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Molluscs in Kongsfjorden (Spitsbergen, Svalbard): a species list and patterns of distribution and diversity

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Mollusca; glacial fjord; species list; species distribution; diversity; Svalbard.

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Abstract

This paper presents a survey of the mollusc fauna in Kongsfjorden, an Arctic glacial fjord in Spitsbergen, Svalbard, based on 197 samples collected with van Veen grabs, dredges, scuba-diving collections and baited traps at depths ranging from 5 to 390 m. Eighty-seven mollusc species were recorded. The species distribution accords well with the distribution of the main substrata: barren rock, kelp bed, gravel and soft bottom. For the most common substrate type, the soft bottom, the distribution and diversity of molluscs were analysed in relation to environmental factors. Glacial activity (particularly the inflow of glacial meltwater loaded with mineral solids) is responsible for the main gradients of environmental variables in the fjord. Silt concentration in sediments, the water temperature near the bottom and inorganic suspensions in the surface water best predict the species distribution of the soft bottom. Two faunal associations located in glacial bays and three faunal associations in the central basin of the fjord can be distinguished for the fauna of the soft bottom. Molluscs are much more abundant in glacial bays (200–300 individuals (ind.) 0.1 m^2) than in the central basin assemblages (30–40 ind./0.1 m^2). Yoldiid (*Yoldiella solidula*, *Y. lenticula* and *Yoldia hyperborea*) and thyasirid bivalves (*Thyasira dunbari*, *T. gouldi* and *Axinopsida orbiculata*) cope particularly well with glacial sedimentation and occur in high quantities in glacial bays. Although there is no effect of glacial disturbance on the molluscan sample species richness and species diversity, there are significant clines of evenness and taxonomic distinctness in areas near to the glacier. The patterns of molluscan diversity are not fully consistent with the patterns described for complete macrobenthic communities.

Kongsfjorden is situated on the west coast of Spitsbergen, which is the largest island of the Svalbard archipelago. Despite its high latitude location (79 °N) the fjord has a sub-Arctic character (Hop et al. 2002). The outer and central basins of Kongsfjorden are influenced by the warm Atlantic waters of the West Spitsbergen Current (Svendsen et al. 2002). Three tidal glaciers terminate in the fjord. Kongsbreen, situated in the innermost part of the fjord, is the most active glacier in the Svalbard archipelago (Lefauconnier et al. 1994). There is an international research centre in the settlement of Ny-Ålesund, which makes Kongsfjorden one of the most intensively studied high latitude fjords. The physical and biological settings of the fjord have been reviewed by Svendsen et al. (2002) and Hop et al. (2002). The Implementation and Networking of Large-scale Long-term Marine Biodiversity in Europe (BIOMARE) project selected Kongsfjorden as one of the European Marine Biodiversity Research Sites, which provide reference localities for large-scale European biodiversity studies (Warwick et al. 2003).

The biota inventory in selected sites is a crucial starting point for large-scale studies of temporal and spatial changes of coastal biodiversity (Stork et al. 1996). Species richness records are largely dependent on the sampling effort (Magurran 2004). The assessment of species richness of a marine bay, an inlet or an island requires intensive sampling using a variety of sampling techniques, and preferably covering several sampling seasons (Bouchet et al. 2002).

Molluscs are widely distributed and can be abundant in a variety of marine habitats ranging from rocky shores to abyssal muddy plains. Molluscs can be highly responsive to local human activities (Terlizzi et al. 2005) as well as to either long-term or large-scale climatic changes (Mieszkowska et al. 2006), and have been proposed as possible surrogates for the study of the distribution and diversity of the whole macrobenthic community (Anderson et al. 2005; Smith 2005). In Arctic fjords molluscs exhibit the highest preservation potential among the marine macrobenthic biota (Aitken 1990). Between 30 and 60% of the modern Arctic mollusc fauna is represented in Quaternary marine Arctic macrofossils, and understanding the environmental factors controlling the distribution of living communities is crucial for reconstructing the palaeoecology of Quaternary glaciations and interglaciations (Gordillo & Aitken 2000).

The macrobenthic communities of Kongsfjorden have been described in several publications. Kendall et al. (2003), Włodarska-Kowalczuk & Pearson (2004), Włodarska-Kowalczuk et al. (2005) and Somerfield et al. (2006) studied the distribution and diversity of subtidal communities of the soft bottom at depths ranging from 30 to 300 m. The shallow subtidal macrofauna has been described by Kaczmarek et al. (2005) and Bick & Arlt (2005). Lippert et al. (2001) studied the phytophylous macrofauna at a single location close to the island of Blomstrandhalvøya. Jorgensen & Gulliksen (2001) investigated the fauna of the hard bottom at the Kvadehuken at a depth of 20–30 m using a suction sampler and underwater photography. Rozycki (1991) published a list of molluscs found at 12 stations sampled with grabs and dredges. Those studies were limited in scope to a single location, habitat or depth range within the fjord.

The published information on mollusc diversity and distribution in Kongsfjorden is scattered and incomplete. In the present study I bring together extensive distributional data of molluscs collected in several benthic surveys carried out in Kongsfjorden by the Institute of Oceanology, Polish Academy of Sciences, in 1996–2000. The material contains 197 samples taken with a variety of sampling gear at a range of depths and habitats, and is likely to give a reliable assessment of the mollusc diversity and distribution patterns in the fjord. The aims of the paper are to (1) present a mollusc species list for Kongsfjorden; (2) identify the environmental predictors of the mollusc species distribution; (3) identify the species characteristic for fjord habitats/mollusc associations; (4) quantify the response of molluscs at the soft bottom to glacial disturbance and compare it with the perturbation signal in the whole macrobenthic community (as described by Włodarska-Kowalczuk et al. 2005).

Study area

Kongsfjorden is an open fjord located on the north-west coast of Spitsbergen in the Svalbard archipelago (12 °E, 79 °N; Fig. 1). The fjord is 26 km long, with an area of 231 km^2. Depths rarely exceed 400 m. Two tidal glaciers (Kongsbreen and Conwaybreen) terminate in the inner basin, whereas a third one, Blomstrandbreen, is situated on the northern mid-fjord coast.

The hydrology of Kongsfjorden is shaped by the interplay among: (1) warm saline Atlantic waters entering the fjord from the shelf [temperature (T) > 1 °C, salinity (S) > 34.7]; (2) local fjord waters ($T < 1$°C, salinity $S > 34.4$); (3) freshwater input from the glaciers (Svendsen et al. 2002). In the inner basin there are deep depressions in which very cold winter waters ($T < -0.5$ °C, $S > 34.4$), which are the remnants of winter cooling and deep convection, can be also observed (Svendsen et al. 2002).

Fairly uniform fine sediments cover much of the Kongsfjorden subtidal region, particularly in the inner basin where high sediment deposition rates are accompanied by relatively weak currents (Włodarska-Kowalczuk & Pearson 2004). Gravel beds occur in some parts of the outer fjord where strong bottom currents winnow out fine sediments. Ice rafted pebbles and stones (drop-stones), typical of Arctic glaciated fjords (Dale et al. 1989), are distributed all over the fjord. At the edge of the fjord there are rocky shelves (Jorgensen & Gulliksen 2001) that gradually change into mixed bottom (hard bottom with macroalgae and bedrock with pockets of soft sediment) in the shallow subtidal region in the middle of the fjord (Kaczmarek et al. 2005). Kelp forests (*Alaria esculenta, Laminaria saccharina* and *L. digitata*) are restricted to sites sheltered from drifting icebergs and with limited grazing by sea urchins (Lippert et al. 2001; Hop et al. 2002).

