Soft bottom community structure and diversity in Kongsfjorden (Svalbard)

J. Laudien[1*], M. Herrmann[2] and W.E. Arntz[1]

1 Alfred Wegener Institute for Polar and Marine Research, P.O. Box 120161, 27515 Bremerhaven, Germany

2 Leibniz Institute of Marine Sciences at Kiel University (IFM-GEOMAR), Wischhofstr. 1-3, 24148 Kiel, Germany

*E-mail: jlaudien@awi-bremerhaven.de

Introduction

Marine diversity is currently one of the most studied topics in ecology especially under the frame of global and regional environmental changes. In the marine realm biodiversity declines from the tropics to the Arctic (Thorson 1957, Brattegard & Holthe 1997, Roy *et al*. 1996, 1998, Gray 2001). Habitat and environmental heterogeneity generally favour biodiversity; additionally, intermediate physical disturbance enhances heterogeneity (Connell 1978, Connell & Keough 1985, Zacharias & Roff 2001). Shallow water systems are particularly interesting, because they are affected by environmental changes first and act as small-scale laboratories (Dayton 1990, Arntz *et al.* 1997). In marine polar habitats a common structuring disturbance is ice scouring (Dayton 1990, Gutt 1991, Dowdeswell & Forsberg 1992, Dayton *et al.* 1994, Gutt *et al.* 1996, Conlan *et al.* 1998, Sahade *et al*. 1998, Gutt & Piepenburg 2003). Hereby the benthic community is affected differently varying with latitude, depth, local current regimes, substrates, geography and site exposure resulting in a high variability both on spatial and temporal scales.

In northwest Spitsbergen five tidewater glaciers calve icebergs (incl. bergy bits *sensu* Armstrong *et al.* 1966) into the Arctic glacial Kongsfjorden (Liestøl 1988, Dowdeswell & Forsberg 1992). When icebergs contact the sea floor, scouring and associated sediment reworking takes place, which has been recognized as strongly affecting the local benthic fauna distribution and diversity (e.g., Holte *et al.* 1996, Wlodarska *et al.* 1996). The benthic soft bottom fauna inhabiting such dynamic areas has been described from a number of glacial or glaciofluvial fjords of Spitsbergen (e.g., Gromisz 1983, Gulliksen *et al.* 1984, Kendall-Aschan 1993, Wlodarska *et al.* 1996, Holte *et al.* 1996, Wlodarska-Kowalczuk *et al.* 1998). However, data on depths shallower than 25m are scarce and only cover Hornsund and Skoddebukta (Gromisz 1983, Wlodarska *et al*. 1996). Community analyses from Kongsfjorden start at 50m depth (Wlodarska-Kowalczuk *et al*. 1998).

The present study encompasses six different depth zones of a soft-sediment biotope and compares the macrobenthic communities for taxonomic and zoogeographical composition, biomass and diversity as well as feeding modes of dominant species. Variations in faunal associations are detected by cluster analysis of similarity from abundance and biomass data. Assuming that diversity is affected by iceberg scouring and in accordance with the 'intermediate disturbance hypothesis' (Connell 1978) depth zones affected by moderate iceberg scouring should show enhanced heterogeneity. In contrast areas of high scouring frequencies should host pioneer, physically controlled macrofaunal assemblages whereas more mature, less diverse communities should dominate areas of low disturbance frequency.

Material and methods

Study area

The study area, Brandal (78°58.53'N, 11°51.35'E), is situated in the inner part of the Arctic glacial Kongsfjorden on the western coast of Spitsbergen. It is located on the northeastern fringe of the Brøgger Peninsula, which forms the southern coast of Kongsjord. The latter is 20km long, its width varies from 4km to 10km at the mouth between Kvadehuken and Kapp Guissez. Maximum depth is close to 350m, and the outer part of the fjord connects directly with the North Atlantic Ocean via the Kongsfjord-Renna trough (Bluhm *et al.* 2001, Jørgensen & Gulliksen 2001, Svendsen *et al.* 2002).

The range of the semidiurnal tides is from 1.5 to 2m with weak currents. Mean sea surface temperature is just above 0°C, but can rise to 6°C in summer, while the temperature at 20m is 3.6°C (Bluhm *et al.* 2001). During summer the 34 psu isohaline may reach 5m depth. A review of the physical environment was presented in Svendsen *et al.* (2002; see also Hanelt *et al.;* this issue), the marine ecosystem is reviewed in Hop *et al.* (2002).

