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ORIGINAL PAPER

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Soft-bottom macrobenthic faunal associations and factors affecting species distributions in an Arctic glacial fjord (Kongsfjord, Spitsbergen)

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Abstract The Kongsfjord (west Spitsbergen) hosts the most active glacier on the island. Therefore the glacial impact on the marine ecosystem is very pronounced and easily recognisable. The study examines the influence of the steep glacier-derived environmental gradients on dominant macrofaunal species distributions and faunal associations in the fjord. The macrobenthic fauna was sampled by van Veen grab at 30 stations situated throughout the fjord (at depths 38–380 m). Two major communities were recognised. An inner basin receives the outflows from three glaciers and is occupied by a Glacial Bay Community dominated by small, surface detritus-feeders, with *Chone paucibranchiata* and a set of thyasirid and nuculanid bivalves (*Thyasira dunbari*, *Yoldiella solidula*, *Y. lenticula*) as characteristic species. An outer basin of the fjord is characterised by a common set of dominant species, including *Heteromastus filiformis*, *Maldane sarsi*, *Levinsenia gracilis*, *Lumbrineris* sp. and *Leitoscoloplos* sp. Three associations may be distinguished within the Outer Basin Community. Association TRANS is of transitional character, with *Nuculoma tenuis* and *Terebellides stroemi*. Association CENTR is the most typical for the community. It is dominated by tube-dwelling *Prionospio* sp., *Clymenura polaris*, *Galathowenia oculata* and *Spiochaetopterus typicus*. Association ENTR contains shelf benthos elements, e.g. *Ophiura robusta* and *Lepeta caeca*. An opportunistic eurytopic *Chaetozone* group is present throughout the fjord and its density and dominance increase with proximity to the glaciers. Dominant species distribution is discussed in relation to environmental factors, of which sediment stability, inorganic particle concentration, sedimentation rate and amount of organic matter in sediments are considered to be most important in structuring the communities.

Introduction

A homogenous and temporarily stable environment is found in subtidal basins in many fjords. Such areas have low hydrodynamic energy and are dominated by "biologically accommodated" communities of evenly distributed large, long-lived organisms resistant to changes in community structure (Valderhaug and Gray 1984; Syvitski et al. 1987). However, that system may be greatly stressed, either anthropogenically or naturally. A number of fjordic benthic communities disturbed by pollution or organic enrichment have been described (e.g. Pearson and Rosenberg 1978; Rosenberg et al. 1987; Holte et al. 1996; Wiegers et al. 1998; Blanchard et al. 2002). In the Arctic, tidal glaciers, often situated in the innermost parts of the fjords, strongly affect basin ecosystems. Seasonal or continuous inflows of fresh glacial meltwater, loaded with mineral material, influence the structure and circulation of water masses and turbidity, primary productivity, sedimentation processes and sediment characteristics. The scale and magnitude of the impact depend on the activity of the glacier. Benthic organisms are affected by glacier activity in several ways. These include: high concentration and sedimentation rate of mineral suspensions, poorly consolidated and easily re-suspended sediments, fluctuating salinities, low levels of available organic matter, which is diluted by the sedimentation of inorganic material, and catastrophic events such as ice-berg scouring or sediment slides and slumps (Gorlich et al. 1987; Syvitski et al. 1989; Kendall 1994).

The Kongsfjord (West Spitsbergen) is a high-latitude Arctic fjord, but the waters are influenced by the

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Atlantic water masses of the West Spitsbergen Current (Svendsen et al. 2002). Three tidal glaciers terminate in fjord waters. Kongsbreen, situated in the innermost part of the fjord, is the most active glacier in the Svalbard archipelago (Lefauconnier et al. 1994). The existing data on the physical and biological features of the fjord are summarised in Svendsen et al. (2002) and Hop et al. (2002). The hard-bottom faunas associated with macroalgae and bryozoans of the Kongsfjord are described in Jorgensen and Gulliksen (2001), Lippert et al. (2001) and Kuklinski (2002). Hitherto, studies of the soft-bottom fauna have been restricted to inner bay (Wlodarska-Kowalczuk et al. 1998; Kendall et al. 2003) or to juvenile benthic forms (Fetzer et al. 2002). The aim of the present study is to describe the benthic communities and associations inhabiting the subtidal sediments throughout the entire fjord, discriminate the characteristic and dominant species, and discuss their distribution in relation to environmental factors, especially the steep physical gradients resulting from glacial activity.

Physical settings

The Kongsfjord is situated between 78°52′ and 79°04′N and 11°20′ and 12°35′E. It is divided into two basins by a shallow sill connected with an archipelago of small rocky islands, the Lovenoyanne. Depths in the outer basin reach 428 m (on average 200–300 m), whereas the inner basin is considerably shallower, with a maximum depth of 94 m (on average 50–60 m).

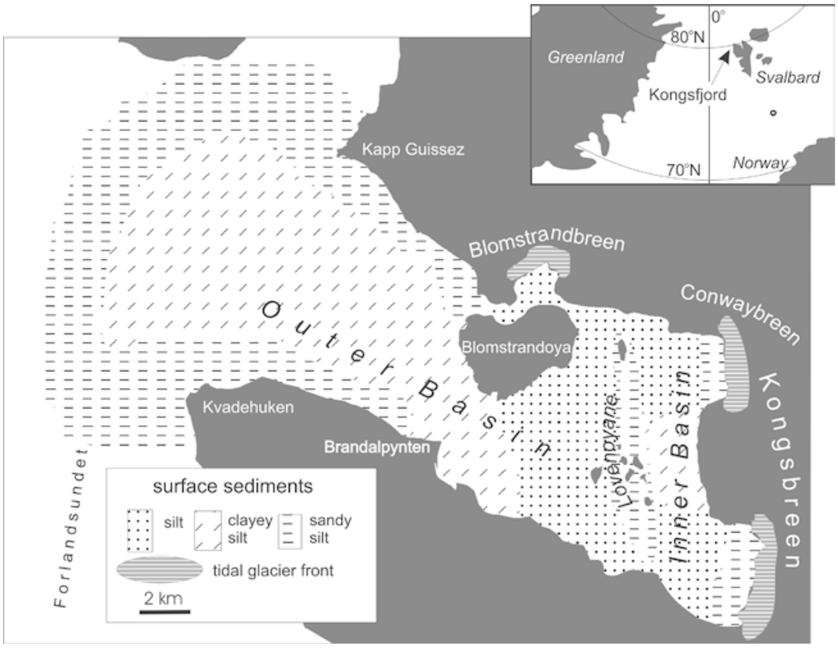
The water masses in the Kongsfjord are described in Svendsen et al. (2002). The deepest water layers throughout the fjord are influenced by Local Fjordic Waters ($T < 1°C$, $S > 34.4$ psu) or Transformed Atlantic Waters ($T > 1°C$, $S > 34.7$ psu). In the deepest depressions of the inner basin, Winter Waters of very low temperature ($T < -0.5°C$, $S > 34.4$ psu) may occur.

Icebergs and growlers are observed all over the fjord the whole year round. The icebergs rarely exceed 20 m in length or 5 m in height (Dowdeswell and Forsberg 1992). A few larger icebergs (up to 10 m high) circulate or stay anchored in the inner basin, where they are retained by the Lovenoyanne shallows.

The input of mineral material into the fjord from the Kongsbreen meltwaters is estimated to be 2.6×10^5 m^3 per season (Elverhøi et al. 1980). The sedimentation rate of mineral material in the surface waters is highest close to the glacier front (over 800 g m^{-2} day^{-1}), and then decreases to 200 g m^{-2} day^{-1} at a distance of 4–5 km from the glacier front, and in the outer parts of the fjord does not exceed 25 g m^{-2} day^{-1} (Zajaczkowski 2000). The sediment accumulation rates follow the gradient of sedimentation rates in the water column. The rate decreases sharply by about 1 order of magnitude from the glacier bay (20,000 g m^{-2} a^{-1}) to the central part of the fiord (1,800–3,800 g m^{-2} a^{-1}) and, again, by another order of magnitude towards the outer fiord (200 g m^{-2} a^{-1}; Svendsen et al. 2002).