The meltwater inflows from the Kongsfjorden glaciers result in a steep gradient in both the concentration of mineral suspensions and the sedimentation rates in the water column (Svendsen et al. 2002). The sediment accumulation rate decreases by about one order of magnitude from the Kongsbreen glacial bay (20 000 g m^{-2} a^{-1}) to the central part of the fjord (1800–3800 g m^{-2} a^{-1}) and, again, by another order of magnitude towards the outer fjord (200 g m^{-2} a^{-1}; Svendsen et al. 2002). Intensive sedimentation results in the formation of unconsolidated labile sediments (Syvitski et al. 1987). Near-glacier sediments may be scoured by icebergs (of up to 10 m in height) that either circulate or stay anchored in the inner basin (Dowdeswell & Forsberg 1992).

The organic matter supply to benthic biota decreases towards the inner basin, where primary productivity is

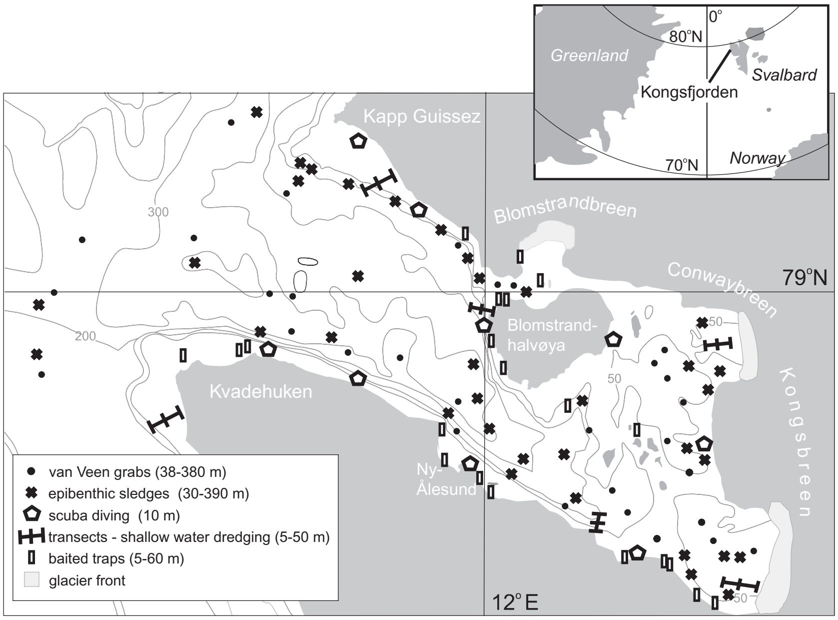

Figure 1 Location of sampling stations.

limited by high levels of water turbidity and where the available organic matter is diluted by the huge mineral sedimentation (Gorlich et al. 1987). The outer fjord and shelf waters are influenced by Atlantic waters and have an enhanced marine organic matter supply (Winkelman & Knies 2005). The particulate organic carbon (POC) concentration in Kongsfjorden sediments increases along the fjord axis from 0.1–0.2 mg g^{-1} in the Kongsbreen glacial bay and 0.3–0.5 mg g^{-1} in Blomstrandbreen glacial bay to 1.1–2.4 mg g^{-1} in the outer fjord and shelf sediments (Fetzer et al. 2002; Włodarska-Kowalczuk & Pearson 2004).

Materials and methods

Material was collected during cruises with the RV *Oceania* and land expeditions based at the Norwegian Polar Institute station in Ny-Ålesund during the summer seasons from 1996 to 2000. Samples were collected throughout the fjord (Fig. 1) using a range of techniques (Table 1). Eighty quantitative samples were taken using van Veen grabs, 117 samples were collected using qualitative methods (dredges, scuba-diving and baited traps). Three replicate samples were collected at van Veen grab and scuba-diving stations (with the exception of a few van Veen grab stations where only one replicate was taken because of navigational difficulties). One replicate was taken at each station sampled using either an epibenthic sledge or baited traps. Either five or six samples from sites situated along the depth transect (5, 10, 15, 20, 30 and 50 m) were taken at six stations using a small rectangular dredge. The small dredge, epibenthic sledge and baited traps were constructed with 1 mm mesh size nets. Samples were sieved on either 0.5 mm mesh (van Veen grabs and samples collected by a diver) or 1 mm mesh (all samples from dredges and baited traps). All animals were sorted, identified to the lowest possible taxonomic level and counted. Some individuals could not be identified to species level as either the shells were damaged or the organisms were juvenile and specific traits were not fully developed. The species names and taxonomic affiliations are consistent with the European Register of Marine Species (available at www.marbef.org/data/erms.php).

The number of observed species (S_{obs}) was plotted as a function of the sampling effort. A species accumulation curve with 95% confidence intervals was computed using the formulae of Colwell et al. (2004). Two alternative approaches can be applied to estimate true species richness: the extrapolation of the accumulation curve (to predict an asymptote); non-parametric techniques based on the concept that rare and uncommon species carry information about the number of species missing in samples. The Michaelis-Menten (*MM*) function was used to generate an asymptotic curve that fitted the species accumulation curve (Magurran 2004). *Chao2*, a non-parametric estimator based on species occurrence data ($Chao2 = S_{obs} + Q_1^2/2Q_2$, where Q_1 is the number of species that occur in just one sample and Q_2 is the number of species that occur in exactly two samples) was also calculated (Chao 2004). The *MM* asymptote estimation and *Chao2*, along with log-linear 95%

Table 1 Sampling effort and basic information on samples used in the Kongsfjorden mollusc study. The table includes references to papers with details of sampling methods and the locations of stations.

Sampling year	Sampling gear	Number of stations	Number of samples	Depths (m)	Reference
1997	van Veen grab, catching area of 0.1 m^2	14	33	38–380	Włodarska-Kowalczuk & Pearson 2004
1998		16	47	40–355	
1996	Epibenthic sledge	9	9	30–300	—
1997		8	8	35–390	
1999		12	12	35–300	
2000		5	5	140–330	
1999	Small rectangular dredge (80 × 30 cm)	6	32	5–50	Kaczmarek et al. 2005
2001	Collection by diver, frame 0.25 m^2	9	27	10	Kuklinski & Porter 2004
1998–2000	Baited traps	24	24	5–60	Legezynska 2001, 2002

confidence intervals as suggested by Chao (1987), were computed using EstimateS (Colwell 2005).

Constrained ordination techniques were used to explore the relationship between mollusc species distribution and environmental settings (ter Braak & Smilauer 2002). The data collected using quantitative (van Veen grabs) and qualitative (dredges and scuba-diving) methods were treated separately. The material obtained with baited traps differed much from other samples and was not considered in the analyses. Only presence/absence data were used for qualitative material. The quantitative data (van Veen grabs) were square-root transformed prior to analyses. The set of environmental variables used in the analyses of qualitative mollusc samples included depth, longitude (as a proxy for distance to the glacier) and six nominal variables, namely, presence of rock, mud, sand, gravel, kelp and drop stones. The analyses of the grab data were performed only with data from a 1998 benthic cruise. The following environmental variables were recorded: depth, longitude (as a proxy for distance to the glacier), temperature and salinity of the water near the bottom, concentration of mineral and organic suspensions in surface waters, occurrence of drop stones, percentage of gravel, sand, silt and clay, mean grain size and the concentration of POC and the POC : particulate organic nitrogen concentration in sediment (PON) ratio in sediments.