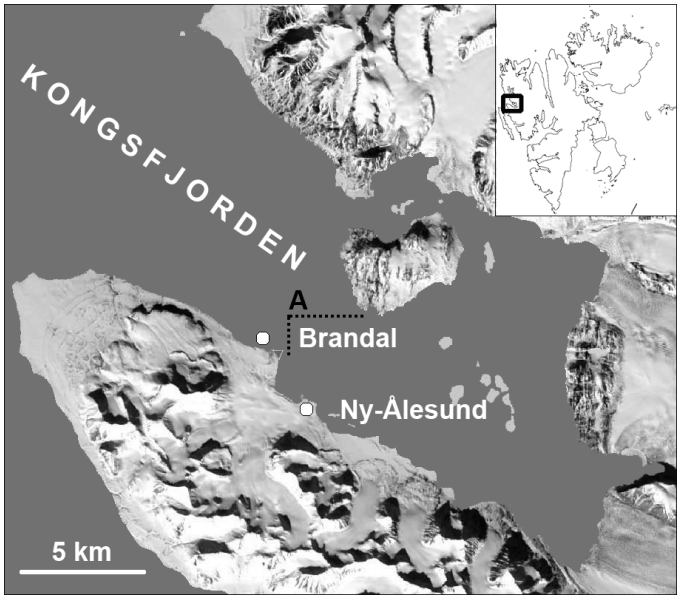

Fig. 1: Landsat TM image of Kongsfjord on Spitsbergen, (Svalbard archipelago) (modified from Svendsen *et al.* 2002). The study site Brandal, the village Ny-Ålesund and transect A of Dowdeswell and Forsberg (1992, see Discussion) are indicated.

Brandal (Fig. 1) is a soft-sediment habitat. The bottom inclines only gradually within the first 50m from the beach, followed by a steeper slope. Sediments are composed of a sand-clay mixture and are apparently well aerated. Occasionally ice-rafted stones overgrown by macrofauna and macroalgae (e.g. *Laminaria digitata*, *Palmaria palmata*) can be found.

Macrofauna

Macrozoobenthos was sampled in five replicates along six transects (5m, 10m, 15m, 20m, 25m, 30m) by pressing a corer of 20cm in diameter 20cm deep into the substrate. The enclosed sediment was sucked with an airlift system consisting of a tube (6cm in diameter, 80cm long with a n-end at the upper end), a compressed-air injection device coupled to a dive tank and a connected 0.5mm mesh retaining bag. All remaining material was sorted in the laboratory and animals preserved in 70% ethanol.

Thereafter all macrofaunal organisms were sorted using a binocular microscope, identified and counted. Biomass was estimated from a preserved subsample by weighing after blotting on filter paper, including valves of shelled organisms. Thereafter sub-samples were dried to constant mass at 60°C, weighed again and ignited in a muffle furnace at 500°C for 24h in order to es-

timate ash free dry mass (AFDM). Percentages of animals in the total faunal abundances were calculated for the five different depth zones separately. Shannon-Wiener diversity indices (H', Log e) were calculated for abundance values for each sample. Multivariate analysis was applied using the *PRIMER v5* package (Clarke & Gorley 2001). Data were square root transformed and Bray-Curtis similarities calculated. Classification (using group average linking) of samples was performed and groups of samples distinguished based on the resultant dendrogram. Statistical differences were analysed by means of an analysis of similarity (one-way ANOSIM, 95% confidence interval, Clarke & Gorley 2001). Species with the highest frequency (>75%) and significant dominance (>1%) within a group were identified as characteristic of that group using SIMPER (Clarke & Gorley 2001).

Results

Figure 2 shows that the number of cores taken was sufficient to detect >90% of the soft bottom fauna as the species-accumulation curves (*sensu* Gray 2001) flattened out at three to four cores. Annelids made up 79%, molluscs 11%, crustaceans 8%, echinoderms 1%, others (including priapulids, sipunculids, anthozoans and ascidians) made up less than 1% of 45 species and the additional 18 families not identified further. Regarding the number of individuals, annelids made up 84% of the fauna, molluscs 10%, crustaceans 3%, echinoderms 1% and others <2%. All taxa and their biomasses are listed in Table 1. Eleven species inhabited the complete depth range. The majority of all individuals of amphipods (80%) occurred at 5m. The bivalve *Cyrtodaria siliqua* was only collected at the shallow transect. In contrast the bivalve *Ciliatocardium ciliatum*, the gastropod *Oenopota* sp. and the polychaetes *Amphitrite cirrata* and *Orbinia* sp. were only present at 30m. At 5m the dominant species were: *Crassicorophium crassicorne* (32%) and *Spio armata* (26%). *Scoloplos armiger* (11-22%) and *Dipolydora quadrilobata* (14-31%) dominated all other depth zones, *Euchone analis* 10m and 15m (10%, 14%), *Spio armata* 10m, 20m-30m (11-14%) and *Chaetozone setosa* 20m-30m (11-14%). Five species were classified as Arctic species, 34 as Arctic-boreal, and 20 as cosmopolitans, 3 taxa were not classified. At all depths the zoogeographical species composition was very similar, with around 8% Arctic representatives, 58% Arctic-boreal, and 34% cosmopolitans. Comparable biogeographical relationships have been found for macroalgae of Kongsfjorden (Wiencke *et al*.; this issue).