Muds dominate the subtidal sediments throughout the fjord (Fig. 1). Sediments of the inner and outer basins are similar in terms of their granulometry. Differences lie in their deposition rates, which are much higher in the inner basin, and bioturbation traces (traces of polychaetes are found only in the outer basin) (Elverhøi et al. 1983). In glacial bays, intensive sedimentation of mineral material results in the formation of unconsolidated, labile sediments (Syvitski et al. 1987). In these conditions, the deposited material is not compacted, water trapped between flocks cannot escape and a layer

Fig. 1 Sediments in Kongsfjord according to Elverhøi et al. (1983) and M. Zajaczkowski (unpublished data). Location of glaciers and other features within the area



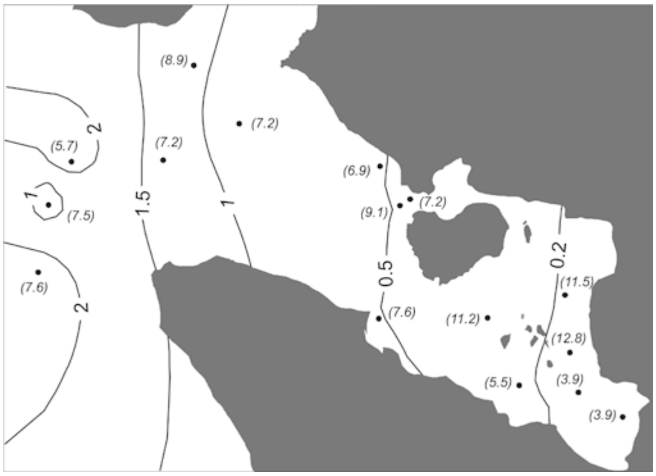


Fig. 2 POC in surface sediments according to M. Zajaczkowski (unpublished data). The *dots* represent the stations sampled for sediments; the values in *parentheses* present values of POC/PON ratio

of very condensed suspension overlying the bottom is formed (Dyer 1989). In addition, the stability of sediments in glacial marine environments is decreased by frequent sediment slides and gravity flows (Dowdeswell 1987).

In the inner basin of the Kongsfjord in summer, primary production is limited by high amounts of mineral suspensions. Keck et al. (1999) observed much lower abundances of phytoplankton in the inner basin compared to the central and outer parts of the Kongsfjord. Similar patterns were observed in the distribution of Particulate Organic Carbon (POC) in surface sediments (Fig. 2), with low values in the inner basin increasing towards the fjord mouth. This gradient results from the impact of mineral suspensions on light penetration in the water column and hence on primary production, and from intensive mineral suspension sedimentation, which "dilutes" organic matter in the sediments (Gorlich et al. 1987). The POC/PON values throughout the fjord mostly varied between 4 and 9 (Fig. 2), which indicates fresh detritus of marine origin.

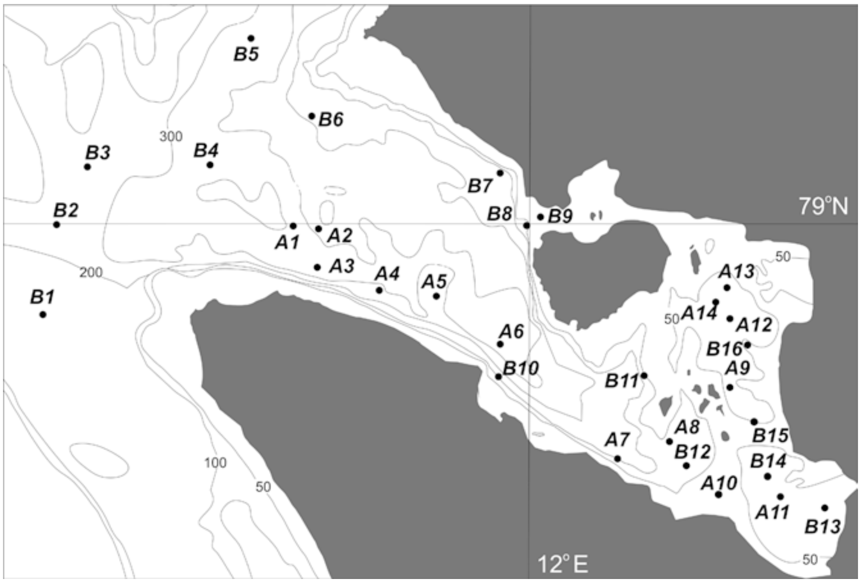
Materials and methods

Material was collected during two cruises of r/v "Oceania" on 17–27 July 1997 and 7–17 July 1998. Samples were collected throughout the fjord at 30 stations (at depths 38–380 m) (Fig. 3). The samples were taken with a van Veen grab with 0.1 m^2 (0.301×0.330 m) catching area. The material was sieved on a 0.5-mm sieve and fixed in buffered 4% formaldehyde. Altogether 80 samples were collected, with 3 replicates per station, except at stations B7 and A5 (2 replicates) and A12, A13, A14 and A6 (1 sample).

Animals were sorted, identified to the lowest possible taxonomic level and counted. Copepoda, the demersal crustaceans *Thysanoessa* and *Themisto*, Decapoda larvae and Foraminifera were not included. The *Chaetozone* group includes polychaetes of the family Cirratulidae (*Chaetozone*, *Cauleriella*, *Tharyx*). The taxonomy of this family is presently under revision (Woodham and Chambers 1994). The majority of specimens appeared to be *Chaetozone setosa* s.l. (at least 70–80%); however, the material was often badly damaged and not all individuals could be identified to genus or species.

Frequency of occurrence (percentage of samples where a species was found in total number of samples) and dominance (percentage of the individuals of a particular species in total number of all animals found in all samples) were calculated for all species. Multivariate analyses have been performed on a data matrix of species abundances in the samples. A number of transformations were applied to the data, including square root, double root, log (1 + x), as well as presence/absence. These provide different views of the community structure—from the very superficial view at no transformation when only a few of the most abundant species are decisive for similarities, up to an analysis with presence/absence data, which takes into account all species regardless of their abundance in a sample (Clarke and Warwick 1994). The similarities between samples were calculated using the Bray-Curtis index. Clustering (using group-average linking) and Multidimensional Scaling (MDS) of double-root transformed data for all samples

Fig. 3 Bathymetry of Kongsfjord and location of sampling stations. Stations named *A1*, *A2*, *A*... were sampled in 1997, stations *B1*, *B2*, *B*... in 1998



were carried out. The resulting dendrogram and MDS-plots were used to distinguish groups of stations with similar species composition. For this analysis, the moderate double-root transformation was used. It downplays the dominants, but retains the basic quantitative information (Clarke and Warwick 1994). MDS was used to view the similarities between samples while using raw data, all transformations of data and presence/absence data. Multivariate analyses were performed with the use of the PRIMER package (Clarke 1993).

There are many concepts and definitions of a community and terms for faunal assemblages of different degrees of integration. In the present study, the approach and definition of Mills (1969) is followed: "community means a group of organisms occurring in a particular environment, presumably interacting with each other and with the environment and separable by means of ecological survey from other groups". We presume that there is some discontinuity in species distribution between the communities. Here the term "association" has been used for groups of samples that can be distinguished within communities.

The frequency of occurrence, dominance, average abundance and indices of community fidelity of each species in each group were calculated. The indices of fidelity included: DAS—degree of association between stations, i.e. the number of stations within the association at which the species concerned occurred as a percentage of the total number of stations at which this species occurred; DAI—degree of association between populations, i.e. the number of individuals of the species concerned within the group as a percentage of the number of individuals of that species found in the whole study area (Salzwedel et al. 1985).

The following criteria were used in assessing the community fidelity of any species: typical species for a group—frequency > 75%, dominance > 2%; characteristic species for a group—typical + DAI or DAS > 66%; eurytopic species—species typical in all groups.

Results

The fauna comprised 30,967 individuals and 213 taxa. Over 90% of the taxa belong to Annelida (111 taxa), followed by Arthropoda (45) and Mollusca (44). Twenty-two taxa had a frequency of occurrence exceeding 50%—six of which occurred with a frequency exceeding 75%, i.e. the polychaetes *Chaetozone* group, *Lumbrineris* sp., *Cossura longocirrata* and *Heteromastus filiformis*, and the bivalve molluscs *Yoldiella lenticula* and *Y. solidula*. Together with two other taxa, *Prionospio* sp. and *Chone paucibranchiata*, they made up over 50% of all individuals. The *Chaetozone* group and *Y. solidula* composed 14.9 and 9.5% of dominance, respectively, of the whole material. In single samples, they accounted for up to 56 and 50% of dominance, respectively.

