

Soft bottom species richness and diversity as a function of depth and iceberg scour in Arctic glacial Kongsfjorden (Svalbard)

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Abstract Macrozoobenthic soft-sediment communities of central Arctic Kongsfjorden inhabiting six depth zones between 5 and 30 m were sampled using SCUBA-diving during June–August 2003 and analysed comparatively. About 63 taxa were found, nine of which had not been reported for Kongsfjorden and four for Svalbard. Suspension feeding or surface and sub-surface detritivorous polychaetes and deposit-feeding amphipods were dominant. Only 11 of the 63 taxa (45 species and additional 18 families not further identified) inhabited the complete depth range. Biomass ranged from 3.5 to 25.0 g ash free dry mass m^{-2} and mean Shannon diversity ($\log e$) was 2.06. Similarity clustering from abundance and biomass data showed a significant difference between the shallow station (5 m) and the rest. The latter formed two sub-groups (10–20 and 25–30 m). Depth is irrevocably correlated with ice-scouring. Thus the differences in diversity together with the predicted iceberg scour intensity support the ‘intermediate disturbance hypothesis’ indicating that habitats impacted by moderate iceberg scouring enable higher diversity. In contrast, biotopes frequently affected only host pioneer communities, while mature, less diverse assemblages dominate depths of low impact.

Keywords Biodiversity · Feeding modes · Ice-scouring · Intermediate disturbance hypothesis · Macrozoobenthos · Soft-sediment

Introduction

Descriptions of species assemblages and biodiversity are crucial to understand faunistic community modifications in the frame of global and regional environmental changes. Marine species diversity in the northern hemisphere generally declines from low to high latitudes (Thorson 1957; Brattegard and Holthe 1997; Roy et al. 1998; Gray 2001). However, environmental and biotope complexity may favour biodiversity on small scale. Furthermore, intermediate biological and physical disturbance increases diversity (Connell 1978; Connell and Keough 1985; Zacharias and Roff 2001). In this vein coastal shallow water communities are particularly attractive for biodiversity studies since these sites are primarily affected by environmental changes and serve as small-scale *in situ* laboratories (Dayton 1990; Arntz et al. 1997).

Shallow coastal communities within the polar range experience relatively constant temperatures and salinity, but have seasonal pulses of primary production and siltation. The light regime, currents and water depth are further structuring factors. Water depth is important (e.g. Gutt et al. 1999; Sahade et al. 1998; Barnes and Brockington 2003) however often superposed by other factors (Gulliksen and Svensen 2004) like therewith-connected iceberg scouring. As a disruptive force this has a huge structuring effect on benthic communities, both in the Antarctic (e.g. Conlan et al. 1998; Peck et al. 1999; Gutt 2001; Gutt and Piepenburg 2003) and the Arctic (e.g. Holte et al. 1996; Barnes 1999; Weslawski et al. 1999; Laudien et al. 2004). The

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impact on benthic communities varies, however, with latitude, geography, depth, site exposure, local current regimes and substrates reflected in a high variability both on temporal and regional scales.

The Arctic glacial Kongsfjorden (northwest Spitsbergen) receives icebergs (including bergy bits *sensu* Armstrong et al. 1966) calved from five tidewater glaciers (Liestøl 1988; Dowdeswell and Forsberg 1992) including Kongsbreen, which is the most active glacier in the Svalbard archipelago (Lefauconnier et al. 1994). Regularly, icebergs score the benthic realm leading to ploughing up of the sediment and thus strongly affecting the benthic faunal distribution and diversity in small-scale (e.g. Holte et al. 1996; Wlodarska et al. 1996). Benthic soft bottom communities populating these unstable bottoms at medium and deeper zones have been described from several glacial or glaciofluvial fjords of Spitsbergen (e.g. Gulliksen et al. 1984; Kendall and Aschan 1993; Wlodarska-Kowalczyk et al. 1998). However, information on benthic communities inhabiting grounds shallower than 25 m is scarce and covers Hornsund and Skoddebukta (Gromisz 1983; Wlodarska et al. 1996) whereas Sahade et al. (2004) analysed only soft sediment macroepifauna of shallow Kongsfjorden. Descriptions of macrozoobenthic infaunal communities of this fjord exist from areas exceeding 30 m depth, available for ship operations (Wlodarska-Kowalczyk et al. 1998, 2005; Kendall et al. 2003; Wlodarska-Kowalczyk and Pearson 2004). Shallow water soft bottom macrofaunal communities have only recently received attention but, were not sampled quantitatively (Kaczmarek et al. 2005).