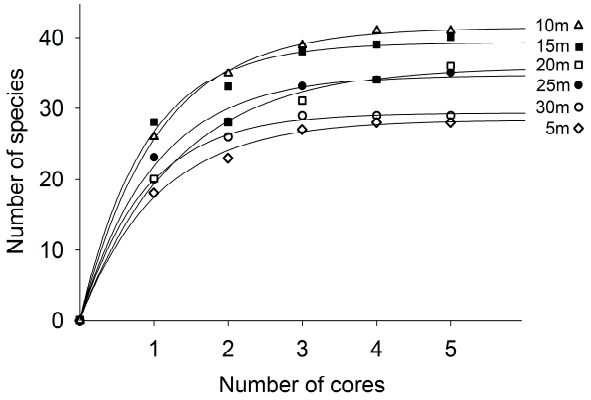

Fig. 2: Species-accumulation curves of six depths (5-30m) showing that curves flatten out at three to four cores.

The total mean faunal abundance was 6296 ind. m^{-2}. The lowest value was recorded at the shallowest transect with 2260 ind. m^{-2} (28 species), followed by the deepest transect with 5443 ind. m^{-2} (29 species), intermittant depths showed higher abundances and species richness (10m: 5969 ind. m^{-2}, 42 species; 15m: 8802 ind. m^{-2}, 41 species; 20m: 6781 ind. m^{-2}, 36 species; 25m: 8521 ind. m^{-2}, 35 species) (Figure 3, Table 1). Significant differences in species richness were detected between the 5m and the 10 and 15m station, respectively (ANOVA $p<0.05$). The diversity ranged between 1.85 (0.28 SE) at 25m and 2.19 (0.29 SE) at 10m, overall diversity was 2.06 (0.12 SE). Highest evenness was found at 5m (0.82 ± 0.01 SE) and lowest at 25m (0.67 ± 0.02 SE). Biomass ranged between 3.5 g m^{-2} (5m) and 25.0 g m^{-2} (15m) AFDM.

Cluster analysis both of abundance and biomass data showed that the samples from 5m depth differed greatly from the rest. The latter formed two subgroups: the medium depth stations (10m-20m) and the deeper stations (25m, 30m) (Fig. 4, dendrogram for biomasses looks similar, not shown).

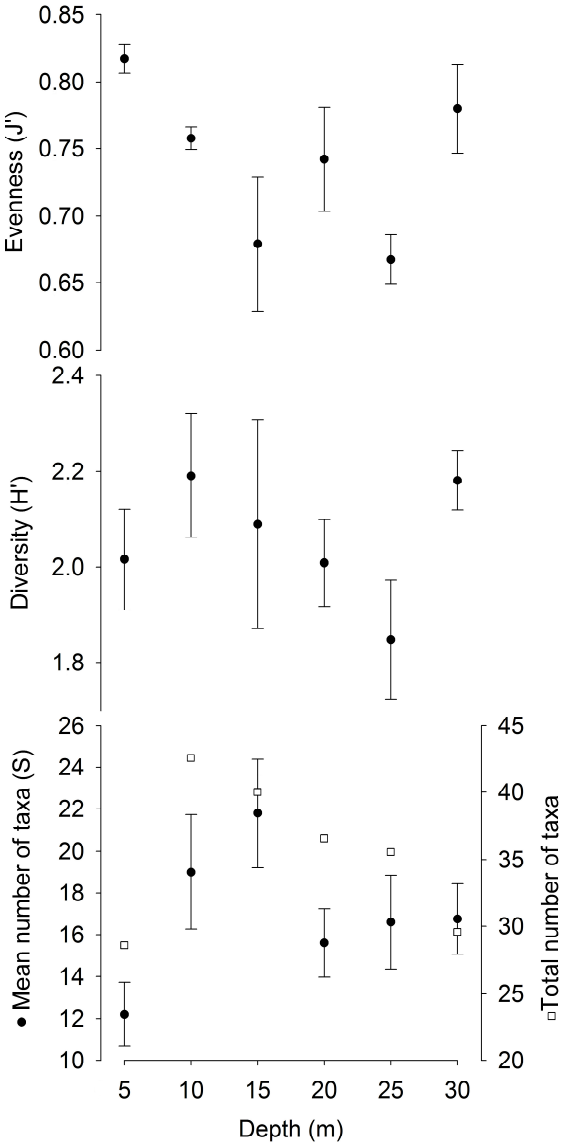

Fig. 3: Mean (●) and total (□) number of taxa, Shannon diversity (H', Log e) and Evenness (J') of soft bottom macrobenthos at six different depths (5m-30m) of the soft-bottom habitat Brandal (Kongsfjord, Spitsbergen).

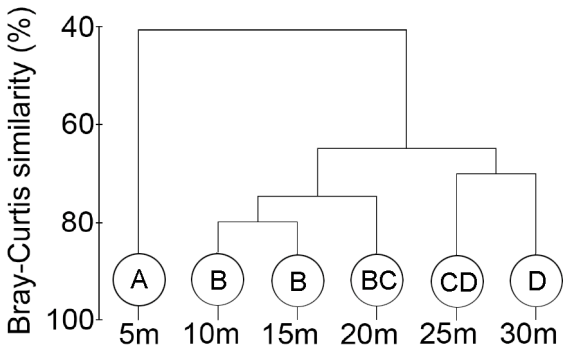

Fig. 4: Dendrogram resulting from cluster analysis of Bray-Curtis similarities using abundance data of soft bottom macrobenthos. Depth zones sharing a letter do not differ significantly (one-way ANOSIM, $p<0.05$).