The results of a preliminary de-trended correspondence analysis (DCA) pointed to canonical correspondence analyses (CCA) as the most appropriate for the qualitative data, and to redundancy analyses (RDA) as the best suited for the grab data (ter Braak & Smilauer 2002). The forward selection of environmental variables was used to identify and rank their importance of variables in determining the species distribution (ter Braak & Smilauer 2002). The forward selection method performs the following functions:it estimates the fit of each variable separately (marginal effects); it selects the best variable; and it ranks all the remaining variables on the basis of the fit that each variable gives in conjunction with the selected variable(s) (conditional effects). In the case of grab data, a subset of best fitted variables was selected. The selection of best fitted variables was performed via repeated forward selection analyses and the progressive elimination of variables with non-significant conditional effects until a set of variables with only significant effects was attained. The significance of the ordination axis in CCA and in RDA, and the effects of environmental variables, were tested employing Monte Carlo permutation tests using 499 unrestricted permutations. The analyses were carried out using Canoco v. 4.5 software (ter Braak & Smilauer 2002).

Clustering (using group-average linking) of Bray-Curtis similarities was used to visualize the patterns of mollusc distribution. Again presence/absence qualitative data and square root transformed quantitative data were used. Based on the resulting dendrograms, groups of samples of similar composition (mollusc associations) were distinguished.

The frequency, dominance, average abundance and indices of the community fidelity (Salzwedel et al. 1985) of each species were calculated for mollusc associations defined by multivariate analyses. The indices of fidelity included *DAS* (degree of association regarding stations, i.e. the number of stations within the association at which the species concerned occurred as the percentage of the total number of stations at which this species occurred) and *DAI* (degree of association regarding individuals, 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 have been used to select the species that are the best descriptors of the associations on the soft bottom: *typical* species (frequency > 75%, dominance > 2%) and *characteristic* species (typical + either *DAI* or *DAS* > 60%). In the case of qualitative data only frequency and *DAS* was considered, and species of frequency > 25% and *DAS* > 60% were regarded as *characteristic* species.

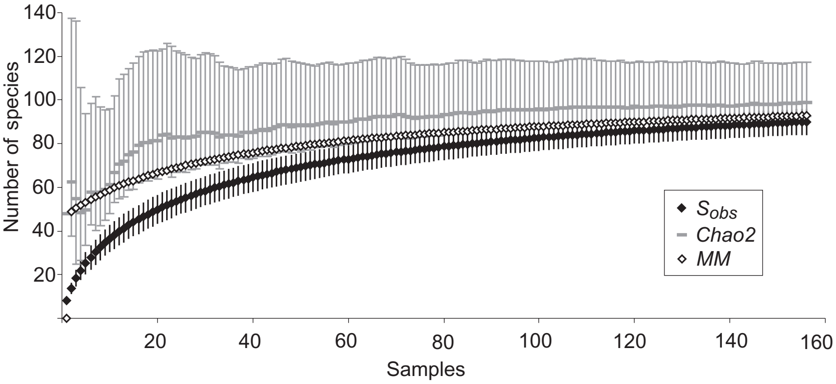

Figure 2 Species accumulation curves plotted for observed number of species (S_{obs}) and the true number of species estimated using *Chao2* and the Michaelis-Menten (*MM*) equation. S_{obs} and *Chao2* are plotted with 0.95 confidence intervals.

The differences in *N* (number of individuals per sample) between associations distinguished based on grab samples were tested using the non-parametric Kruskal-Wallis test, as even after transformation variances could not be homogenized. Post-hoc testing of differences between pairs of associations was performed using pair-wise Mann-Whitney U tests. Species richness defined as the total number of species in a sample (*SP*), species diversity measured using the Shannon-Wiener index (*H*) and the evenness (equitability) of distribution of individuals between species as estimated by the Pielou index (*J*) were calculated for quantitative samples. The differences in *SP*, *H* and *J* between the associations were tested using a one-way ANOVA. The Fisher's LSD (least significant difference) tests were used for post-hoc multiple comparisons.

To explore the taxonomic diversity of samples, two measures of taxonomic distinctness were calculated: *avTD* (average taxonomic distinctness of presence/absence data) and *varTD* (variation in taxonomic distinctness) (Clarke & Warwick 2001). The taxonomic diversity measures differ from other metrics of species richness and species diversity, because they include information on the taxonomic position of species. *avTD* describes the average taxonomic distance (the "path length" between two species following Linnean taxonomy) of all the species in the association. *varTD* is defined as the variance of the taxonomic distances between all pairs of species in the association. Five taxonomic levels were used in calculations: species, genus, family, order and class, and equal step levels between successive taxonomic levels were assumed. The differences between soft-bottom associations in *AvTD* and *varTD* were identified with the use of a one-way ANOVA. The post-hoc testing was carried out using Fisher's LSD tests.

Results

The material contained 35 398 individual molluscs representing 87 species of 56 genera and 43 families. One species of Caudofoveata, five species of Polyplacophora, 38 species of Gastropoda and 43 species of Bivalvia were recorded. A full taxonomic list is presented in the Appendix. The species accumulation curves tended to stabilize towards an asymptotic value in the cases of both the observed and the estimated numbers of species (Fig. 2). The *MM* estimator of the asymptotic value of total species richness gave 93 species. *Chao2* gave an estimate of 99 species (with 95% confidence intervals from 93 to 117).

The shallow waters of the Kongsbreen glacial bay were very poor in the numbers of molluscs: samples collected by scuba-diving at 10 m and in baited traps deployed at depths from 5 to 50 m yielded no mollusc specimens. Samples collected with small dredges at 5–15 m contained only a few specimens. Samples from baited traps located along the coast in the central and outer parts of the fjord contained only scavenging buccinid gastropods (*Buccinum glaciale*, *B. undatum*, *B. scalariforme*, *B. polare* and *Colus kroeyeri*).

Species–environment relationship

In the CCA of qualitative data the first two ordination axes explained about 50% of the variance of the species–environment relationship. The first canonical axis was significant at $P = 0.002$, the second axis was not significant ($P > 0.05$). The occurrence of rock and mud was significantly correlated to the first axis (0.85 and –0.80, respectively, Fig. 3). Five variables were selected as significant predictors of species distribution by the forward selection analyses: rock, depth, mud, gravel and sand (Table 2). Two groups of species can be delineated on the CCA diagram: species situated on the left-hand side of the diagram with an occurrence restricted to muddy sediments (*Y. solidula*, *Y. lenticula*, *Thyasira dunbari*, *Nuculana pernula*, *Ciliatocardium ciliatum*, *Frigidoalvania cruenta*, *Ennucula tenuis*, *Arctinula groenlandica* and *Y. hyperborea*); species situated on right-hand side of the plot, with an

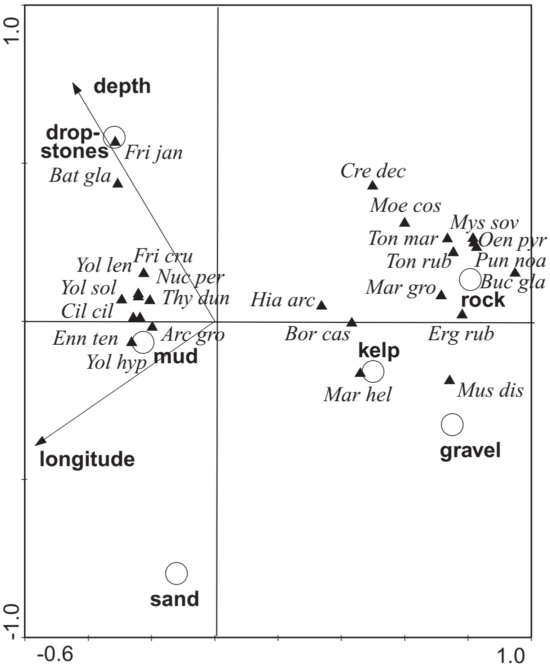

Figure 3 Ordination diagram based on the canonical correspondence analyses of mollusc species occurrences with respect to environmental variables in Kongsforden. Circles represent centroids of dummy variables, arrows are linear variables and triangles are species. Only species with a 10% minimum fit to the lower axis are plotted. The species names are coded by the first three letters of the generic and specific name (for species names consult the Appendix).