With the present study we aim to quantitatively describe macrobenthic soft-sediment epi- and infaunal associations of six contiguous zones from 5 to 30 m. We compare the taxonomic and zoogeographical composition, biomass and diversity as well as feeding modes of the dominating species. Dissimilarities in communities are determined by cluster analysis using abundance and biomass data. Assuming that biodiversity is modulated by iceberg scouring and in line with the 'intermediate disturbance hypothesis' (Connell 1978), benthic habitats impacted by moderate iceberg scouring should enable higher diversity. In contrast, biotopes frequently affected by scouring should primarily host pioneer communities.

Materials and methods

Study area

Sampling was carried out at Brandal (78°58.53'N, 11°51.35'E), a site located in central, glacial Kongsfjorden (west coast of Spitsbergen, Arctic). The study area is situated on the north-eastern edge of the Brøgger Peninsula,

which forms the southern coast of the fjord. Kongsfjorden has an extension of 20 km in length and between 4 and 10 km (at the mouth between Kvadehuken and Kapp Guisez) in width. It reaches depths of ~350 m (on average 200–300 m). The fjord is directly connected with the North Atlantic Ocean via the Kongsfjord-Renna trough (Bluhm et al. 2001; Jørgensen and Gulliksen 2001; Svendsen et al. 2002).

Semidiurnal tides of the fjord system range between 1.5 and 2 m and only weak currents prevail. Mean sea surface temperature slightly exceeds 0°C, while maximal values may reach 6°C in summer; the temperature at the 20 m isobath is 3.6°C (Bluhm et al. 2001). During summer the 34 isohaline is located at 5 m depth. Icebergs and growlers are present throughout the year and rarely exceed 20 m in length or 5 m in height (Dowdeswell and Forsberg 1992). A comprehensive description of the physical environment can be found in Svendsen et al. (2002) and Hanelt et al. (2004); ecological information on Kongsfjorden is broadly compiled in Hop et al. (2002).

Off Brandal (Fig. 1), the extensive flat soft-sediment bottom of apparently uniform character slopes only slowly within the first 50 m from the coast, followed by a steeper incline. Sediments consist of a sand-clay mixture of quite homogenous granulometric characteristics throughout the fjord (Wlodarska-Kowalczyk and Pearson 2004) and appear well oxygenated. In a nearby station (<1 km distance) M. Zajackowski (unpublished data, *fide* Wlodarska-Kowalczyk and Pearson 2004) measured a POC/PON value of 7.6, which indicates the existence of fresh marine detritus. Irregularly ice-transported boulders can be found forming

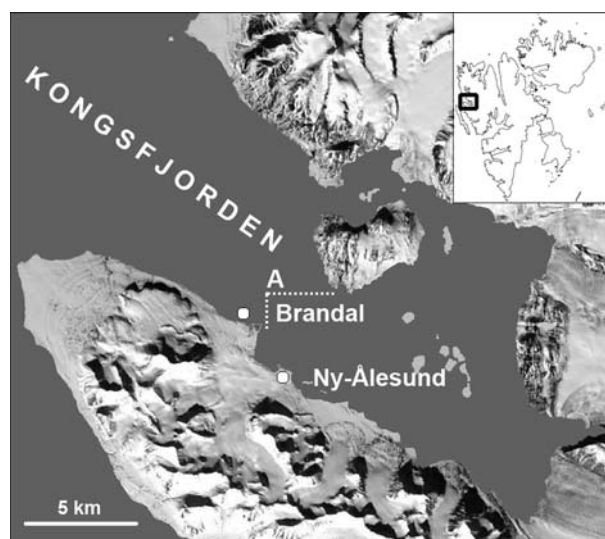


Fig. 1 Landsat TM image of Kongsfjorden on Spitsbergen, Svalbard archipelago (modified from Svendsen et al. 2002). The study site Brandal, the village Ny-Ålesund and transect A of Dowdeswell and Forsberg (1992, see Discussion) are indicated

substrate for hard-bottom fauna and flora (e.g. *Acrosiphonia* aff. *flagellata*, *Laminaria digitata* and *Phycodrys rubens*) communities in the soft bottom habitat (Whittington et al. 1997; Lippert et al. 2001).