Table 1 Mean abundance (A, ind. m^{-2}) and biomass (B, g AFDM m^{-2}), n.d. = not determined

	5m		10m		15m		20m		25m		30m	
Taxon	A	B	A	B	A	B	A	B	A	B	A	B
PRIAPULIDA												
Priapulus caudatus[1]			21	0.085	10	0.042	21	0.085	21	0.085		
SIPUNCULIDA												
Sipunculida indet.					10	n.d.						
ANTHOZOA												
Edwardsia fusca[1]			63	8.682	10	1.447	10	1.447				
MOLLUSCA												
Astarte borealis									10	3.104		
Astarte sulcata[1]	21	0.075	21	0.075	31	0.113	10	0.038				
Axinopsida orbiculata[1]	10	0.003	10	0.003	271	0.073	10	0.003	302	0.081	326	0.087
Chaetoderma nitidilum[1]									10	n.d.		
Ciliatocardium ciliatum											13	n.d.
Crenella decussata[1]	21	0.001	313	0.148	448	0.196	73	0.051	156	0.077	273	0.129
Cryptonatica affinis[1]			10	0.012	21	0.024						
Cylichna cf *arctica*[1]	52	0.060	21	0.024	73	0.083	52	0.060	10	0.012	26	0.030
Cyrtodaria siliqua[2]	52	0.040										
Hiatella rugosa[2]	42	0.635	52	0.005	135	0.040	115	0.203			39	0.005
Liocyma fluctuosa[1]	73	0.378	10	0.054	10	0.054	10	0.054				
Macoma sp.			31	0.035	31	0.035	21	0.023	52	0.058	13	0.014
Montacuta sp.[1]	94	0.011					42	0.029			78	0.008
Oenopota simplex[1]	42	0.048	21	0.024	10	0.012	10	0.012				
Oenopota sp.											26	0.030
Polinices pallidus									10	0.012	13	0.015
Serripes groenlandicus[1]			31	0.882	42	1.176	10	0.294	31	0.882		
Thracia septentrionalis[2]	10	0.002	10	0.002	10	0.002			10	0.002	13	0.003
POLYCHAETA												
Ampharete cf. *baltica*[2]					42	0.045	31	0.034	229	0.249	378	0.410
Amphitrite cirrata											13	1.679
Apistobranchus tullbergi[1]					10	n.d.			10	n.d.	65	n.d.
Brada villosa[1]			52	0.117	21	0.298	10	0.006	31	0.005		
Chaetozone setosa	10	0.004	354	0.151	531	0.351	635	0.572	781	0.234	469	0.141
Chone sp.[1]					10	0.073	42	0.291	52	0.363		
Dipolydora quadrilobata[1]	73	0.012	1188	0.198	2344	0.390	1906	0.317	3583	0.596	2018	0.336
Eteone spetsbergensis[1]			10	0.127								
Eteone flava[1]			94	0.247	198	0.668	198	0.623	135	0.397	117	0.344

Table 1 continued

Taxon	5m, A	B	10m, A	B	15m, A	B	20m, A	B	25m, A	B	30m, A	B
Euchone analis[1]	167	0.435	1031	1.278	1000	1.039	365	0.540	167	0.208	117	0.146
Glycera capitata							10	n.d.				
Lumbrineris sp.	10	0.133	73	0.933	83	1.066	31	0.400	146	1.865	130	1.665
Maldanidae 1 indet.*									31	0.299		
Maldanidae 2 indet.			177	1.692	417	3.982	271	2.588	188	1.792	65	0.622
Marenzelleria wireni[2]	10	0.017	10	0.017								
Ophelia limacina	10	n.d.	52	n.d.	42	n.d.			21	n.d.		
Ophelina sp.	10	n.d.	83	n.d.	63	n.d.	10	n.d.	73	n.d.	39	n.d.
Orbinia sp.[2]											13	0.259
Paraonidae indet.									10	n.d.		
Phyllodoce groenlandica[1]			52	1.935	42	1.781	10	0.393				
Polynoinae indet.			31	0.098	21	0.065					13	0.041
Praxillella praetermissa[1]	10	n.d.	31	n.d.			21	n.d.				
Scalibregma inflatum	21	0.121	21	0.121			10	0.060	10	0.060	39	0.227
Scoloplos armiger	83	0.138	1271	2.097	1927	1.985	1906	2.217	1167	0.612	534	0.280
Sigalionidae indet.					21	0.344	10	0.172			13	0.215
Spio armata[1]	365	0.317	385	0.335	323	0.281	750	0.652	1083	0.942	508	0.442
Spio filicornis[1]			10	0.028	10	0.028	21	0.056	42	0.111		
Travisia forbesii[1]	115	0.699	156	0.783	167	0.349	63	0.082	42	0.019	13	0.006
CRUSTACEA												
Anonyx nugax[1]	63	0.167	10	0.066					10	0.066	26	0.165
Crassicorophium crassicorne[1]	729	0.079	10	0.001								
Onisimus edwardsi[1]	31	0.009			10	0.003	10	0.003	21	0.006		
Paroediceros lynceus[1]	42	0.066	10	0.016								
Protomedia sp.[1]	42	0.013	10	0.003			21	0.006			52	0.016
Priscilla armata[2]	52	0.011	10	0.002								
Monoculodes sp.									31	n.d.		
Ischyrocerus megalops			10	0.003	21	0.007						
Synidothea nodulosa[1]			21	0.048	31	0.071			21	0.048		
Sclerocrangon boreas									10	1.65		
ECHINODERMATA												
Chiridota laevis			31	1.936	104	6.442	21	1.290				
Holothurioidea indet.					10	n.d.						
Ophiura robusta			135	0.801	208	1.232	31	0.185	10	0.062		
ASCIDIACEA												
Pelonaia corrugata			21	0.830	31	1.246	10	0.415				