Table 2 Marginal and conditional effects obtained from the forward selection of environmental variables. λ_1 is a fit with an eigen value with one variable only, λ_A is an additional fit with an increase in the eigen value, *P* is the significance level obtained with a Monte Carlo simulation using 499 unrestricted permutations.

Variable	Marginal effects λ_1	Conditional effects λ_A	*P*
Qualitative data			
Rock	0.52	0.52	0.002
Depth	0.31	0.26	0.012
Mud	0.49	0.21	0.034
Gravel	0.25	0.21	0.022
Sand	0.25	0.2	0.034
Kelp	0.14	0.14	0.102
Longitude	0.31	0.13	0.08
Drop stones	0.23	0.08	0.574
Grab data			
Silt	0.29	0.29	0.002
Temperature	0.28	0.08	0.004
Mineral suspensions	0.13	0.13	0.002
Depth	0.16	0.05	0.004
POC/PON	0.02	0.03	0.018
Organic suspensions	0.14	0.04	0.004
Drop stones	0.03	0.02	0.066
Salinity	0.22	0.03	0.018
Gravel	0.10	0.03	0.022
POC	0.19	0.05	0.002
Longitude	0.26	0.03	0.008
Sand	0.26	0.02	0.002
Mean grain size	0.10	0.01	0.04

POC, particulate organic carbon concentration in sediment; PON, particulate organic concentration in sediment.

affinity to occurrence at the hard bottom (*Erginus rubellus, Margarites groenlandicus, Tonicella rubra, T. marmorea, Buccinum glaciale, Puncturella noachina, Oenopota pyramidalis, Mysella sovaliki* and *Moelleria costulata*). *Margarites helicinus* was placed close to the kelp variable centroid. *Bathyarca glacialis* and *Frigidoalvania janmayeni* were located close to the drop stones centroid.

In the RDA of grab data the first two ordination axes were significant ($P = 0.002$) and explained about 89% of the variance of the species–environment relationship. A third axis was not significant ($P > 0.05$). The concentration of silt (0.68) and the longitude (0.62) had the highest positive correlation to the first axis (Fig. 4a). The salinity at the bottom was negatively correlated to the first axis (−0.63). The temperature at the bottom was negatively correlated to the second axis (−0.63). Forward selection, applied to the full set of environmental variables considered, discriminated 10 variables with significant conditional effects (Table 2). The small conditional effect of longitude, temperature, salinity and sand compared with their large marginal effect results from the high correlation of these variables to silt concentration. The extra fit of the variables mentioned above is very small, as a large part of the effect is already explained by a strongly co-varying variable: silt. Five environmental variables were selected in repeated forward selection analyses by progressive elimination of the variables with non-significant conditional effects: silt, temperature, mineral and organic suspensions and POC/PON in sediments. Three groups of species can be distinguished on the RDA diagram: (1) species that correlated positively with silt, mineral suspensions and longitude (*Y. solidula, Y. lenticula* and *T. dunbari*); (2) species that correlated negatively with longitude (distance along the fjord) and its co-variables (*Lepeta caeca, Margarites costalis* and *Ischnochiton albus*); (3) species not correlated to environmental variables considered in the analyses (*Mya truncata, Y. hyperborea* and *T. gouldi*).

Molluscan associations

Four groups of stations were distinguished on the dendrogram resulting from clustering the presence/absence data from samples taken by qualitative methods (Fig. 5): (1) *ROCK*, samples collected at shallow stations (5–20 m) situated on rocky shelves at two Kongsfjorden capes

(Kvadehuken and Kapp Guissez); (2) *KELP*, samples collected in the shallow sublittoral on different types of bottom covered with kelp (*L. saccharina*, *L. digitata* and *A. esculenta*); (3) *SEDIMENT*, samples collected on soft bottom at depths ranging from 5 to 300 m; and (4) *GRAVEL*, samples collected on gravel/stones at the entrance of the fjord (depths below 150 m).

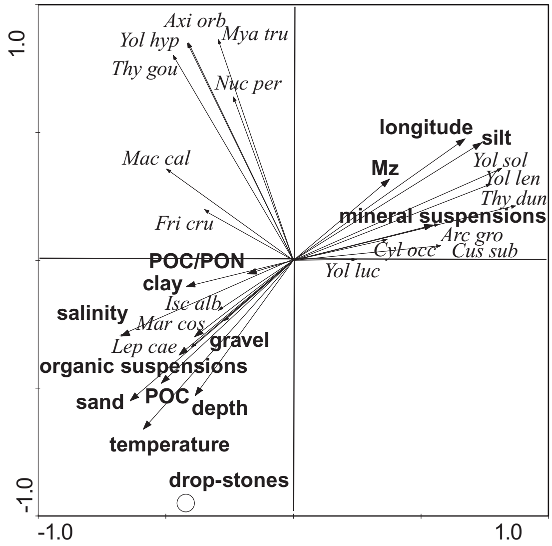

Figure 4 Ordination diagram based on redundancy analyses of square root transformed mollusc species densities in grab samples with respect to environmental variables. Circles represent centroids of dummy variables, small arrowheads indicate species and large arrowheads indicate linear variables. Only species with a 5% minimum fit to the lower axis are plotted. The species names are coded by the first three letters of the generic and specific name (for species names consult the Appendix). POC, particulate organic carbon concentration in sediments; POC/PON, particulate organic carbon/particulate organic nitrogen ratio; Mz, mean grain size in sediments.

There were six species characteristic for the *ROCK* association: the chitons *T. rubra* and *T. marmorea*; the gastropods *M. costulata, P. noachina* and *M. groenlandicus*; and the bivalves *Crenella decussata* and *M. sovaliki* (Table 3). Only the gastropod *M. helicinus* could be classified as characteristic for the group of samples collected at sites with kelp. The gastropods *Lepeta caeca*, *Margarites costalis* and *Trophon clathratus* and the chiton *Ischnochiton albus* were characteristic for the *GRAVEL* association. Thirteen species could be identified as characteristic for the *SEDIMENT* association (Table 3).

Five groups of samples could be distinguished on the dendrogram of Bray-Curtis similarities of square-root transformed quantitative data (Fig. 6): (1) *G1*, samples collected in the Kongsbreen glacial bay; (2) *G2*, samples collected in the Blomstrandbreen glacial bay; (3) *CB*, samples collected in the central basin; (4) *CD*, a small number of stations in the central basin where drop stones were common; (5) *CE*, samples from three stations situated at the mouth of the fjord.