Macrozoobenthos

Five replicated soft bottom samples were collected along six isobathic transects (5, 10, 15, 20, 25 and 30 m) using SCUBA-diving. A quadratic metal frame (20 cm side length and 20 cm deep) was used to surround a small area of soft bottom, which was thereafter removed by an airlift system. This device was constructed using a pvc tube (6 cm in diameter and 80 cm of length with an “n”-shaped end at the upper edge), a compressed-air injection unit connected to a 200 bar dive tank and an attached retaining bag (0.5 mm mesh size). The collected material was immediately separated in the laboratory and species preserved in 70% ethanol. Thereafter, organisms were identified and counted under a binocular microscope. Species accumulation curves (sensu Gray 2001) were plotted to exploit the cumulative number of different species observed—as each a priori ordered new sample is added—against increased sampling area. The plots indicate the minimum number of cores needed to detect >90% of the soft bottom fauna (Magurran 2004). After blotting on filter paper biomass (including shells) of the different taxa was assessed from a preserved sub-sample before drying to mass constancy at 60°C, estimations of the dry mass (DM) and ignition in a muffle furnace at 500°C for 24 h for ash free dry mass (AFDM). Percentages of species in comparison to the total faunal abundances were estimated for the five bathymetric zones separately. For each sample the Shannon–Wiener diversity index (H' , $\log e$) was determined from abundance data. Thereafter, multivariate community analyses were employed utilizing the PRIMER Version 6 package (Clarke and Gorley 2006). Before calculating Bray–Curtis similarities, data were square root transformed. Using group average linkage, sample classifications were achieved and thereafter samples related to each other identified based on the resulting dendrogram. By means of a similarity analysis (one-way ANOSIM, 95% confidence interval, Clarke and Gorley 2006) statistical differences were identified. Thereafter, SIMPER (Clarke and Gorley 2006) was used to identify characteristic species, which are contributing most to the statistical dissimilarity among samples. Differences in species richness between the six bathymetric transects were tested using one-way ANOVA. Furthermore, species were classified into five feeding modes (omnivores, carnivores, sub-surface detritivores, surface detritivores and suspension feeders) according to the literature (Syvitski et al. 1989; Aitken 1990; Gromisz and Legezyńska 1992; Schmid and Piepenburg 1993). Species

were assigned to four zoogeographical groups (Arctic, Arctic-boreal, boreal and cosmopolitan) according to the literature (Gajewska 1948; Rózycki 1991; Weslawski 1991; Anisimova et al. 1992; Gromisz and Legezyńska 1992). All data of this study are available via the internet (Herrmann 2004; Herrmann and Laudien 2004).

Results

Species-accumulation curves (sensu Gray 2001; Fig. 2) show that the five replicates sampled were sufficient to include >90% of the soft-sediment species as they already level at 3–4 cores. Annelids comprise 79%, molluscs 11%, crustaceans 8%, echinoderms 1%, and others (including priapulids, sipunculids, anthozoans and ascidians) contribute less than 1% of the 45 known species and additional 18 families not further identified. Concerning the number of individuals, annelids made up 84% of the specimens, molluscs 10%, crustaceans 3%, echinoderms 1%, and others <2%. Table 1 summarizes all taxa and their biomasses, also showing that eleven species populated the full depth range studied. The bulk of amphipods (80%) inhabited the 5 m depth zone in association with the bivalve *Cyrtodaria siliqua*, which was only found at shallow depth. In contrast the bivalve *Ciliatocardium ciliatum*, the gastropod *Oenopota* sp. and the polychaetes *Amphitrite cirrata* and *Orbinia* sp. only occurred at 30 m.

The SIMPER analyses revealed that *Scoloplos armiger* (11–22%) and *Dipolydora quadrilobata* (14–31%) characterize the community of all other depth zones, while the shallow habitat was dominated by *Crassikorophium crassicornes* (32%) and *Spio armata* (26%). *Euchone analis* dominated at 10 and 15 m (14 and 10%), *S. armata* at 10 and 20–30 m (11–14%) and *Chaetozone setosa* at 20–30 m (11–14%). Only five species were categorized as Arctic species, 34 as Arctic-boreal, and 20 as cosmopolitans (three taxa could not be classified). The whole depth range was