[1] taxon not reported for Kongsfjord or [2] for Svalbard according to Gulliksen *et al*. (1999)

*most likely *Praxillella praetermissa* (A. Bick, Univ. Rostock, pers. comm.)

Discussion

The species list presented includes 63 taxa, of which 30 were not reported for Kongsfjorden and seven not for Svalbard yet. The remaining 32 taxa make up a rather low proportion (16%) of the entire benthic Kongsfjorden macroinvertebrates summarised by Gulliksen *et al*. (1999) and comprising almost 200 invertebrates. Both the analyses of only a single biotope (sand-clay bottom 5m-30m deep), and the small sample area do not permit the presentation of a complete description of the soft bottom benthos of Kongsfjorden. However, the aim of this study was to reveal differences in the diversity between depth zones differently impacted by ice-scouring. Only some of the abundant species found in the present study were also reported from a study conducted on deeper soft bottom macrofauna at Kongsfjorden (50-70m, Wlodarska-Kowalczuk *et al*. 1998). In both surveys the bivalve *Axinopsida orbiculata* was present in lower abundances. The values of *Chaetozone setosa* and *Paraonidae* indet. at 25m (781 and 10 ind. m^{-2}) are in good accordance with the value of 739 and 11 ind. m^{-2} respectively found by Wlodarska-Kowalczuk *et al*. (1998). Our values of *Eteone flava* and *Lumbrineris* sp. exceed the abundance of *Eteone longa* and *Lumbrineris fragilis* given by the deeper study. The bivalves *Macoma* sp. and *Liocyma fluctuosa* were found in the present study, although they were absent in the previous survey of Kongsfjorden, but found in Julibukta, Skoddebukta and Bettybukta (Wlodarska-Kowalczuk *et al*. 1998). This could be due to the distance of the sample location to the glacier front as the present study area was located approximately 8.5 nautical miles (nm) from the front, while the previous Kongsfjorden study was carried out up to 1nm from the glacier. In contrast the three other fjords were sampled up to 2nm, 1.9nm and 2.5nm, respectively from the front. Svendsen *et al.* (2002) measured the highest flux of particulate inorganic matter (PIM, 800 g m^{-2} d^{-1}) in front of the Kongsbreen glacier. The value successively declined with distance and was lower than 20g m^{-2} d^{-1} at 5.5nm from the front. Inorganic material is particularly stressful to suspension feeders, affecting their feeding by clogging of filtering organs (e.g., Moore 1977). Therefore sedimentation can have a significant effect on the distribution of these bivalves. Likewise the polychaetes *Ophelina* sp. and *Maldanidae* 1 indet. (only parts available, most likely belonging to *Praxillella praetermissa*, A. Bick, pers. comm.) were found in the present study and in fjords sampled in maximal distances ranging between 1.7 and 4nm from the glacier front (Wlodarska-Kowalczuk *et al*. 1998). Similar patterns were found for benthic decapod fauna in front of the South Patagonian Icefield (Mutschke & Gorny 1999). Accordingly, in Potter Cove (King George Island, South Shetlands) the benthic communities are dominated by ascidians, which are able to flush their filtration unit by contraction and therefore substitute sponges not being able to clean their filtering chambers (Sahade *et al*. 1998).

Polychaete worms and molluscs dominated the fauna, both in number of species (28 and 18) and individuals (4544 and 820 ind. m^{-2}). Crustaceans occurred only in lower numbers (10 species, 78 ind. m^{-2}). While the same proportions for annelids and molluscs were found by Wlodarska-Kowalczuk *et al*. (1998), they observed a lower percentage of crustaceans (annelids : molluscs : crustaceans = 8 : 5 : 1 as opposed to 8 : 5 : 2.9 in the present study). Similarly Holte *et al*. (1996) found low proportions of crustaceans in Gronfjord and Adventfjord and Görlich *et al*. (1987) in glacier-impacted parts of Hornsund. As the identified crustaceans are highly mobile organisms the results