The molluscs of the Kongsbreen glacial bay (*G1*) were dominated by the bivalves *Y. solidula, Y. lenticula* and *T. dunbari* (Table 4). Both species of *Yoldiella* were also numerous in the glacial bay of the Blomstranbreen (*G2*), but the characteristic species of this association included only *Y. hyperborea*, *A. orbiculata* and *Thyasira gouldi*. All the species already mentioned were also present, although much less numerous, in the *CB* association, where *Chaetoderma nitidulum* was the characteristic species. *B. glacialis*

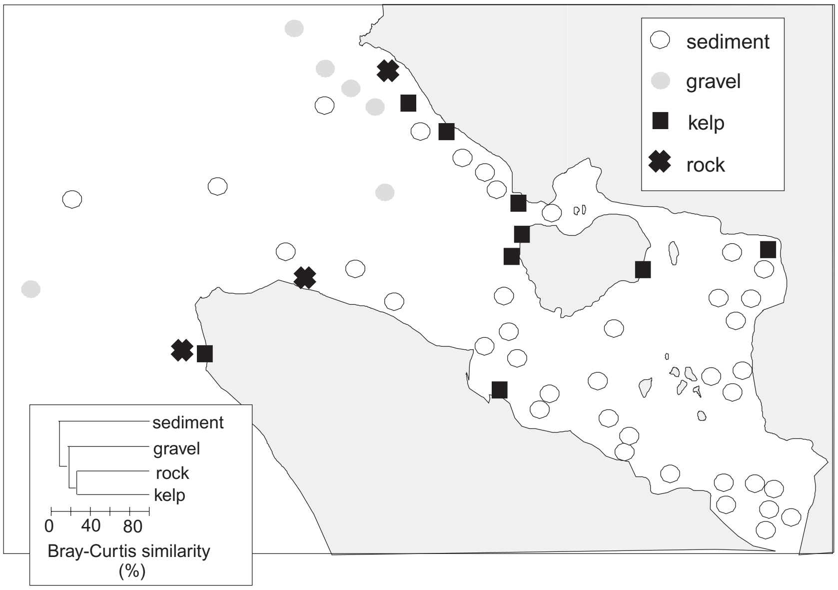

Figure 5 Distribution of associations distinguished on a dendrogram, plotted using the group average linking of Bray-Curtis similarities of presence/absence data of species occurrences in samples taken using qualitative methods (dredges and scuba-diving). The simplified dendrogram is presented.

Table 3 The most common species in associations distinguished in multivariate analyses of qualitative data. *F* is frequency (%), *NI* is number of all individuals. Species with frequency exceeding 25% are presented. Characteristic species [degree of association regarding stations (DAS) exceeding 50%] are in boldface.

	ROCK		*KELP*		*GRAVEL*		*SEDIMENT*	
	NI	*F*	*NI*	*F*	*NI*	*F*	*NI*	*F*
Tonicella rubra	**113**	**78**	1	5	1	17	1	3
Crenella decussata	**92**	**33**					2	3
Moelleria costulata	**48**	**33**					1	3
Mysella sovaliki	**51**	**33**						
Puncturella noachina	**8**	**33**						
Margarites groenlandicus	**14**	**78**	12	25			32	3
Astarte borealis	34	33					35	15
Cingula castanea	11	33	3	5			3	5
Erginus rubellus	90	89	19	35			2	3
Hiatella arctica	45	89	18	35	29	67	44	28
Tonicella marmorea	**39**	**56**	5	5	48	33		
Margarites helicinus	11	22	**3316**	**95**			15	10
Lepeta caeca					**16**	**83**		
Astarte montagui					6	50	69	20
Margarites costalis					**2**	**33**		
Ischnochiton albus	13	22			**13**	**17**		
Trophon clathratus					**2**	**33**	1	3
Yoldiella solidula					1	17	**2479**	**68**
Yoldiella lenticula							**7333**	**73**
Nuculana pernula							**1837**	**78**
Arctinula groenlandica							**869**	**63**
Mya truncata	34	33	7	20			**351**	**60**
Ennucula tenuis	1	11	1	5			**1448**	**55**
Ciliatocardium ciliatum							**219**	**50**
Thyasira dunbari							**418**	**43**
Frigidoalvania cruenta					6	17	**344**	**40**
Axinopsida orbiculata	15	22					**1129**	**38**
Bathyarca glacialis					5	17	**304**	**38**
Macoma calcarea	2	11			12	17	**302**	**33**
Cuspidaria subtorta							**381**	**28**

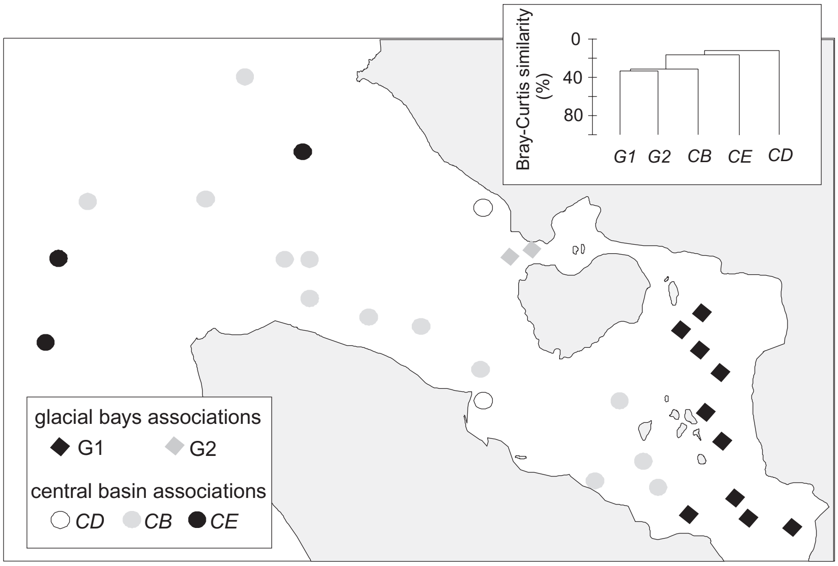

Figure 6 Distribution of associations distinguished on a dendrogram, plotted using the group average linking of Bray-Curtis similarities of square root transformed densities of species in quantitative samples from the soft bottom. The simplified dendrogram is presented.

Table 4 The dominant species in mollusc associations at the soft bottom. *D* is dominance (%), *avN* is average density (ind./0.1 m^2). The five most abundant species are presented for each association. Characteristic species [either degree of association regarding individuals (DAI) or DAS > 60%] are in boldface.

	G1		***G2***		***CB***		***CD***		***CE***	
	avN	*D*	*avN*	*D*	*av N*	*D*	*avN*	*D*	*avN*	*D*
Yoldiella solidula	**116.0**	**54**	24.2	6	5.2	16	0.3	1	0.3	1
Yoldiella lenticula	**53.0**	**25**	9.0	2	7.7	24	0.5	2	0.1	1
Thyasira dunbari	**24.7**	**12**	1.0	0	0.2	1	0.3	1	0.1	1
Ennucula tenuis	8.7	4	29.0	8	2.3	7			1.1	4
Nuculana pernula	3.6	2	15.8	4	2.7	8			0.9	3
Axinopsida orbiculata	1.0	1	**177.2**	**46**	0.6	2			0.5	2
Yoldia hyperborea	0.1	0	**48.3**	**13**	0.2	1				
Thyasira gouldi			**48.2**	**12**	0.1	0			2.8	10
Macoma calcarea	0.1	0	8.7	2	0.2	1			8.3	30
Frigidoalvania cruenta	0.5	0	6.3	2	2.0	6				
Chaetoderma nitidulum	0.9	0	0.7	0	**3.7**	**11**	1.8	6	1.1	4
Bathyarca glacialis	0.1	0			2.3	7	**23.3**	**78**		
Frigidoalvania janmayeni					1.4	4	2.0	7		
Oenopota sp.	0.0	0			0.4	1	1.5	5		
Lepeta caeca					0.7	2			**8.0**	**29**