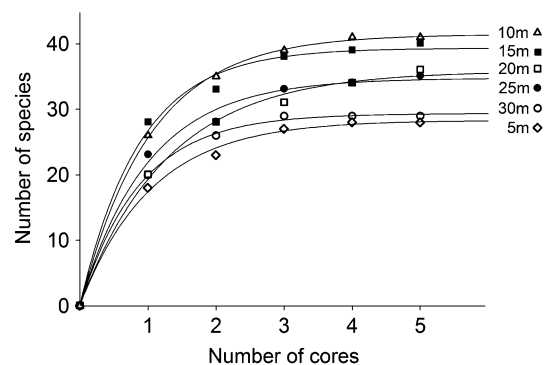


Fig. 2 Species-accumulation curves of six depths (5–30 m) showing that curves flatten out at 3–4 cores

Table 1 Mean abundance (*A*, individuals m⁻²) and biomass (*B*, g AFDM m⁻²), *nd* not determined

Taxon	5m		10m		15m		20m		25m		30m	
	<i>A</i>	<i>B</i>	<i>A</i>	<i>B</i>	<i>A</i>	<i>B</i>	<i>A</i>	<i>B</i>	<i>A</i>	<i>B</i>	<i>A</i>	<i>B</i>
Priapulida												
<i>Priapulus caudatus</i> ^d			21	0.085	10	0.042	21	0.085	21	0.085		
Sipunculida												
<i>Sipunculida</i> indet.					10	n.d.						
Anthozoa												
<i>Edwardsia fusca</i> ^{a,d}			63	8.682	10	1.447	10	1.447				
Mollusca												
<i>Astarte borealis</i>									10	3.104		
<i>Astarte sulcata</i> ^{a,d}	21	0.075	21	0.075	31	0.113	10	0.038				
<i>Axinopsida orbiculata</i> ^d	10	0.003	10	0.003	271	0.073	10	0.003	302	0.081	326	0.087
<i>Chaetoderma nitidulum</i> ^d									10	n.d.		
<i>Ciliatocardium ciliatum</i> ^d											13	n.d.
<i>Crenella decussata</i> ^d	21	0.001	313	0.148	448	0.196	73	0.051	156	0.077	273	0.129
<i>Cryptonatica affinis</i> ^d			10	0.012	21	0.024						
<i>Cylichna</i> cf. <i>arctica</i> ^{a,d}	52	0.060	21	0.024	73	0.083	52	0.060	10	0.012	26	0.030
<i>Cyrtodaria siliqua</i> ^{b,d}	52	0.040										
<i>Hiatella rugosa</i> ^{b,d}	42	0.635	52	0.005	135	0.040	115	0.203			39	0.005
<i>Liocyma fluctuosa</i> ^d	73	0.378	10	0.054	10	0.054	10	0.054				
<i>Macoma</i> sp.			31	0.035	31	0.035	21	0.023	52	0.058	13	0.014
<i>Montacuta</i> sp. ^d	94	0.011					42	0.029			78	0.008
<i>Oenopota simplex</i> ^{a,d}	42	0.048	21	0.024	10	0.012	10	0.012				
<i>Oenopota</i> sp. ^d											26	0.030
<i>Polinices pallidus</i> ^d									10	0.012	13	0.015
<i>Serripes groenlandicus</i> ^d			31	0.882	42	1.176	10	0.294	31	0.882		
<i>Thracia septentrionalis</i> ^{a,d}	10	0.002	10	0.002	10	0.002			10	0.002	13	0.003
Polychaeta												
<i>Ampharete</i> cf. <i>baltica</i>					42	0.045	31	0.034	229	0.249	378	0.410
<i>Amphitrite cirrata</i>											13	1.679
<i>Apistobranchnus tullbergi</i> ^d					10	n.d.			10	n.d.	65	n.d.
<i>Brada villosa</i> ^d			52	0.117	21	0.298	10	0.006	31	0.005		
<i>Chaetozone setosa</i> ^d	10	0.004	354	0.151	531	0.351	635	0.572	781	0.234	469	0.141
<i>Chone</i> sp.					10	0.073	42	0.291	52	0.363		
<i>Dipolydora quadrilobata</i> ^a	73	0.012	1188	0.198	2344	0.390	1906	0.317	3583	0.596	2018	0.336
<i>Eteone spetsbergensis</i>			10	0.127								
<i>Eteone flava</i>			94	0.247	198	0.668	198	0.623	135	0.397	117	0.344
<i>Euchone analis</i> ^d	167	0.435	1031	1.278	1000	1.039	365	0.540	167	0.208	117	0.146
<i>Glycera capitata</i> ^d							10	n.d.				
<i>Lumbrineris</i> sp.	10	0.133	73	0.933	83	1.066	31	0.400	146	1.865	130	1.665
Maldanidae 1 indet. ^c									31	0.299		
Maldanidae 2 indet.			177	1.692	417	3.982	271	2.588	188	1.792	65	0.622
<i>Marenzelleria wireni</i> ^b	10	0.017	10	0.017								
<i>Ophelia limacina</i> ^d	10	n.d.	52	n.d.	42	n.d.			21	n.d.		
<i>Ophelina</i> sp.	10	n.d.	83	n.d.	63	n.d.	10	n.d.	73	n.d.	39	n.d.
<i>Orbinia</i> sp.											13	0.259
Paraonidae indet.									10	n.d.		
<i>Phyllodoce groenlandica</i> ^d			52	1.935	42	1.781	10	0.393				

