and saline tolerance are in general lower in juveniles than in adults, although field observations showed that they are within larval tolerance (Day and McEdward 1984). It is not clear, however, whether the thermal tolerance limits of early juveniles are exceeded, especially in polar regions (Gosselin and Qian 1997).

Tube-building animals like *Pectenaria* sp., whose tubes consist of sand grains of a special size, have to cope with the lack of suitable building material when only fine material is present. Although Burkovsky et al. (1997) found that juveniles were not significantly correlated with the granulometric composition of the sediments, although young individuals of *Maldane sarsi*, which live in tubes buried in the sediment, rather suffer from the instability of the sediment (Moore 1979). This might be a reason why no juveniles of this species are found at the inner station.

Indirect effects of sedimentation

The redox front in the sediment gets closer the surface as one moves out of the fjord. Görlich et al. (1987) made

similar observations in Hornsund Fjord. Anaerobic bacterial breakdown of the organic matter in the sediments leads to depletion of oxygen in the sediments and may severely restrict the niches available to settling larvae and the survival of juveniles that are obligate aerobes. Only opportunistic species, such as *Chaetozone setosa* or *Cossura longocirrata*, may survive under such conditions (Pearson and Rosenberg 1978). This might be an additional reason for the low mean abundance and the low number of species at station 0.

The TOC level and the mean number of juvenile polychaetes were highly correlated ($r=0.971$) within the fjord. About 71% of the polychaetes, 73% of the crustaceans and all of the oligochaetes were deposit feeders. Five of seven of the taxa in the "Varia" group were considered to be deposit feeders. The dilution of TOC may constrain the distribution and/or survival of deposit feeders close to the glacier. Piepenburg et al. (1996) suggested that sediment properties, in particular the TOC level, have a strong influence in structuring megabenthic adult communities in the Svalbard area. This seems not to be the case for deposit-feeding oligochaetes and species within the "Varia" group. They seem to thrive at the food-impooverished sites close to the glacier.

The turbid waters near the glacier are thought to be disadvantageous for filter feeders, but their numbers, particularly that of bivalves, did not decrease substantially. Farrow et al. (1983) found, in a highly turbid fjord in British Columbia, the greatest numbers of suspension feeders in the upper inlet. The animals were able to select digestible from non-digestible particles, and the researchers observed that suspension feeders (e.g. sabellids and brachiopods) took up grains $<8 \mu\text{m}$, probably utilising the associated bacteria.

Deposit feeders dominated the juvenile communities of all sites. A comparison of the adult benthic fauna in an arctic fjord at Franz Josef Land and a subarctic Spitsbergen fjord indicates that this may be an overall trait of arctic-influenced fjords (Włodarska et al. 1996).

Predation may influence both the presence and the survival rate of juveniles (Thorson 1966; Gosselin and Qian 1997). Here, the predatory meiobenthic organisms may also play an important role (Watzin 1983, 1986). This has not been considered in this study. Juvenile species composition and abundance may also be affected by the shrimp fishing that takes place in the deeper outer parts of the Kongsfjord (Hop 1995). Depending on the intensity and frequency of trawling, this may alter or decrease the diversity of the community (Clarke and Warwick 1994; Begon et al. 1996). Trawling-related disturbances may provide new settling areas for juveniles, or may destroy already established juvenile communities. Species reproducing late in the year may gain an advantage as trawling occurs mostly in the period April to June (Hop 1995).

This study shows that although sedimentation is an important structuring element influencing juvenile communities in this glacial fjord, other associated factors also have strong effects. To gain a more detailed

picture of which factors shape the patterns found, studies of seasonal variability in both the environmental factors and the juvenile and adult benthic populations are necessary.

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