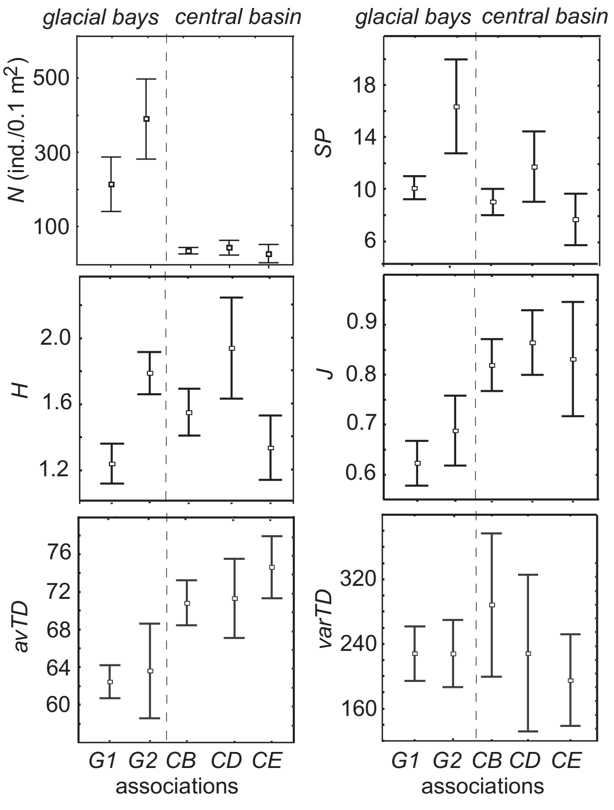

Figure 7 Density (*N*, number of individuals per 0.1 m^2) and diversity (*SP*, number of species per sample; *H*, Shannon-Wiener index; *J*, Pielou index; *avTD*, average taxonomic distinctness; *varTD*, variance of taxonomic distinctness) in mollusc assemblages of the soft bottom (mean and 95% confidence intervals).

was both the most abundant and characteristic species in the *CD* association, whereas the gastropod *L. caeca* was characteristic for the *CE* association. *E. tenuis, N. pernula* and *Macoma calcarea* were not characteristic for any of the associations—they were common in soft sediments all over the fjord.

Density and diversity in the quantitative samples from the soft bottom

The number of individuals *(N)* was significantly higher in the glacial bays (214 ind./0.1 m^2 on average in *G1*, 387 ind./0.1 m^2 in *G2*) than in the central basin associations (32 ind./0.1 m^2 in *CB*, 40 ind./0.1 m^2 in *CD*, 27 ind./0.1 m^2 in *CE*; Fig. 7). *SP* was at the highest level and significantly different from most other assemblages in *G2* (Fig. 7; Table 5). *H* was higher in *G2*, *CB* and *CD* than in *G1* and *CE*. *J* was lower in glacial bays (*G1* and *G2*) than in the central basin assemblages, *CB, CD* and *CE*. *avTD* was significantly lower in glacial bays (*G1* and *G2*) than in the central basin assemblages (*CB, CD* and *CE*; Fig. 7; Table 5). There was no significant difference in *varTD* at $P < 0.05$ (one-way ANOVA).

Discussion

The survey of Kongsfjorden molluscs yielded 87 mollusc species. Rozycki (1991) reported 39 mollusc species in 18 samples collected in Kongsfjorden in 1988. His list included nine species (*Littorina saxatilis, Nucella lapillus,*

Table 5 Results of Kruskal-Wallis test comparing density (*N*, number of individuals per 0.1 m^2) and ANOVA comparing diversity measures (*SP* is the number of species per sample, *H* is Shannon-Wiener index, *J* is Pielou index, *avTD* is average taxonomic distinctness, *varTD* is variance of taxonomic distinctness) of mollusc associations at the soft bottom. Pairwise contrasts determined by Mann-Whitney U tests for *N* and post-hoc Fisher's LSD tests for *SP*, *H*, *J* and *avTD*. *G1* and *G2* are glacial bay associations, *CB*, *CE* and *CD* are central basin associations.

	F or *H*	*P*	Significant contrasts in pairs of assemblages (at $P < 0.05$)
N	47.5 (*H*)	0.000	*G1, G2 > CB,CD,CE; G2 > G1*
SP	13.0 (*F*)	0.000	*G2 > G1,CB,CD,CE; G1,CD > CE; CD > CB*
H	9.4 (*F*)	0.000	*G1 < CB,CD,G2; CB < CD; CD,G2 > CE*
J	13.9 (*F*)	0.000	*G1, G2 < CB,CD, CE*
avTD	17.2 (*F*)	0.000	*G1,G2 < CB,CD, CE*
varTD	1.1 (*F*)	0.382	—

Buccinum hydrophanum, *Colus latericus*, *Turbonilla interrupta*, *Thyasira ferruginea*, *Macoma loveni*, *Kellyella miliaris* and *Poromya subtorta*) that were absent in material I have studied here. Combining the data, there have been 96 species recorded in Kongsfjorden to date. This number of species lies within the confidence interval of the *Chao2* estimate of the true species richness in the fjord, and is a quarter of all the Arctic species (436 species of molluscs, excluding Nudibranchia and Cephalopoda) listed by Sirenko (2001). It is difficult to compare the assessment of Konsfjorden molluscan species richness to other Arctic localities as there are few studies of comparative sampling effort covering the full range of fjordic habitats and depths. Seventy nine mollusc species were identified in 106 benthic samples collected with the use of grabs and dredges at depths from 2 to 190 m in Jørgen Brønlund Fjord, North Greenland (Schiøtte 1989). Only 26 mollusc species were found in 27 dredge samples in Expedition Fiord, Northwest Territories, Canada (Aitken & Gilbert 1996). Odhner (1915) recorded 130 mollusc species (cephalopods and nudibranchs excluded) in a comprehensive study of Isfjorden (west Spitsbergen) based on 130 stations sampled with various dredges at depths ranging from 2 to 406 m. Rozycki (1993) added another nine bivalve species to Odhner's list. Isfjorden is about four times longer and much larger in area than Kongsfjorden, so it can host a higher number of species, but its species richness is nevertheless dramatically lower than that found in lower latitude sites of a similar area. A species inventory of a tropical coastal site with an area of 295 km^2 off the coast of New Caledonia recorded as many as 2738 species of marine molluscs (Bouchet et al. 2002). The differences between the mollusc species richness in polar and tropical sites are enormous. The huge latitudinal cline of diversity, more pronounced in molluscs than in some other taxa, may be related to the increased cost of calcification in low temperatures, as suggested by Clarke (1992).

The majority of mollusc species in Kongsfjorden showed strong preferences towards a single substratum type; only a few (e.g. *Hiatella arctica* and *Mya truncata*) were abundant both on soft and hard substrata. The major discontinuity in mollusc species distributions separated the biota of rocky shelves, gravel beds and the soft bottom. Multivariate analyses distinguished the kelp associated fauna as the fourth association, but kelp bed samples differed from the rocky shelf material mostly in the common occurrence and dominance of *M. helicinus*, a well-known dweller of kelp cauloids and phylloids in the shallow waters of Spitsbergen (Rozycki & Gruszczynski 1986). The substrate dictates the taxonomic and functional organization of mollusc associations. The rocky shelf fauna is dominated by grazing chitons (*Tonicella*) and gastropods (*Erginus* and *Margarites*), and suspension feeding sedentary bivalves (*Crenella*, *Astarte* and *Hiatella*), the gravel beds are inhabited by grazers, surface deposit feeders and suspension feeders (*Ischnochiton*, *Lepeta* and *Astarte*), whereas mobile deposit feeding bivalves (*Yoldiella*, *Yoldia*, *Nuculana*, *Ennucula* and *Axinopxida*) dominate in soft sediments. Such distribution of functional groups agrees well with the model patterns described for Boreal coastal macrobenthic communities by Pearson & Rosenberg (1987).