Two main groups of samples were distinguished both on the dendrogram and the MDS-plot of double-root transformed data (Fig. 4a,b). These were: samples taken in the inner basin, considered as representing the Glacial

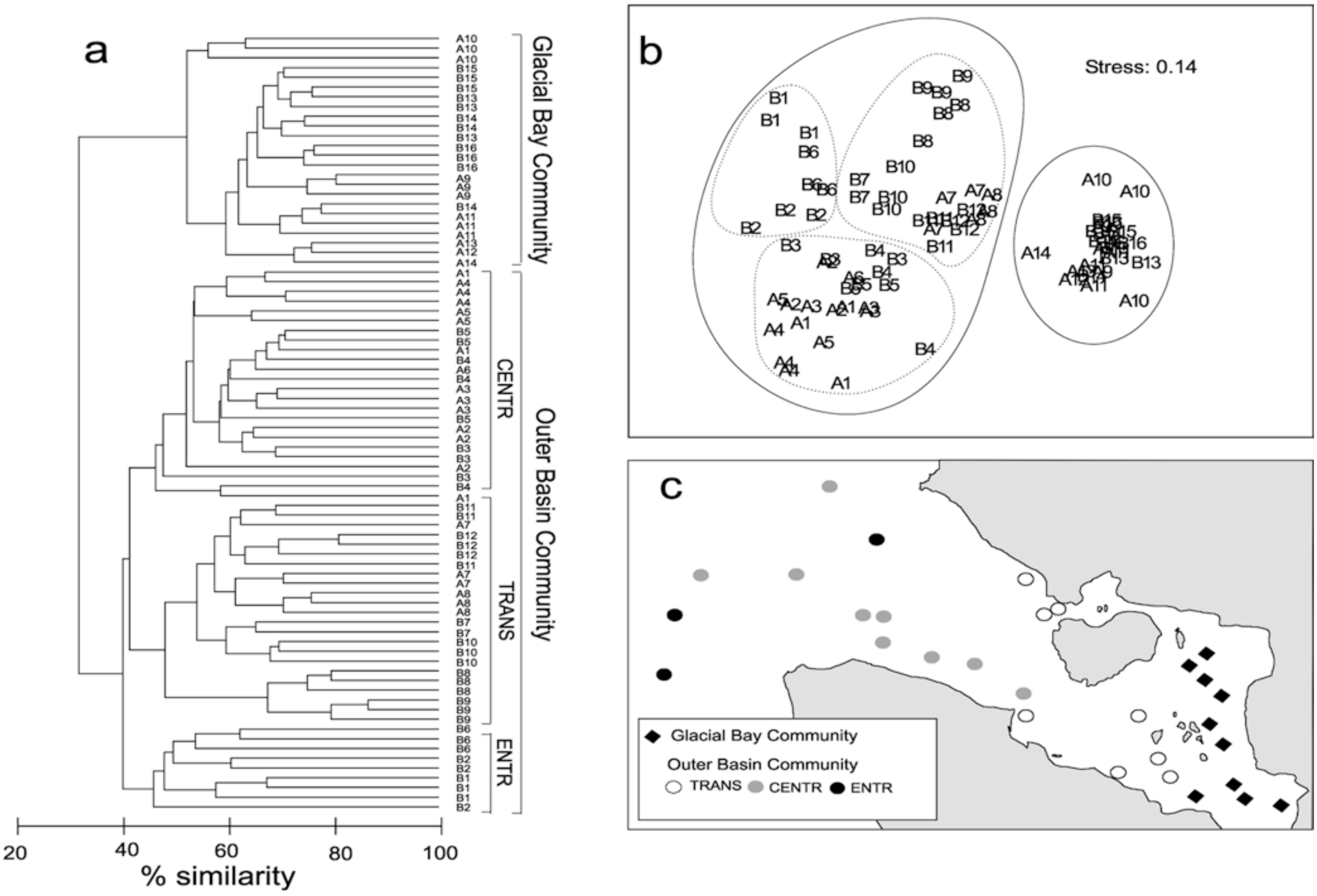


Fig. 4a–c Multivariate analyses for double-root-transformed data of species abundance in samples: **a** dendrogram, **b** MDS plot, **c** map of associations

Bay Community, and samples taken in the central and outer parts of the fjord, designated as the Outer Basin Community. On the dendrogram, this main division is made at quite a low level of similarity, not exceeding 30%. The Glacial Bay Community includes samples taken at stations situated in the inner basin and station A10 situated on the Lovenoyane sill. The Outer Basin Community is divided at similarity levels of between 40 and 43% into three associations: i.e. TRANS—stations situated in the outer basin between Lovenoyane and the Blomstrandoya/Brandalpynten line and stations B8, B9 situated close to Blomstrandoya; CENTR—stations situated in the central part of the fjord; and ENTR—stations situated at the entrance to the fjord (Fig. 4c). In the application of other transformations to the data, the results were very similar—the main division into two groups of samples (Glacial Bay and Outer Basin) was identical (Fig. 5). In all cases, the Outer Basin group could be again divided into three subgroups with only slight differences in their sample composition (Fig. 5).

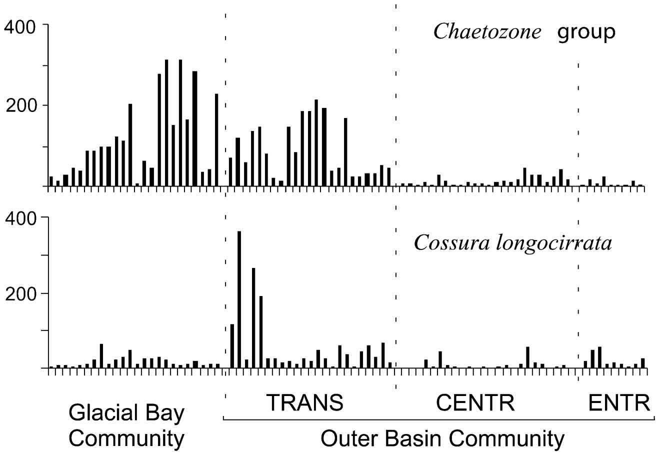


Fig. 6 Distribution of individuals of eurytopic taxa in samples [ind./0.1 m^2]: *Chaetozone* group, *Cossura longocirrata*

Two taxa have been classified as eurytopic: the *Chaetozone* group and *Cossura longocirrata*. They are typical (have high dominance and frequency) in all associations, but their distribution is not uniform. The *Chaetozone* group (Fig. 6) occurs in much higher numbers in samples from Glacial Bay Community and TRANS Association (average—121 and 92 ind./0.1 m^2) than in the CENTR and ENTR Associations (15 and 9

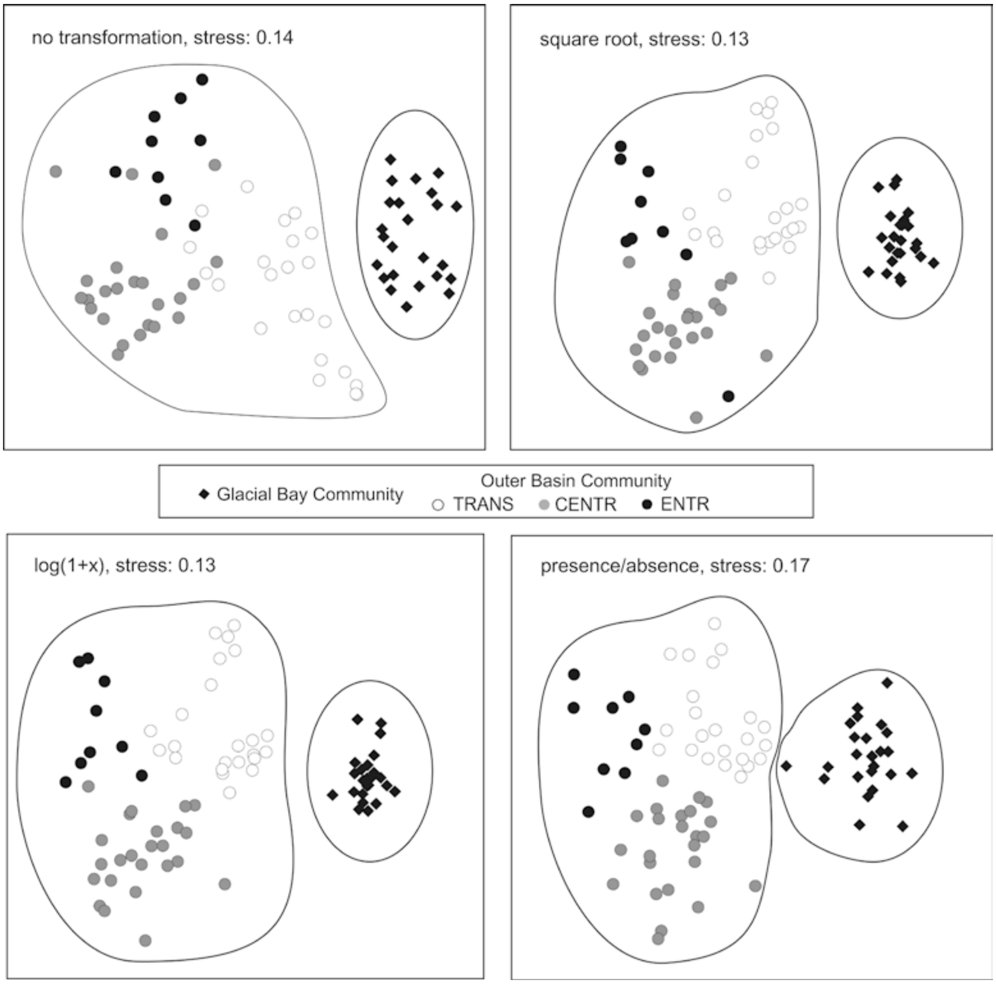


Fig. 5 Multidimensional Scaling (*MDS*) plots for data of species abundance in samples. Plots for raw data, square-root transformed, log(1 + x) transformed, presence/absence data. Symbols represent associations distinguished on Fig. 4