Table 1 continued

Taxon	5m		10m		15m		20m		25m		30m	
	A	B	A	B	A	B	A	B	A	B	A	B
Polynoinae indet.			31	0.098	21	0.065					13	0.041
<i>Praxillella praetermissa</i> ^d	10	n.d.	31	n.d.			21	n.d.				
<i>Scalibregma inflatum</i>	21	0.121	21	0.121			10	0.060	10	0.060	39	0.227
<i>Scoloplos armiger</i> ^d	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
<i>Spio armata</i>	365	0.317	385	0.335	323	0.281	750	0.652	1083	0.942	508	0.442
<i>Spio filicornis</i>			10	0.028	10	0.028	21	0.056	42	0.111		
<i>Travisia forbesii</i> ^d	115	0.699	156	0.783	167	0.349	63	0.082	42	0.019	13	0.006
Crustacea												
<i>Anonyx nugax</i> ^d	63	0.167	10	0.066					10	0.066	26	0.165
<i>Crassicorophium crassicorne</i> ^{a,d}	729	0.079	10	0.001								
<i>Onisimus edwardsi</i> ^d	31	0.009			10	0.003	10	0.003	21	0.006		
<i>Paroediceros lynceus</i> ^d	42	0.066	10	0.016								
<i>Protomeia</i> sp. ^a	42	0.013	10	0.003			21	0.006			52	0.016
<i>Priscilla armata</i> ^b	52	0.011	10	0.002								
<i>Monoculodes</i> sp.									31	n.d.		
<i>Ischyrocerus megalops</i>			10	0.003	21	0.007						
<i>Synidothea nodulosa</i> ^{a,d}			21	0.048	31	0.071			21	0.048		
<i>Sclerocrangon boreas</i> ^d									10	1.65		
Echinodermata												
<i>Chiridota laevis</i>			31	1.936	104	6.442	21	1.290				
Holothuroidea indet.					10	n.d.						
<i>Ophiura robusta</i> ^d			135	0.801	208	1.232	31	0.185	10	0.062		
Ascidacea												
<i>Pelonaia corrugata</i>			21	0.830	31	1.246	10	0.415				

^a Taxon not reported for Kongsfjorden

^b Taxon not reported for Svalbard according to Gulliksen et al. (1999), Kaczmarek et al. (2005) and <http://www.iopan.gda.pl/projects/biodaff/EMBS-04.html>

^c Most likely *Praxillella praetermissa* (A. Bick, Univ. Rostock, personal communication)

^d Referenceexemplar (for numbers see Herrmann 2004) of the Museum für Naturkunde der Humboldt-Universität zu Berlin

characterised by a similar zoogeographical species composition with around 8% Arctic representatives, 58% Arctic-boreal and 34% cosmopolitans, which is consistent with biogeographical relationships of macroalgae in the same fjord (Wiencke et al. 2004).

The overall mean macrozoobenthos abundance was 6,296 individuals m⁻² with minimal values at 5 m depth (2,260 individuals m⁻² and 28 species), followed by the 30 m transect (5,443 individuals m⁻² and 29 species). Intermediate depths showed increased abundances and species richness (10 m: 5,969 individuals m⁻² and 42 species; 15 m: 8,802 individuals m⁻², 41 species; 20 m: 6,781 individuals m⁻², 36 species; 25 m: 8,521 individuals m⁻² and 35 species) (Fig. 3; Table 1). Species richness differed significantly between the shallowest and the 10 and 15 m transects, respectively (ANOVA, $P < 0.05$). Mean diversity was 2.06 (0.12 SE), and ranged between 1.85 (0.28 SE) at

25 m and 2.19 (0.29 SE) at 10 m. Highest evenness was detected at 5 m (0.82 ± 0.01 SE) and lowest at 25 m (0.67 ± 0.02 SE). Minimal biomass was 3.5 g m⁻² (5 m) and maximum biomass 25.0 g m⁻² (15 m) AFDM.