of the previous fjord studies may be underestimations in presence and number as all samples were taken by grab-sampling. The SCUBA operated airlift may be a more adequate method for quantitative sampling of these species. Other methods like dredge sampling or underwater photography have also shown abundant populations of motile crustaceans and ophiuroid species (Syvitsky *et al.* 1989, Wlodarska *et al.* 1996) and support our results. The dominant species were surface detritivorous and suspensivorous polychaetes (*Dipolydora quadrilobata*, *Spio armata, Euchone analis*), the subsurface detritivorous polychaete *Scoloplos armiger* and the surface detritivorous and carnivorous amphipod *Crassicorophium crassicorne*. The previous study of Wlodarska-Kowalczuk *et al*. (1998) carried out closer to the glacier front (up to 1nm) and therefore in the area of higher impacts derived from sedimentation of PIM revealed that approx. 50% of the soft-sediment fauna was deposit feeding and sub-surface detritivorous, while this proportion declined in the present study (36%) and suspensivorous species increased from 14% (Wlodarska-Kowalczuk *et al*. 1998) to 27%. These findings agree well with the general trend of increasing dominance of deposit feeding infauna with a decreasing distance from the glacier front and increasing level of glacier activity (Farrow *et al*. 1983, Syvitsky *et al.* 1989, Holte *et al*. 1996, Wlodarska *et al.* 1996). These findings again can be explained with the higher load of PIM towards the glacier front and the unfavourable conditions for filter feeders. Our biomass values ranged between 51 and 248 g m^{-2} wet mass and 3.5 and 25.0 g m^{-2} AFDM, respectively. Kowalczuk *et al*. (1998) observed for their two Kongsfjorden samples 6 and 11 g m^{-2} wet formalin masses. These values are significantly lower than the present ones, which again can be explained by the different impacts of sedimentation on the communities sampled. Low faunal biomass near the glacier fronts has also been related to the scarcity of food available to subsurface detritivorous species as a consequence of low levels of primary production and the dilution of organic matter in the substrate by high sedimentation (Görlich *et al*. 1987). Furthermore, the different sampling technique (van Veen grab in their case) and the low sample number are also mentioned by Kowalczuk *et al*. (1998) to possibly result in some underestimation. Compared to hard-bottom areas from Kongsfjorden our biomass values are about one order lower than values (380-2300 g m^{-2} wet mass) estimated by Jørgensen and Gulliksen (2001). This is due to the relatively small size of soft-bottom fauna.

Table 2 Ranges of Shannon index (H', Log e), from different glacial or glaciofluvial Spitsbergen bays at sampling depths ranging from 2 to 80m, modified from Wlodarska-Kowalczuk *et al*. 1998 (1 Wlodarska-Kowalczuk *et al*. 1998, 2 Kendall-Aschan 1993, 3 Gromisz 1983, 4 Wlodarska *et al*. 1996, 5 Gulliksen *et al*. 1984, 6 Holte *et al*. 1996).

Site	Depth	H'
Kongsfjord (present study)	5-30	1.85-2.19
Kongsfjord (1)	50-70	1.49
Skoddebukta (1)	30-75	1.49-2.54
Yoldiabukta (1)	57-75	1.26-1.48
Julibukta (1)	30-50	2.22-2.30
Ekmanfjord (1)	30-55	2.22-2.31
Tempelfjord (1)	40-80	1.85-2.01
Bettybukta (1)	40-80	0.43-2.11
Sassenfjord (2)	30-95	2.6-2.9
Hornsund at Hyrnebreen (3)	5-53	0.7-1.38[a]
Hornsund at Storbreen (3)	18-37	1.2-2.07[a]
Skoddebukta (4)	2-60	0.38-2.49
Van Mijenfjord (5)	25-75	2-2.5[a]
Raudfjord (5)	25-75	2.7-3.2[a]
Adventfjord (6)	26-52	1.38-1.79

[a]Values taken from charts

Shannon diversity ranged between 1.85 and 2.19 with lower diversity at shallow depth and highest diversity at 10m. Our values are somewhat higher than the previous estimates (Kowalczuk *et al*. 1998), but corre-

spond well with results published from different Spitsbergen glacial or glaciofluvial bays (Table 2). Variations in diversity of similar habitats have been related again to differences in inorganic sedimentation levels (Kendall & Aschan 1993, Wlodarska *et al*. 1996). The differences in diversity along the depth range of the present study, where transects were located very close to each other (total distance between the 5m and 30m transects <100m) and differences in sedimentation level should have been negligible, must have another reason. Obviously the differences are related to water depth. Analysing the biodiversity of soft-bottom fauna from the Norwegian continental shelf Ellingsen (2002) found that species richness (for all 508 species pooled) was not correlated with depth or median grain size. However, the frequency and extent of disturbance due to iceberg scouring (which is related to water depth) might explain the observed differences in diversity: Iceberg depth can be calculated from observations of freeboard and given assumptions concerning the density and shape of the iceberg. Dowdeswell and Forsberg (1992) found that the frequency of icebergs along their transect A (Fig. 1) with a freeboard high enough to scour the ground at 5m was 17%, while 4% could ground at 10-15m depth and only 0.5% could scour below 21m (value taken from their Fig. 3). Thus, it is more probable that shallower areas are disturbed by scouring than deeper zones.