Table 1 Basic quantitative characteristics of species dominating in Glacial Bay Community (*D* dominance, *F* frequency, *AA* average abundance in sample, *DAI* degree of association regarding individuals, *DAS* degree of association regarding stations). Ten species of the highest dominance are presented. Typical species marked with **bold type**, characteristic—**bold and underlined**

	D	*F*	AA	DAI	DAS
***Chaetozone* group**	27.3	100	120.9	53	30
Yoldiella solidula	26.2	100	115.8	80	36
Chone paucibranchiata	13.0	96	57.7	68	42
Yoldiella lenticula	11.2	100	49.6	73	37
Thyasira dunbarii	6.7	96	29.5	84	58
Cossura longocirrata	4.1	100	18.0	19	30
Tanaidacea n. det.	1.8	88	8.0	66	42
Lumbrineris sp.	1.7	100	7.7	6	30
Eudorella emarginata	1.1	88	5.0	52	36
Aglaophamus malmgreni	0.8	75	3.5	96	82

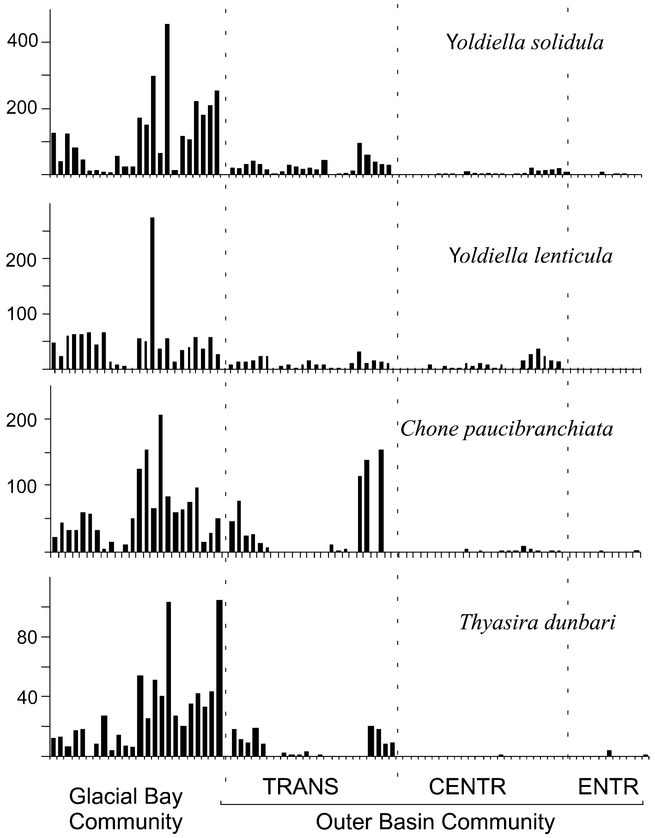


Fig. 7 Distribution of individuals of taxa characteristic for Glacial Bay Community in samples [ind./0.1 m^2]: *Yoldiella solidula*, *Yoldiella lenticula*, *Chone paucibranchiata*, *Thyasira dunbarii*

Table 2 Basic quantitative characteristics of species dominating in Outer Basin Community (*D* dominance, *F* frequency, *AA* average abundance in sample, *DAI* degree of association regarding individuals, *DAS* degree of association regarding stations). Ten species of the highest dominance are presented. Typical species marked with **bold type**, characteristic—**bold and underlined**. DAS was not considered in classification of characteristic species, as number of samples in this group composes 70% of all samples

	D	*F*	AA	DAI	DAS
Prionospio sp.	11.3	57	52.4	100	91
***Lumbrineris* sp.**	10.7	100	49.4	94	70
***Chaetozone* group**	9.9	100	45.8	47	70
Cossura longocirrata	7.3	98	33.9	81	70
***Leitoscoloplos* sp.**	6.8	91	31.7	100	96
Heteromastus filiformis	5.5	98	25.5	99	85
Axinopsida orbiculata	4.2	25	19.5	100	100
Maldane sarsi	3.7	89	17.2	100	98
Levinsenia gracilis	3.4	84	15.7	97	90
Terebellides stroemi	2.7	71	12.4	98	83

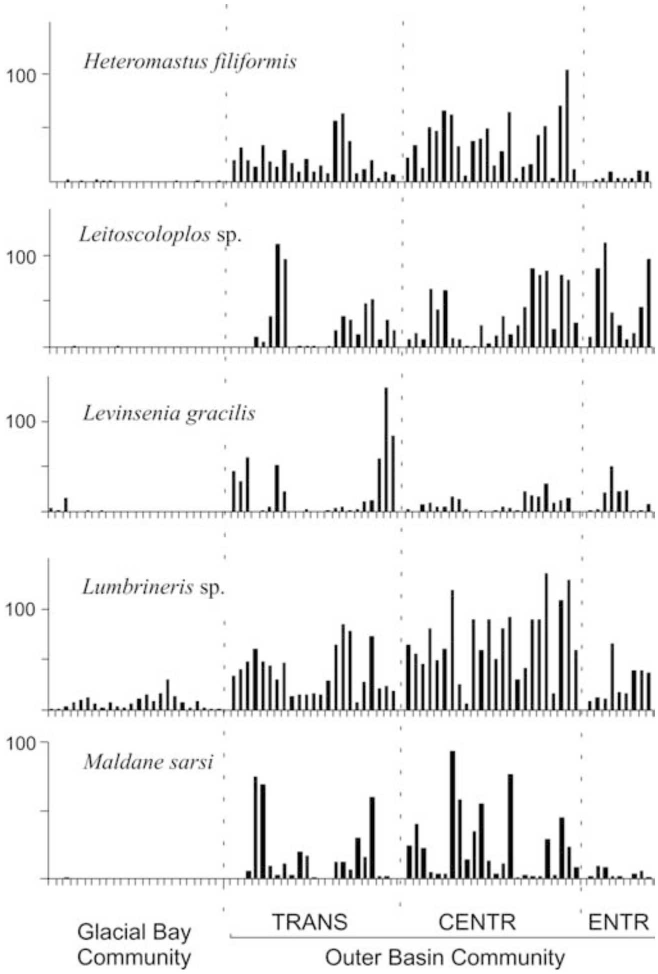


Fig. 8 Distribution of individuals of taxa characteristic for Outer Basin Community in samples [ind./0.1 m^2]: *Heteromastus filiformis*, *Leitoscoloplos* sp., *Levinsenia gracilis*, *Lumbrineris* sp., *Maldane sarsi*

ind./0.1 m^2). Numbers of *Cossura longocirrata* (Fig. 6) are very high in some samples of Association TRANS (65 ind./0.1 m^2 on average), especially on stations A7, and A8. Much lower numbers of *Cossura longocirrata* were noted in Glacial Bay Community and Associations CENTR and ENTR (on average—18, 8, 22 ind./0.1 m^2, respectively).

The Glacial Bay Community fauna is strongly dominated by two taxa, the *Chaetozone* group and *Y. solidula*, which together constitute 53.5% of all animals. *Chone paucibranchiata* and *Y. lenticula* constitute together the next 24% of the community (Table 1). The most numerous taxon, the *Chaetozone* group, is eury-

Table 3 Basic quantitative characteristics of species characteristic for Outer Basin Community Associations TRANS, CENTR, ENTR (*D* dominance, *F* frequency, *AA* average abundance in sample, *DAI* degree of association regarding individuals, *DAS* degree of association regarding stations). The species of dominance exceeding 1% are presented

	D	F	AA	DAI	DAS
TRANS					
Terebellides stroemi	4.6	100	27.1	88	48
Nuculoma tenuis	3.0	100	17.9	81	41
Sipunculida n.det.	2.1	83	12.5	90	68
CENTR					
Prionospio sp.	28.6	100	121.6	99	69
Leiochone polaris	3.2	79	13.7	71	44
Galathowenia oculata	2.0	96	8.6	74	46
Bathyarca glacialis	1.5	75	6.3	98	90
Spiochaetopterus tipicus	1.0	54	4.1	91	72
ENTR					
Ophiura robusta	8.3	78	20.0	100	100
Lepeta caeca	3.0	78	7.1	77	58
Syrrhoe crenulata	1.3	56	3.2	88	56

topic, i.e. a taxon typical in all associations (even if highest density and dominance were observed in Glacial Bay Community), and therefore had a relatively low DAI value (53). Four species were classified as characteristic for this association: *Y. solidula*, *Chone paucibranchiata*, *Y. lenticula* and *Thyasira dunbari*. *Y. solidula* was found also in relatively high numbers and with high frequency in samples of the Association TRANS (Fig. 7). *Chone paucibranchiata* was recorded with high densities in some samples of the TRANS Association—at stations A7, A8, B11 and B12, all situated in an area west of the Lovenoyane archipelago. *Aglaophamus malmgreni* had the highest values of DAI and DAS in the Glacial Bay Community.