Five separate assemblages distinguished in soft sediments could be regarded as different expressions of the same species pool, as any differences were largely a result of the varying patterns of dominance of the same set of species. The changes in the relative dominance of the infaunal molluscs could be largely explained in terms of the distance that any particular assemblage lies from the head of the fjord and from the most active glacier, Kongsbreen. Although RDA analysis showed that there are many factors that were related to the distribution of faunal assemblages, the significant factors were co-variable and the overall influence of the glacier was predominant. The granulometric characteristics, the quantity of organic carbon and the stability of sediments all reflect the glacial sedimentation gradients in an Arctic glacial fjord (Gorlich et al. 1987; Syvitski et al. 1987; Włodarska-Kowalczuk & Pearson 2004). Similarly the salinity and temperature gradients are produced by the inflow of fresh and cold glacial meltwaters, and are controlled by the glacier activity (Svendsen et al. 2002).

High levels of mineral sedimentation and sediment deposition have been shown to be an acute disturbance agent causing a dramatic decrease in benthic densities and diversity (e.g. Airoldi 2003; Anderson et al. 2004; Thrush et al. 2004; Włodarska-Kowalczuk et al. 2005). Arctic molluscs cope surprisingly well with the glacial

Table 6 Dominant mollusc taxa in subtidal sediments in inner (either glacial or glaciofluvial sedimentation influenced) basins versus outer parts of Arctic fjords.

Location	Inner fjord	Outer fjord
Expedition Fiord, Northwestern Territories, Canada (Aitken & Gilbert 1996)	*Portlandia arctica*, *Thyasira gouldi*	*Astarte borealis, Astarte warhami, Hiatella arctica, Mya sp., Trichotropis sp.*
McBeth and Itirbilung fiords (Syvitski et al. 1989, Aitken& Fournier 1993)	*Portlandia arctica, Hiatella arctica, Axinopsida orbiculata*	*Axinopsida orbiculata, Bathyarca glacialis, Astarte spp.*
Cambridge Fiord (Aitken & Fournier 1993)	*Yoldiella intermedia, Yoldiella lenticula, Axinopsida orbiculata*	*Axinopsida orbiculata, Bathyarca glacialis, Astarte spp.*
Yoldiabukta, Isfjorden, Spitsbergen (Włodarska-Kowalczuk et al. 1999)	*Yoldiella fraterna*	—
Hornsund, unpublished data	*Portlandia arctica*	*Ennucula tenuis, Ciliatocardium ciliatum*
van Mijenfjorden, Svalbard (Gulliksen et al. 1985, Renaud et al. 2007)	*Portlandia arctica, Yoldiella solidula*	*Macoma calcarea*
Jørgen Brønlund Fjord, North Greenland (Schiøtte 1989)	*Portlandia arctica*	*Hiatella arctica*
Scoresby Sund, Greenland (Thorson 1934)	*Portlandia arctica*	*Astarte crenata, Bathyarca glacialis*
Young Sound, East Greenland (Sejr et al. 2000)	—	*Astarte* spp., *Hiatella arctica*

sedimentation disturbance. In Kongsfjorden, the mollusc numbers are ten times higher in glacial bays than in the stable sediments of the central basin because of the high abundance of a few species of *Yoldiella* and *Thyasira*. Protobranch bivalves are the most common dominants in the sediments influenced by either glacial or glaciofluvial inputs in several other Arctic and sub-Arctic sites, whereas suspension feeding bivalves *Astarte, Hiatella* and *Bathyarca* seem to prefer the outer basins of fjords of high latitude (Table 6). Several *Yoldiella* species (*Y. intermedia, Y. fraterna* and *Y. lenticula*) were also reported as pioneer species populating defaunated sediments in succession following the onset of deglaciacion in late Pleistocene shelf sediments off the coast of northern Norway (Thomsen & Vorren 1986). This pioneer community was later replaced by an "established low-Arctic community" comprising *B. glacialis, Astarte crenata, Frigidoalavania janmayeni, T. gouldi* and *A. groenlandica* (Thomsen & Vorren 1986). The common features of yoldiid and thyasirid bivalves successful in glacial bays include small, simple, smooth and thin shells with no external ornamentation, which facilitate movement and the maintenance of the proper position in unstable quickly accumulating sediments (Rhoads 1974). Yoldiid bivalves possess a large and muscular foot and are known to move into and through a soft substratum (Yonge 1939). They collect detritus particles from the sediment surface with the use of long palp proboscides, and can very efficiently sort the particles (Stasek 1965). The efficient mechanism of elimination of pseudofaeces protects the respiratory organs of protobranch bivalves from being clogged by mineral particles accumulating in the mantle cavity (Rhoads 1974). All of these traits of yoldiid bivalves (small size, high mobility, selective deposit feeding and the efficient elimination of mineral particles) obviously facilitate their survival in glacial bays. What makes thyasirids well-suited to high sedimentation and instable sediments is less clear. Some *Thyasira* species construct a complicated system of mucus-lined tunnels, host symbiotic chemoautotrophic bacteria and are nutritionally dependent on hydrogen sulphides in sediments (Dando & Southward 1986; Dando & Spiro 1993). The Spitsbergen fjordic sediments are well oxygenated (Jorgensen et al. 2005), and the local thyasirids must depend on energy sources other than energy derived from the oxidation of sulphur compounds. The high sedimentation does not favour the construction of stable tunnels. The life habits of the Kongsfjorden thyasirid dominant species must differ from those of the temperate Atlantic species described by Dando & Southward (1986) and Dando & Spiro (1993).

The dominants in two Kongsfjorden glacial bays are different, although closely related: *Y. solidula* and *T. dunbari* in Kongsbreen glacial bay (*G1*) and *Y. hyperborea, A. orbiculata* and *T. gouldi* in Blomstrandbreen glacial bay (*G2*). The Blomstrandbreen glacial bay is located closer to the fjord mouth and has a much higher concentration of organic matter in the sediments than the sediments of Kongsbreen glacial bay (Włodarska-Kowalczuk & Pearson 2004). Włodarska-Kowalczuk et al. (1998) reported the similar separation of protobrach bivalves in a survey of six west Spitsbergen glacial bays—*Y. hyperborea* domination in two locations situated at either the open coast or close to the fjord mouth and *Yoldiella solidula* (erroneously identified as *Yoldiella fraterna*) in four sites situated in inner fjord basins. Ockelmann (1958) suggested that *Y. hyperborea* has fairly high energetic demands and therefore occurs primarily at either the open coast or in the outer parts of the fjords, where the supply of organic matter is larger than in the inner fjord basins. Domination by *Y. hyperborea* was reported for open shelf waters influenced by the terrigenous inflows off Svalbard (Włodarska et al. 1996), as well as off southern Greenland and Iceland (Peres 1982). Similarly, *T. gouldi* was reported to occur in large numbers in Chukchi Sea shelf sediments (Feder et al. 1994), and may be less suited to survival in inner basin glacial bay sediments that are poor in organic matter.