The 'intermediate disturbance hypothesis' (Connell 1978) may explain the observed species richness (Fig. 5). In situations where disturbance is minimal, species richness (SR_S *sensu* Gray 2000) is reduced because of competitive exclusion between species, which can explain the lower total number of taxa at 30m (29 species). With an increasing level or frequency of scouring — more icebergs ground in shallower areas, since the majority of icebergs is smaller — competition is relaxed, resulting in increasing species richness (intermittant depth zones: 35-42 species). At higher or more frequent levels of disturbance species start to be eliminated by stress (5m: 28 species) so that diversity falls again. Thus, it is at intermediate levels of scouring activity that species richness is highest. In the Antarctic icebergs are much bigger and therefore scouring impact reaches areas up to 400m depths. The results are however comparable: in the Antarctic habitat many different succession stages can be found in the same areas (Gutt & Piepenburg 2003) resulting in a very high diversity, but on a wider scale.

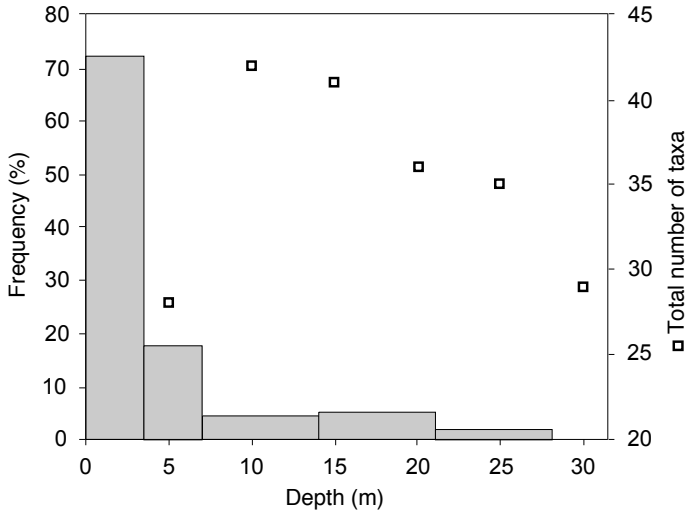

Fig. 5: Iceberg depth-frequencies (gray bars, calculated from Dowdeswell and Forsberg 1992, Fig. 3) and total number of soft-bottom taxa (□) from Brandal.

However, since our data is restricted to a small area within Kongsfjorden, future studies on a wider area are needed, including the direct quantification of disturbance resulting from scouring of icebergs from tidewater glaciers in Kongsfjorden, before generality can be attached to our findings.

Conclusions

63 macrobenthic taxa were found in the soft bottom habitat of Kongsfjorden (Svalbard), 30 of which had not been reported for Kongsfjorden and seven not for Svalbard before. Suspensivorous or surface and sub-surface detritivorous polychaetes and deposit-feeding amphipods were dominant. Only eleven of 45 species and an additional 18 families inhabited the complete depth range (the polychaetes *Dipolydora quadrilobata*, *Chaetozone setosa*, *Euchone analis*, *Lumbrineris* sp., *Ophelina* sp., *Scoloplos armiger*, *Spio armata, Travisia forbesii*, the bivalves *Axinopsida orbiculata* and *Crenella decussata,* and the opistobranch *Cylichna* cf *arctica*). Similarity clustering of samples showed a significant difference between the shallow station (5m) and the rest. The latter formed two subgroups, the medium depth stations (10m, 15m, 20m) and the deeper stations (25m, 30m). The biomass ranged from 3.5 to 25.0 g ash free dry mass m^{-2} and Shannon diversity was 2.06 (0.12 SE). Observed differences in diversity together with information on ice-scouring support the 'intermediate disturbance hypothesis'.

Acknowledgements

We are grateful to the scientific diving group of the Alfred Wegener Institute for Polar and Marine Research (AWI) for assistance during the sampling, especially to Tilman Alpermann, Saskia Brandt, José Velez and Dr. Michael Assmann. Our deepest thanks are due to Dr. Andreas Bick who was a great support in identifying polychaetes, Dr. Jørgen Berge who helped to identify amphipods and Dr. Jon-Arne Sneli with the molluscs. We are grateful to Dr. Eike Rachor and Prof. Dr. C. Wiencke for their comments on an earlier version of the manuscript.

References

Arntz WE, Gutt J, Klages M (1997) Antarctic marine biodiversity: an overview. In: B Battaglia, J Valencia, D Walton (eds) Antarctic communities. Proc 6th SCAR Biology Symposium, Venice 1994, Cambridge Univ Pr, Cambridge pp 3-14

Armstrong T, Roberts B, Swithinbank C (1966) Illustrated Glossary of Snow and Ice. Scott Polar Research Institute, Cambridge, pp 60

Bluhm B, Iken K, Laudien J, Lippert H (2001) German activity in cold water scientific diving, S.C. Jewett (ed.). Cold Water Diving for Science. Proceedings of the 21st Annual Scientific Diving Symposium, American Academy of Underwater Sciences. University of Alaska Sea Grant, AK-SG-01-06, Fairbanks pp 1-4

Brattegard T, Holthe T (1997) Distribution of marine, benthic macro-organisms in Norway. A tabulated catalogue. Preliminary edition. Research Report No. 1991-1 Directorate for Nature Management, Trondheim, Norway, pp 409

Clarke KR, Gorley RN (2001) PRIMER v5: User Manual/Tutorial, PRIMER-E: Plymouth.