Five polychaetes, *H. filiformis*, *Leitoscoloplos* sp., *Levinsenia gracilis*, *Lumbrineris* sp. and *Maldane sarsi* are characteristic species for the Outer Basin Community (Table 2, Fig. 8). High abundance and dominance were observed for *Prionospio* sp.; however, it occurred in only 57% of samples. The other quantitatively important taxon is the eurytopic *Chaetozone* group. For 15 of 19 most numerous species, DAI exceeded 80%, and for 8 of them it was 100%, indicating that they occurred only in this group of samples. All characteristic species, except for *Lumbrineris* sp., were recorded with very high values of DAI and DAS. These occurred almost exclusively in samples of the Outer Basin Community. *Lumbrineris* sp., a species with high values of DAI and DAS in the Outer Basin Community, was also common in the Glacial Bay Community. It occurred there with an average abundance of 7.7 ind./0.1 m^2, a dominance of 1.7 and 100% frequency. *H. filiformis* and *M. sarsi* were much more numerous in associations TRANS and ENTR than in association ENTR of the Outer Basin Community (Fig. 8).

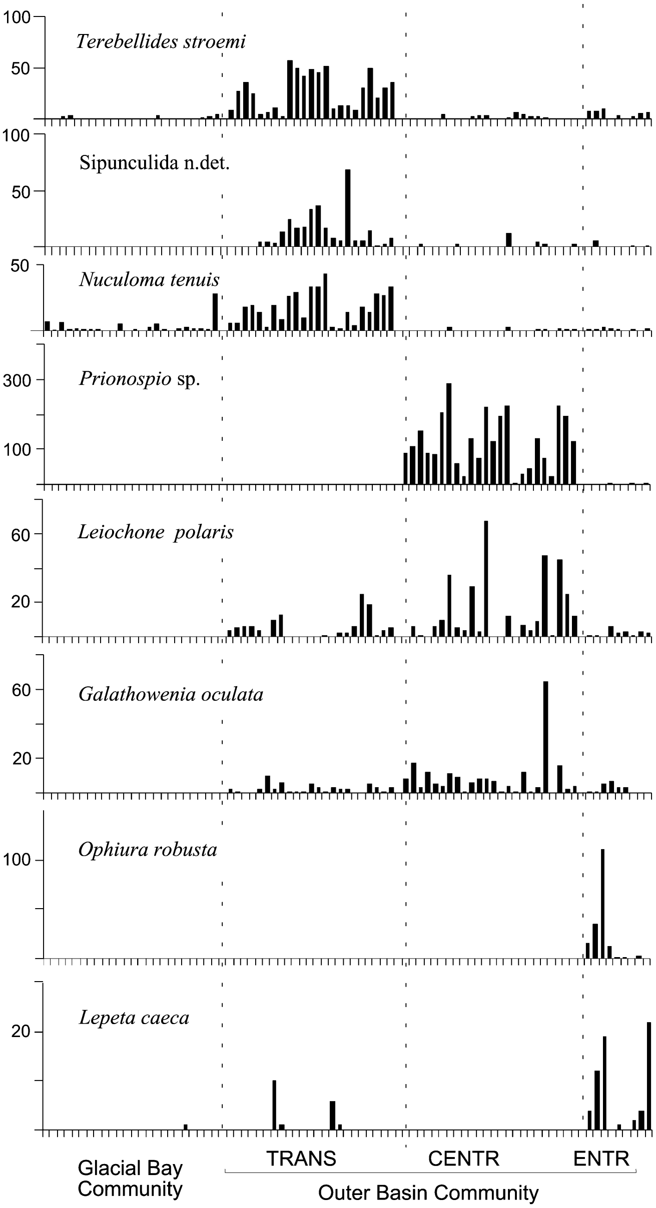


Fig. 9 Distribution of individuals of taxa characteristic for Association TRANS (*Terebellides stroemi*, Sipunculida n.det., *Nuculoma tenuis*), Association CENTR (*Prionospio* sp., *Leiochone polaris*, *Galathowenia oculata*) and Association ENTR (*Ophiura robusta*, *Lepeta caeca*) in samples [ind./0.1 m^2]

In addition to the species characteristic for the whole Outer Basin Community, which are present in each of the three associations within the community, species characteristic for each association can be defined (Table 3). Three taxa are classified as characteristic for Association TRANS: the polychaete *Terebellides stroemi*, the bivalve *Nuculoma tenuis* and Sipunculida n. det. (Table 3, Fig. 9). All three occurred in this association with high fidelity. The small bivalve molluscs *Axinopsida orbiculata*, *Thyasira gouldii* and *Yoldia hyperborea* were noted with high DAI but low frequency. These species were abundant at the only two stations (B8 and B9 situated close to Blomstrandoya) where they occurred.

Prionospio sp. made up almost 30% of Association CENTR fauna. It was noted with very high values of

DAI and DAS (99 and 69, Table 3, Fig. 9). *Leiochone polaris* and *Galathowenia oculata* were also characteristic of this association (Fig. 9), but their fidelity was lower (DAI around 70). Very high values of DAI were noted for the less numerous *Bathyarca glacialis* and *Spiochaetopterus typicus* (Table 3).

Almost all species exceeding 1% dominance in Association ENTR showed very low values of degree of association. The only exceptions were the ophiurid *Ophiura robusta*, (DAI and DAS = 100), the less numerous gastropod *Lepeta caeca* and the amphipod *Syrrhoe crenulata* (Table 3, Fig. 9). The large bivalve *Macoma calcarea* occurred with high abundance but only at station B1.

Discussion

Faunal communities

On MDS plots, the samples taken in the inner basin were always separated regardless of the transformation used. Similarly, the analysis of dominants points to the high specificity of this group—four out of five most numerous species are characteristic (with high DAI values). The clear and unequivocal division both at the level of dominants and at the level of the full species lists, as well as the high fidelity to communities of most dominants, indicate the discrete discontinuity between the fauna in the inner glacial bay and in the outer areas of the fjord. Therefore we termed those groups as communities: Glacial Bay Community and Outer Basin Community.

Three associations distinguished within the outer basin were not treated as representing separate communities. The fidelity of species within the associations was low. The differences between associations lay in differences in dominance of species characteristic for the whole Outer Basin Community and the occurrence of a few species specific for particular associations.

The Glacial Bay Community is dominated by small mobile bivalves—nuculanids and thyasirids, while the Outer Basin Community is dominated by larger, often less mobile, mostly tube-dwelling polychaetes (Table 4). This resembles the pattern described by Syvitski et al. (1989) in Baffin Island fjords. They observed a sequence of communities occurring on soft sediments including a *Portlandia arctica* Association close to active glaciers, and a Maldanid Association in the central and outer parts of fjords. Communities dominated by protobranch and thyasirid bivalves are common in Arctic and sub-Arctic soft-bottom localities impacted by terrigenous inflows. Thorson (1957) described *Yoldia arctica* communities as being characteristic of soft bottoms near river mouths or large glaciers in the high Arctic (Svalbard, East Greenland). *Yoldia hyperborea*-dominated communities were observed in the Anadyr River lagoon (Bering Sea, Filatova and Barsanova 1964), as well as in the Skoddebukta glacial bay (Spitsbergen, Wlodarska

Table 4 Biological features of eurytopic taxa and species dominating in the Outer Basin Community