The yoldiid and thyasirid bivalves occurred at most stations with soft bottoms in Kongsfjorden, but it was only in glacial bays that these species were found in large numbers. In central basins, in stable conditions with low inorganic sedimentation, the bivalves are replaced by numerous tube-building polychaetes (*Maldane sarsi* and *Spiochaetopterus typicus*; Włodarska-Kowalczuk & Pearson 2004). The same pattern is observed in Canadian fjords: *Portlandia arctica* is present in large numbers only near glaciers and is much less numerous in central and outer fjord basins inhabited by Maldanid association (Syvitski et al. 1989; Aitken & Fournier 1993). The dense populations of tube-building polychaetes can diminish the numbers of mobile burrowers as a result of the competition for space and food (Wilson 1991). The experimental removal of tube builders results in the dramatic increase in numbers of mobile detritus feeders (Woodin 1974). The high densities of protobranch and thyasirid bivalves in glacial bays may result from the competitive release, as the tube builders are naturally eliminated by high sedimentation and the deposition of mineral material. The weak competitive capabilities of Protobranchia were expressed in the evolutionary history of the group. Protobranchia are numerically dominant and are the most diverse deep sea bivalves known at present (Allen & Sanders 1996). During the Mesozoic the Atlantic Protobranchia migrated to the deep sea as a consequence of competitive exclusion by the eulamellibranch bivalves radiating at that time in shallow waters (Allen 1978).

The patterns of mollusc distribution at the soft bottom and diversity in Kongsfjorden are not fully consistent with those of the whole macrobenthic community described by Włodarska-Kowalczuk et al. (2005). The main discontinuity in patterns of both complete macrobenthos and mollusc species distribution separates the glacial bays and central basin stable sediments, but the dramatic species diversity cline towards the glaciers described for the whole macrofauna was not observed in mollusc assemblages. The high increase of numbers of individuals in assemblages near glaciers was also a pattern unique to molluscs. The taxonomic distinctness showed the contrasting patterns along the glacial sedimentation gradient. *avTD* drops for molluscs, but increases for the whole macrobenthic community the closer one gets to the glacier. It is noteworthy that the discrepancies in taxonomic distinctness patterns for different taxonomic groups may result from different responses to environmental gradients, but also from differences in the hierarchical taxonomic systems of different phyla (Ellingsen et al. 2005). Smith (2005) observed the high correlation of mollusc diversity and the overall benthic community diversity on rocky shores, and recommended using molluscs as surrogates for complete macrobenthic communities in benthic diversity and impact assessment studies. However, the molluscs of the soft bottom seem to react to glacial disturbance in a different way than do other benthic phyla and I would not recommend molluscs as a useful surrogate for the whole macrobenthic community in surveys of sedimentary habitats.

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Appendix

List of mollusc species found in materials collected in Kongsfjorden in 1996–2000.

CAUDOFOVEATA
CHAETODERMATIDAE
Chaetoderma nitidulum Lovén, 1844
POLYPLACOPHORA
LEPTOCHITONIDAE
Leptochiton arcticus (Sars, G.O. 1878)
Leptochiton alvelous (Lovén, 1846)
ISCHNOCHITONIDAE
Tonicella marmorea (Fabricius, O. 1780)
Tonicella rubra (Linné, 1767)
Ischnochiton albus (Linné, 1767)
GASTROPODA PROSOBRANCHIA
FISSURELLIDAE
Puncturella noachina (Linné, 1771)
LOTHIDAE
Erginus rubellus (Fabricius, O. 1780)
LEPETIDAE
Lepeta caeca (Müller, 1776)
TROCHIDAE
*Margarites costali*s (Gould, 1841)
Margarites groenlandicus (Gmelin, 1791)
Margarites helicinus (Phipps, 1774)
Margarites olivaceus Brown, 1827
Solariella varicosa (Mighels & Adams, 1842)
TURBINIDAE
Moelleria costulata (Møller, 1842)
RISSOIDAE
Frigidoalvania janmayeni (Friele, 1878)
Frigidoalvania cruenta (Odhner, 1915)
Boreocingula castanea (Møller, 1842)
ELACHISIMIDAE
Elachisina globuloides (Warén, 1972)
TURRITELLIDAE
Tachyrhynchus reticulatus (Mighels & Adams, 1842)
NATICIDAE
Euspira pallida (Broderip & Sowerby, G.B. 1829)
Cryptonatica affinis (Gmelin, 1791)
MURICIDAE
Trophon clathratus (Linné, 1767)
Boreotrophon truncatus (Ström, 1767)
BUCCINIDAE
Buccinum undatum (Linné, 1758)
Buccinum scalariforme, Møller, 1842
Buccinum glaciale Linné, 1761
Buccinum polare Gray J.E., 1839
Colus kroeyeri (Møller, 1842)
Colus sabini (Gray, 1824)
CANCELLARIDAE
Admete viridula (Fabricius, O. 1780)
CONIDAE
Oenopota pyramidalis (Ström, 1788)
Oenopota exarata (Møller, 1842)
Oenopota impressa (Mørch, 1969)
Oenopota nobilis (Møller, 1842)
Oenopota sp
GASTROPODA HETEROBRANCHIA
MATHILDIDAE
Turitellopsis stimpsoni (Stimpson, 1851)
PYRAMIDELLIDAE
Menestho albula (Fabricius, O. 1780)
Menestho truncatula Odhner, 1915
GASTROPODA OPISTHOBRANCHIA
DIAPHANIDAE
Diaphana sp
RETUSIDAE
Retusa sp.
PHILINIDAE
Philine sp.
CYLICHNIDAE
Cylichna cf *alba* (Brown, 1827)
Cylichna cf *occulta* (Mighels & Adams, 1842)
BIVALVIA
NUCULIDAE
Ennucula tenuis (Montagu, 1808)
NUCULANIDAE
Nuculana pernula Müller, 1779
Nuculana minuta (Müller, 1776)
YOLDIIDAE
Yoldia hyperborea Torell, 1859

Yoldiella solidula Warén, 1989
Yoldiella lucida (Lovén, 1846)
Yoldiella lenticula (Møller, 1842)
Yoldiella frigida (Torell, 1859)
Yoldiella intermedia (Sars, M. 1865)
Portlandia arctica (Gray, 1824)
MYTILIDAE
Crenella decussata (Montagu, 1808)
Musculus corrugatus (Stimpson, 1851)
Musculus discors (Linné, 1767)
Dacrydium vitreum (Møller, 1842)
ARCIDAE
Bathyarca glacialis (Gray, J.E. 1824)
PECTINIDAE
Chlamys islandica (Müller, O.F. 1776)
PROPEAMUSSIIDAE
Arctinula groenlandica (Sowerby, G.B. 1842)
THYASIRIDAE
Axinopsida orbiculata (Sars, G.O. 1878)
Thyasira gouldi (Philippi, 1845)
Thyasira dunbari Lubinsky, 1976
Thyasira sp. n. (Bouchet & Warén, 1979)
UNGULINIDAE
Diplodonta torelli Jeffreys, 1847
KELLIDAE
Kellia sp.
MONTACUTIDAE
Montacuta maltzani Verkrüzen 1876
Montacuta spitzbergensis Knipowitsch, 1901
Mysella sovaliki MacGinitie, 1959
ASTARTIDAE
Astarte crenata (Gray, 1824)
Astarte borealis (Schumacher, 1817)
Astarte elliptica (Brown, 1827)
Astarte montagui (Dillwyn, 1817)
CARDIDAE
Ciliatocardium ciliatum (Fabricius, O. 1780)
Serripes groenlandicus (Bruguière, 1789)
TELLINIDAE
Macoma moesta Deshayes, 1855
Macoma calcarea (Gmelin, 1791)
VENERIDAE
Liocyma fluctuosa (Gould, 1841)
MYIDAE
Mya truncata Linné, 1758
HIATELLIDAE
Hiatella arctica (Linné, 1767)
THRACIIDAE
Thracia myopsis Møller, 1842
Thracia devexa Sars, G.O. 1878
LYONSIIDAE
Lyonsia arenosa (Møller, 1842)
PANDORIDAE
Pandora glacialis Leach, 1819
CUSPIDARIIDAE
Cuspidaria subtorta (Sars, G.O. 1878)
Cuspidaria arctica (Sars, M. 1859)