Conlan KE, Lenihan HS, Kvitek RG, Oliver JS (1998) Ice scour disturbance to benthic communities in the Canadian High Arctic. Mar Ecol Prog Ser 166:1-16

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1303-1310

Connell JH, Keough MJ (1985) Disturbance and patch dynamics of subtidal marine animals on hard substrata. In: STA Pickett, PS White (eds) The ecology of natural disturbance and patch dynamics. Academic Press, Orleando pp 125-147

Dayton PK (1990) Polar benthos. In: WE Smith (ed) Polar Oceanography, part B: Chemistry, Biology and Geology. Academic Press, London pp 631-685

Dayton PK, Mordida BJ, Bacon F (1994) Polar marine communities. Amer zool 34:90-99

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

Ellingsen KE (2002) Soft-sediment benthic biodiversity on the continental shelf in relation to environmental variability. Mar Ecol Prog Ser 232:15-27

Farrow GE, Syvitsky 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

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

Gray JS (2000) The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. J Exp Mar Biol Ecol 250:23-49

Gray JS (2001) Marine diversity: the paradigms in patterns of species richness examined. Sci Mar 65(2):41-56

Gromisz S (1983) Bottom fauna communities of glacial bays situated at glaciers Hyrne and Stor (Spitsbergen-Hornsund) (in Polish). In: Polish Polar Research 1970-1982. Uniwersytet M Kopernika, Torún, pp 267-276

Gulliksen B, Holte B, Jakola KJ (1984) The soft bottom fauna in Van Mijenfjord and Raudfjord, Svalbard. In: J Gray, ME Christiansen (eds) Marine biology of polar regions and effects of stress on marine organisms. Wiley, Oslo, pp 199-215

Gulliksen B, Palerud R, Brattegard T, Sneli J-A (eds) (1999) Distribution of marine benthic macroorganisms at Svalbard (including Bear Island) and Jan Mayen. Research Report for DN 1999-4. Directorate for Nature Management, Trondheim: 1-148

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

Gutt J, Piepenburg D (2003) Scale-dependent impacts of catastrophic disturbances by grounding icebergs on the diversity of Antarctic benthos, Mar Ecol Progr Ser 253:77-83

Gutt J, Starmans A, Dieckman G (1996) Impact of iceberg scouring on polar benthic habitats. Mar Ecol Prog Ser 137:311-316

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 RJG, Lønne OJ, Zajaczkowski M, Falk-Petersen S, Kendall M, Wängberg S-A, Bischof K, Voronkov AY, Kovaltchouk NA, Wiktor J, Poltermann M, di Prisco G, Papucci C, Gerland S (2002) The marine ecosystem of Kongsfjorden, Svalbard. Polar Res 21(1):167-208

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

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

Lefauconnier B, Hagen JO, Rudant, JP (1994) Flow speed and calving rate of Kongsbreen glacier, 70°N Spitsbergen, Svalbard, using SPOT images. Polar Res 13:59-66

Liestøl O (1988) The glaciers of the Kongsfjorden area. Spitsbergen. Norsk Geografisk Tidsskrift 42:231-238

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

Mutschke E, Gorny M (1999) The benthic decapod fauna in the channels and fjords along the South Patagonian Icefield, Southern Chile. Sci Mar 63 (Suppl. 1):315-319

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

Roy K, Jablonski D, Valentine JW (1996) Higher taxa in biodiversity studies: patterns from eastern Pacific marine molluscs. Phil Trans Roy Soc London. Ser B 351:1605-1613

Roy K, Jablonski D, Valentine JW, Rosenberg G (1998) Marine latitudinal diversity gradients: tests of causal hypotheses. Proc Natl Acad Sci USA, 95:3699-3702

Sahade R, Tatián M, Kowalke J, Kühne S, Esnal GB (1998) Benthic faunal associations on soft substrates at Potter Cove, King George Island, Antarctica. Polar Biol 19:85-91

Svendsen H, Beszczynska-Møller A, Hagen JO, Lefauconnier B, Tverberg V, Gerland S, Ørbæk 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 fjord system in Svalbard. Polar Res 21(1):133-166

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

Thorsen G (1957) Treatise on Marine Ecology and Palaeoecology. In: JW Hedgpeth (ed) Mem Geol Soc Soc Amer, pp 461-534

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, Wesawski JM, Kotwicki L (1998) Spitsbergen glacial bays macrobenthos – a comparative study. Polar Biol 20:66-73

Zacharias MA, Roff JC (2001) Explanations of patterns of intertidal diversity at regional scales. J Biogeogr 28(4):471-483