Species	Biology	Reference
Chaetozone group	Mobile surface detritus-feeders, burrowing just below the sediment surface and feeding by means of two large tentacular palps which may select particles from the surface or below the sediment surface	Pearson et al. (1996)
Cossura longocirrata	Mobile, burrowing, detritus-feeder	Fauchald and Jumars (1979)
Leitoscoloplos sp.	Non-selective mobile detritus-feeder burrowing in the sediment	Fauchald and Jumars (1979)
Maldane sarsi	Large detritivorous polychaete, living in a "head down" position in long (up to 50 cm) tubes built of sediment grains and mucus; typical bioturbator	Fauchald and Jumars (1979); Neira and Hopner (1994)
Heteromastus filiformis	"Head-down" detritivorous polychaete frequently found in disturbed sediments	Fauchald and Jumars (1979)
Terebellides stroemi	Inhabits membranous tubes encrusted with mud and sand, and feeds on detritus collected with the use of tentacles	Fauchald and Jumars (1979)
Prionospio sp.	Lives in a tube built of mud grains and feeds on detritus particles, which are collected with use of ciliated palps	Fauchald and Jumars (1979)
Galathowenia oculata	Builds relatively long tubes, does not have feeding appendages typical for other owenids except for a pair of lips, and Fauchald and Jumars (1979) suggested that it probably lives and feeds in a way similar to maldanids; however it was observed to feed in the head-up position—extending its head from the tube and bending over to sweep the surface of the sediment to collect particles (T.H. Pearson, pers. obs.)	Fauchald and Jumars (1979), T.H. Pearson, pers. obs.
Spiocheatopterus typicus	Long, thin polychaete inhabiting a tough parchment-like tube; has two long extensible palps and may be facultative surface deposit and suspension particle-feeder	Fauchald and Jumars (1979)
Bathyarca glacialis	Filtering suspension-feeding bivalve, usually occurring at depths below 100 m, on coarse sediments or drop-stones	Ockelmann (1958)

et al. 1996). Molluscs of the genus *Portlandia* dominate communities characteristic of Arctic estuarine waters of the Siberian seas (Golikov and Averintzev 1977). Aitken and Gilbert (1996) described a similar community of molluscs, composed of *P. arctica*, *Thyasira dunbari* and *Thyasira gouldi*, on muddy bottoms influenced by strong inorganic sedimentation in Expedition fjord on Axel Heiberg Island. A thyasirid bivalve, *Axinopsida*, and the protobranch, *Nuculana*, are abundant in embayments subjected to high sediment loads derived from rivers or tidewater glaciers in Alaskan fjords (Hoskin 1977; Carpenter 1983; Hoberg and Feder 2002). *H. filiformis* and maldanid polychaetes-dominated communities were found in Norwegian fiords not subjected to strong glacial inflow (Holte 1998). Thorson (1957) found the *Maldane sarsi*-*Ophiura sarsi* community widely distributed on muddy sediments of deeper subtidal sediments (80–300 m) in the Barents, White and Japanese Seas, off Iceland and in the Skagerrak. *M. glebifex* and *O. sarsi* are common to abundant in muddy sediments of the northeastern Chukchi Sea (Feder et al. 1994; Ambrose et al. 2001).

Influence of environmental factors

The sediment in the Kongsfjord sublittoral is quite homogenous in terms of its granulometric characteristics. Sediment stability and mineral sedimentation processes appear to be much more important in influencing the distribution of the Kongsfjord macrofauna than the granulometric composition of sediments.

The relationship between the composition and distribution of benthic communities and high inorganic suspension loads of both natural and anthropogenic origin has been observed in several localities (e.g. Farrow et al. 1983; Feder and Jewett 1986; Syvitski et al. 1989; Olsgard and Hasle 1993). The impact of mineral suspensions on macrofauna results from the burial of organisms and their larvae and the clogging of the filtering organs of suspension-feeders (Moore 1977). Burial of organisms is a direct effect of high inorganic sedimentation. The organism's reaction depends on the species, sedimentation rate and particle size (Nichols et al. 1978). Fine sediment with high water content is probably a more difficult barrier to upward burrowing than coarse sediment (Turk and Risk 1981). Suspension-feeders are especially sensitive to inorganic suspensions. The increased load of inorganic particles cause an increase in the energetic expense connected with their elimination, dilutes nutritious particles in a mass of mineral particles, or even clogs filtering mechanisms, which in turn hinders respiration and nutrition (Moore 1977).

Sediment instability is a limiting factor for benthic fauna due to increased resuspension of sediment, the burial of newly settled larvae and interference to the maintenance of the proper positioning in the sediment by an animal (Rhoads and Young 1970; Fetzer et al. 2002). Organisms inhabiting unstable, easily resuspended sediments are subjected to high amounts of inorganic suspensions, even in regions of relatively low sedimentation from the water column. The large icebergs calving from Kongsfjord glaciers and circulating in the inner basin may be another factor of sediment disturbance. The effect of icebergs on sediments may result from direct scouring or from resuspension and sediment transport caused by water circulation around an iceberg (Peck et al. 1999; Gutt 2001).

A unique feature of the Kongsfjord glacial bay is the occurrence of "winter waters" of very low temperature, the remains of winter convection observed in the deepest parts of a bay (Svendsen et al. 2002). These waters may influence the distribution of particular species but they probably do not determine the basic division of fauna into two communities. Similar communities with a similar set of dominants were observed in other glacial bays where winter waters were not recorded (Wlodarska-Kowalczuk et al. 1998). Benthic mortalities caused by the pooling of hypoxic brine in ice gouges in a shallow Arctic bay were reported by Kvitek et al. (1998). It is possible, therefore, that this phenomenon might occur in the inner basin of Kongsfjord, although it has not been directly observed. Such events result in sulphidic sedimentary conditions and could favour those species that utilise symbiotic sulphate-reducing bacteria, such as certain of the thyasirid molluscs.

The amount of available organic matter may also influence Kongsfjord macrofauna distribution. In the case of sediments of low organic content, the ability of a detritus-feeding organism to select particles might be important. Jumars (1993) reported a general trend towards decreased selectivity in large burrowing detritus feeders. The "diluted" organic matter in the inner basin of Kongsfjord may be more available to small surface detritus-feeding bivalves and polychaetes, which dominate the Glacial Bay Community.

Ecological characteristics of dominant species

The *Chaetozone* group, a eurytopic group of species in Kongsfjord, has been recorded as typical and dominant in fjords and open coast glacial bays of Spitsbergen (Gromisz 1983; Gulliksen et al. 1985; Kendall and Aschan 1993; Wlodarska-Kowalczuk et al. 1998, 1999), as well as in muddy sediments in the Storfjord and in the Barents Sea east of Svalbard (Kendall 1996). *Chaetozone setosa* is an opportunistic species and was noted as one of the first species recolonising sediments defaunated by intensive dredging or organic or oil pollution (Hily 1987). In the inner basin, on a transect perpendicular to the face of the Conwaybreen glacier, Kendall et al. (2003) observed an increase in density and dominance of the *Chaetozone* group towards the glacier. It seems to be an omnipresent species that achieves the highest values of density and dominance in areas subjected to disturbance. The cirratulids have been noted in high numbers in areas experiencing high inorganic sedimentation

(Moore 1977). Olsgard and Hasle (1993) noted *Chaetozone setosa* and *Cauleriella* spp., as well as *Cossura longocirrata*, as characteristic species in areas of intensive non-toxic mine wastes disposal.

Bivalves characteristic for the Glacial Bay Community belong to two families: Nuculanidae and Thyasiridae. Bivalves of these two families inhabit the surface layers of sediment (they have short, non-extensible siphons) and are capable of quite effective movement (Ockelmann 1958). Their morphological features (small size and thin, smooth shells) facilitate maintenance of their position and movement in soft sediment (Rhoads 1974). Nuculanidae are very efficient detritus-feeders, collecting organic matter from and below the sediment surface with the use of long palp proboscides (Morton 1983). They sort particles efficiently, and rapidly eliminate pseudofaeces, and hence respiratory functions of the ctenidia are not endangered by the accumulation of mineral particles in the mantle cavity (Rhoads 1974). Some members of the Thyasiridae are known to utilise sedimentary sulphide through the agency of symbiotic bacteria (Dando and Spiro 1993). It is not known if *Thyasira dunbari* is capable of this but as there is no evidence of high levels of sulphide in the inner basin sediments, it seems unlikely. The only characteristic polychaete in the Glacial Bay Community—*Chone paucibranchiata*—is a small, mobile animal, which may feed both on organic particles suspended in water, as well as from the surface of the sediment (Cochrane 2000). High tolerance and high densities in habitats of high inorganic sedimentation have been observed for several species of Sabellidae (Moore 1977). Fabricinae were recorded as dominants in glacial bays of Tempelfjorden and Ekmanfjorden (Wlodarska-Kowalczuk et al. 1998).

The characteristic species of the Outer Basin Community are mostly large tube-dwelling polychaetes (Table 4). The only probable predator—polychaete *Lumbrineris* sp.—is an important component of the Glacial Bay Community as well. *Leitoscoloplos* sp. was not present in the Kongsfjord glacial bay; however, it was one of the dominants in glacial bays in Yoldiabukta, Skoddebukta and Julibukta (Wlodarska-Kowalczuk et al. 1998). Therefore, it should not be considered as characteristic for the outer basin habitat. Similarly, Holte (1998) did not find a relationship between that species' distribution and inorganic sedimentation (of natural or anthropogenic origin) or organic pollution in coastal Norwegian waters. Domination of *Heteromastus filiformis* was observed in habitats disturbed by strong organic pollution (Pearson and Rosenberg 1978), as well as in areas impacted by mine waste (Olsgard and Hasle 1993). However, this species does not tolerate mechanical disturbance of sediment (Beukema 1995), and for this reason may be excluded from glacial bays experiencing sediment slides, gravity flows and ice-berg scouring.

The fauna of the Association TRANS is included in the Outer Basin Community. Some of its characteristics, however, point to its transitional, ecotonic character. These include the high frequency and dominance of *Yoldiella solidula* (characteristic for the Glacial Bay Community) and the high density and dominance of polychaetes of the *Chaetozone* group. *Nuculoma tenuis*, one of the characteristic species of this association, another protobranch, was recorded as characteristic of areas impacted by mine waste disposal (Olsgard and Hasle 1993). In the TRANS Association, there is also a group of species that occur in large numbers, but only in samples taken in the outlet of the straits at Blomstrandoya: *Axinopsida orbiculata*, *Thyasira gouldii*, *Yoldia hyperborea*. These thyasirid and nuculanid bivalves are numerous in glacial bays. In Kongsfjord, they occur close to the Blomstrandbreen glacier. The comparison of dominants in west Spitsbergen glacial bays (Wlodarska-Kowalczuk et al. 1998) shows that *Yoldia hyperborea* is a dominant in glacial bays situated on the open coast (Skoddebukta) or very close to the fjord mouth (Julibukta). However, *Yoldiella* or *Portlandia* are not observed in those places as dominants. The domination of *Yoldia hyperborea* in areas influenced by terrigenous inflows in open shelf waters was also reported by Peres (1982) and Filatova and Barsanova (1964). Ockelmann (1958) related such a distribution of this species to its high energy demands and higher organic-matter input to sediments from open sea.

In the CENTR Association, the characteristic species were mostly large tube-dwelling polychaetes. One of them—*Spiochaetopterus typicus*—composes only 1% of the total abundance, but is a very important and typical component of this group, particularly for its physical structure. The tough tubes protrude one or more centimetres from the sediment surface and remain in place long after the demise of their inhabitants. This greatly increases the topographic complexity of the surface and sub-surface sedimentary habitat in areas where *Spiochaetopterus typicus* is abundant. The CENTR Association seems to be the most typical association of the Outer Basin Community, when compared to the ecotonic Association TRANS, which has several features similar to the Glacial Bay Community and Association ENTR, which is much influenced by shelf waters.

The sedentary, tube-dwelling polychaetes, typical for the whole Outer Basin Community, are much less important in the ENTR Association. This association is dominated by the mobile, burrowing detritus-feeders *Leitoscoloplos* sp. and *Cossura longocirrata*, and a carnivore, *Lumbrineris* sp. This suggests much lower stability in the sediments there that could be linked to the strong currents flowing from the Forlandsund Strait. The brittlestar *Ophiura robusta* and the gastropod *Lepeta caeca*, characteristic species for the ENTR Association, indicate the proximity to deep shelf waters. Larsen (1997) noted the low numbers of echinoderms in fjords in comparison to neighbouring shelf waters. Echinoderms are rare in the deep benthos of Port Valdez, a subarctic fjord in Alaska (Blanchard et al. 2002). The amphipod *Syrrhoe crenulata*, a very characteristic species in Association ENTR, was observed by Weslawski (1990) in Hornsund fjord only in the deeper outer part.

Conclusions

The ecological characteristics of dominants in two communities confirm the significance of inorganic suspension sedimentation and sediment stability for the described fauna. Rhoads (1974) distinguished two groups of organisms: mobile detritus-feeders, whose activity leads to the formation of unstable, easily resuspended sediments, and sedentary tubiculous detritus- or suspension-feeders, which increase the compaction and cohesion of sediment. In a glacial bay, the representatives of the first group dominate. The activity of protobranch bivalves results in the formation of a surface layer of unconsolidated mud and faecal pellets, an increase of water content and finally the intensification of resuspension and increased concentration of inorganic particles in bottom waters (Rhoads and Young 1970). Thus the glacial bay of the Kongsfjord is inhabited by organisms that are adapted to live in unstable sediments, but which also decrease the sediment stability. However, in the outer basin of the Kongsfjord, high numbers of sedentary or discretely motile, tube-dwelling polychaetes were observed. Again, those animals are known to increase the sediment stability (Fager 1964).

There are some trends in the physical structure of communities when the dominants are compared. Mobile small bivalves and polychaetes, which keep on or close to the sediment surface, dominate the Glacial Bay Community. The Outer Basin Community's physical structure is much more complex. The community is structured by large tubiculous, sedentary polychaetes, which penetrate deep into the sediment. They are accompanied by mobile burrowers and animals of varying size and mobility associated with the upper sediments and benthic boundary layer. Thus the size of the organisms, the depth of sediment penetration and the complexity of the physical structure of the community all decrease towards the glacier.

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References

Aitken AE, Gilbert R (1996) Marine Mollusca from Expedition Fiord, Western Axel Heiberg Island, Northwest Territories, Canada. Arctic 49:29–43

Ambrose WG, Clough LM, Tilney PR, Beer L (2001) Role of echinoderms in benthic remineralisation in the Chukchi Sea. Mar Biol 139:937–949

Beukema JJ (1995) Long-term effects of mechanical harvesting of lugworms *Arenicola marina* on the zoobenthic community of a tidal flat in the Wadden Sea. Neth J Sea Res 33:219–227

Blanchard AL, Feder HM, Shaw DG (2002) Long-term investigations of benthic fauna and the influence of treated ballast water disposal in Port Valdez, Alaska. Mar Pollut Bull 44:367–382

Carpenter TA (1983) Pandalid shrimps in a tidewater glacial fjord, Aialik Bay, Alaska. MSc Thesis, University of Alaska, Fairbanks

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143

Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. Natural Environment Research Council, Plymouth

Cochrane SJ (2000) Taxonomy and systematics of selected marine soft-bottom fan-worms (Polychaeta: Sabellidae: Sabellinae). PhD Thesis, University of St. Andrews, Polar Environmental Center

Dando PR, Spiro B (1993) Varying nutritional dependency of the thyasirid bivalves *Thyasira sarsi* and *Thyasira equalis* on chemoautotrophic symbiotic bacteria, demonstrated by isotope ratios tissue carbon and shell carbonate. Mar Ecol Prog Ser 92:151–158

Dowdeswell JA (1987) Processes of glaciomarine sedimentation. Prog Phys Geogr 11:52–90

Dowdeswell JA, Forsberg CF (1992) The size and frequency of icebergs and bergy bits derived from tidewater glaciers in Kongsfjorden, Northwest Spitsbergen. Polar Res 11:81–91

Dyer KR (1989) Sediment processes in estuaries: future research requirements. J Geo Res 94:12339–14327

Elverhøi A, Liestøl O, Nagy J (1980) Glacial erosion, sedimentation and microfauna in the inner part of Kongsfjorden, Spitsbergen. Nor Polarinst Skr 172:33–60

Elverhøi A, Lønne Ø, Seland R (1983) Glaciomarine sedimentation in a modern fjord environment, Spitsbergen. Polar Res 1:127–149

Fager EW (1964) Marine sediments: effects of tube-dwelling polychaete. Science 143:356–359

Farrow GE, Syvitski JPM, Tunnicliffe V (1983) Suspended particulate loading on the macrobenthos in a highly turbid fjord: Knight Inlet, British Columbia. Can J Fish Aquat Sci 40 [Suppl 1]:273–288

Fauchald K, Jumars PA (1979) The diet of worms: a study of polychaete feeding guilds. Oceanogr Mar Biol Annu Rev 17:193–284

Feder HM, Jewett SC (1986) The subtidal benthos. In: Hood DW, Zimmerman ST (eds) The Gulf of Alaska. Physical environment and biological resources. U.S. Minerals Management service, Alaska OCS Region, U.S. Goverment Printing Office, Washington, DC, pp 347–396

Feder HM, Naidu AS, Jewett SC, Hameed JM, Johnson WR, Whitledge TE (1994) The northeastern Chukchi Sea: benthos-environmental interactions. Mar Ecol Prog Ser 111:171–190

Fetzer I, Lønne OJ, Pearson T (2002) The distribution of juvenile benthic invertebrates in an arctic glacial fjord. Polar Biol 25:303–315

Filatova ZA, Barsanova NG (1964) The communities of bottom fauna of the western part of the Bering Sea. Tr Inst Okeanol 69:6–97

Golikov AN, Averintzev VG (1977) Distribution patterns of benthic and ice biocenoses in the high latitudes of the polar basin and their part in the biological structure of the world ocean. In: Dunbar MJ (ed) Polar oceans. McGill University, Montreal, pp 331–364

Gorlich K, Weslawski JM, Zajaczkowski M (1987) Suspension settling effect on macrobenthos biomass distribution in the Hornsund fjord, Spitsbergen. Polar Res 5:175–192

Gromisz S (1983) Bottom fauna communities of glacial bays situated at glaciers Hyrne and Stor (Spitsbergen-Hornsund). Polish Polar Research 1970–1982, Uniwersytet M Kopernika, Torun

Gulliksen B, Holte B, Jakola KJ (1985) The soft bottom fauna in Van Mijenfjord and Raudfjord, Svalbard. In: Gray J, Christiansen ME (eds) Marine biology of polar regions and effects of stress on marine organisms. Wiley, Oslo, pp 199–215

Gutt J (2001) On the impact of ice on marine benthic communities, a review. Polar Biol 24:553–564

Hily C (1987) Spatial-temporal variability of *Chaetozone setosa* (Malmgren) populations on an organic gradient in the Bay of Brest, France. J Exp Mar Biol Ecol 112:201–216

Hoberg M, Feder HM (2002) The macrobenthos of sites within Prince William Sound, Alaska, prior to the Exxon Valdez oil spill. Int Rev Hydrobiol 87:25–45

Holte B (1998) The macrofauna and main functional interactions in the sill basin sediments of the pristine Holandsfjord, Northern Norway, with autecological reviews for some key-species. Sarsia 83:55–68

Holte B, Dahle S, Gulliksen B, Naes K (1996) Some macrofaunal effects of local pollution and glacier induced sedimentation, with indicative chemical analyses, in the sediments of two Arctic fjords. Polar Biol 16:549–557

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

Hoskin CM (1977) Macrobenthos from three fjords in Prince William Sound, Alaska. Report R77-1. Institute of Marine Science, Fairbanks, Alaska

Jørgensen LL, Gulliksen B (2001) Rocky bottom fauna in arctic Kongsfjord (Svalbard) studied by means of suction sampling and photography. Polar Biol 24:113–121

Jumars PA (1993) Gourmands of mud: diet selection in marine deposit feeders. In: Hughes RN (ed) Diet selection—an interdisciplinary approach to foraging behaviour. Blackwell, Oxford, pp 124–156

Keck A, Wiktor J, Hapter R, Nilsen R (1999) Phytoplankton assemblages related to physical gradients in an arctic, glacier-fed fjord in summer. ICES J Mar Sci 56:203–214

Kendall MA (1994) Polychaete assemblages along a depth gradient in a Spitsbergen Fjord. In: Dauvin JC, Laubier L, Reish DJ (eds) Acte de la 4eme Conférence internationale des Polychetes. Mem Mus Natl Hist Nat 162:463–470

Kendall MA (1996) Are arctic soft-sediment macrobenthic communities impoverished? Polar Biol 16:393–399

Kendall MA, Aschan M (1993) Latitudinal gradients in the structure of macrobenthic communities: a comparison of Arctic, temperate and tropical sites. J Exp Mar Biol Ecol 172:157–169

Kendall MA, Widdicombe S, Weslawski JM (2003) A multi-scale study of the biodiversity of benthic fauna of the high latitude Kongsfjord, Svalbard. Polar Biol (in press)

Kuklinski P (2002) Fauna of bryozoans in Kongsfjorden, West Spitsbergen. Pol Polar Res 23:193–206

Kvitek RG, Conlan KE, Iampietro PJ (1998) Black pools of death: hypoxic, brine-filled ice gouge depressions become lethal traps for benthic organisms in a shallow Arctic embayment. Mar Ecol Prog Ser 162:1–10

Larsen L-H (1997) Soft-bottom macro invertebrate fauna of North Norwegian coastal waters with particular reference to sill-basins. Part one: Bottom topography and species diversity. Hydrobiologia 355:101–113

Lefauconnier B, Hagen JO, Rudant JP (1994) Flow speed and calving rate of Kongsbreen glacier, Svalbard, using SPOT images. Polar Res 10:56–65

Lippert H, Iken k, Rachor E, Wiencke C (2001) Macrofauna associated with macroalgae in the Kongsfjord (Spitsbergen). Polar Biol 24:512–522

Mills EL (1969) The community concept in marine zoology, with comments on continua and instability in some marine communities: a review. J Fish Res Board Can 26:1415–1428

Moore PG (1977) Inorganic particulate suspensions in the sea and their effects on marine animals. Oceanogr Mar Biol Annu Rev 15:225–363

Morton B (1983) Feeding and digestion in Bivalvia. In: Saleuddin ASM, Wilbur KM (eds) Mollusca. Academic, New York, pp 65–131

Neira C, Hopner T (1994) The role of *Heteromastus filiformis* (Capitellidae, Polychaeta) in organic carbon cycling. Ophelia 39:55–73

Nichols JA, Rowe GT, Clifford CH, Young RA (1978) In situ experiments of the burial of marine invertebrates. J Sediment Petrol 48:419–425

Ockelmann WK (1958) The zoology of East Greenland, marine Lamellibranchiata. Medd Grønl 122:1–256

Olsgard F, Hasle JR (1993) Impact of waste from titanium mining on benthic fauna. J Exp Mar Biol Ecol 172:185–213

Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr Mar Biol Annu Rev 16:229–311

Pearson TH, Mannvik HP, Evans R, Falk-Petersen S (1996) The benthic communities of the Snorre Field in the northern North Sea (61°30′N 2°10′E). 1. The distribution and structure of communities in undisturbed sediments. J Sea Res 35:301–314

Peck LS, Brockington S, Vanhove S, Beghyn M (1999) Community recovery following catastrophic iceberg impacts in a soft-sediment shallow-water site at Signy Island, Antarctica. Mar Ecol Prog Ser 186:1–8

Peres JM (1982) Major benthic assemblages. In: Kinne O (ed) Marine ecology, vol V. Wiley, New York, pp 373–522

Rhoads DC (1974) Organism-sediment relations on the muddy sea floor. Oceanogr Mar Biol Annu Rev 12:263–300

Rhoads DC, Young DK (1970) The influence of deposit-feeding organisms on sediment stability and community trophic structure. J Mar Res 28:150–178

Rosenberg R, Gray JS, Josefson AB, Pearson TH (1987) Petersen's benthic stations revisited. II. Is the Oslofjord and eastern Skagerrak enriched? J Exp Mar Biol Ecol 105:1–33

Salzwedel H, Rachor E, Gerdes D (1985) Benthic macrofauna communities in the German Bight. Veroff Inst Meeresforsch Bremerhaven 20:199–267

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

Syvitski JPM, Burell CD, Skei JM (1987) Fjords. Processes and products. Springer, Berlin Heidelberg New York

Syvitski JPM, Farrow GE, Atkinson RJA, Moore PG, Andrews JT (1989) Baffin Island fjord macrobenthos: bottom communities and environmental significance. Arctic 42:232–247

Thorson G (1957) Bottom communities. In: Hedgepth JW (ed) Treatise on marine ecology and paleocology, vol 1. Ecol Geol Soc Am Mem 67:1296

Turk TR, Risk MJ (1981) Effects of sedimentation on infaunal invertebrate populations of Cobequid Bay, Bay of Fundy. Can J Fish Aquat Sci 38:642–648

Valderhaug VA, Gray JS (1984) Stable macrofaunal community structure despite fluctuating food supply in subtidal soft sediments of Oslofjord, Norway. Mar Biol 82:307–322

Weslawski JM (1990) Distribution and ecology of south Spitsbergen coastal marine Amphipoda (Crustacea). Pol Arch Hydrobiol 37:503–519

Wiegers JK, Feder HM, Mortensen LS, Shaw DG, Wilson Vj, Landis WG (1998) A regional multiple-stressor ranj-based ecological risk assessment for the fjord at Port Valdez, Alaska. Hum Ecol Risk Assess 4:1125–1173

Wlodarska M, Weslawski JM, Gromisz S (1996) A comparison of the macrofaunal community structure and diversity in two arctic glacial bays—a 'cold' one off Franz Josef Land and a 'warm' one off Spitsbergen. Oceanologia 38:251–283

Wlodarska-Kowalczuk M, Weslawski JM, Kotwicki L (1998) Spitsbergen glacial bays macrobenthos—a comparative study. Polar Biol 20:66–73

Wlodarska-Kowalczuk M, Szymelfenig M, Kotwicki L (1999) Macro- and meiobenthic fauna of the Yoldiabukta glacial bay (Isfjorden, Spitsbergen). Pol Polar Res 20:367–386

Woodham A, Chambers S (1994) Some taxonomic problems of bitentacular cirratulids. Polychaete Res 16:14–15

Zajaczkowski M (2000) Doplyw i sedymentacja zawiesiny w wybranych fiordach zachodniego Spitsbergenu. PhD Thesis, Uniwersytet Gdanski, Gdynia