The cluster analysis of both abundance and biomass data indicated a huge difference between the 5 m samples and all other transects (Fig. 4, dendrogram for biomasses appears similar and is therefore not shown). The latter group can be sub-divided into the medium depth stations (10–20 m) and the deeper stations (25, 30 m).

Discussion

The soft-sediment off Brandal, Kongsfjorden was inhabited by 63 taxa. Nine of these had not previously been identified and published for this fjord and four (the polychaete worm

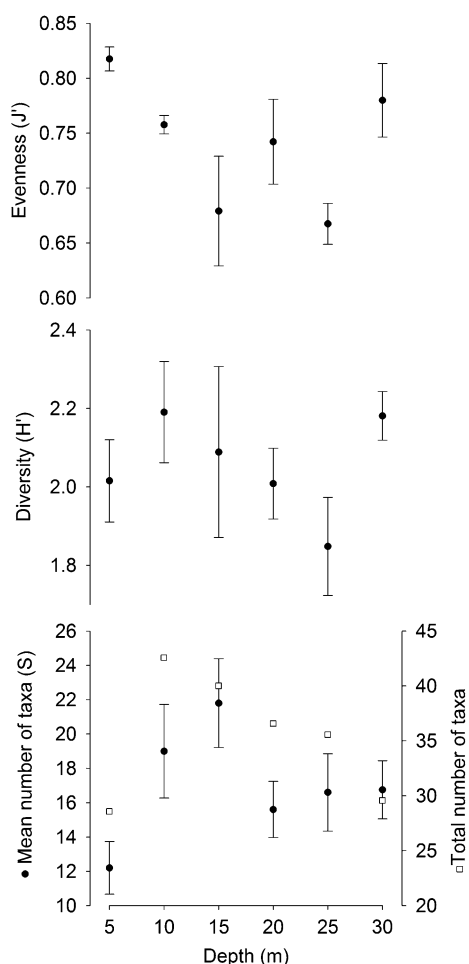


Fig. 3 Evenness (J'), Shannon diversity (H' , Log e) as well as mean (filled circle) and total (open square) number of taxa of macrobenthos at six different depths (5–30 m) of the soft bottom habitat Brandal (Kongsfjorden, Spitsbergen)

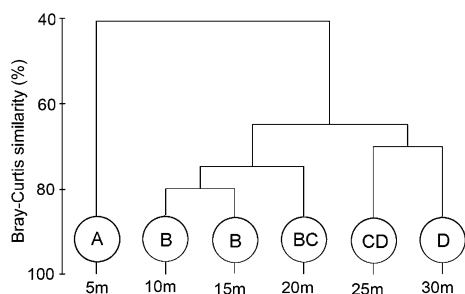


Fig. 4 Dendrogram resulting from cluster analysis of Bray–Curtis similarities using abundance data of soft bottom macrobenthos. Depth zones sharing a letter do not differ significantly (one-way ANOSIM, $P < 0.05$)

Marenzelleria wireni, the amphipod *Priscilla armata* and the bivalves *Hiatella rugosa*, *C. siliqua*) had not been reported for Svalbard yet. However, 45% of the present taxa were also found inhabiting shallow soft bottoms located between 5 and 50 m depth near Blomstrand Island

(distance 5.6 km), Gluudneset (distance 6.3 km) and Dyrevika-Conwaybreen glacial bay (distance 11.0 km) (Kaczmarek et al. 2005). In spite of this, the common taxa constitute a relatively low fraction (23%) of the 122 benthic macroinvertebrates composing the soft bottom association inhabiting the central Kongsfjorden coast recorded during the previous study (Kaczmarek et al. 2005). The present investigation, however, analysed the sand-clay bottom in a narrower depth range (5–30 m versus 5–50 m depth), included a smaller sampling area (two orders of magnitude less), sampled quantitatively by a suction device versus dredging and did not aim to present an overall description of the soft bottom benthos of Kongsfjorden. The main objective of the study was to describe the fauna quantitatively and detect possible diversity dissimilarities between bathymetric zones differently affected by ice-scouring.

Both shallow water surveys revealed that *Axinopsida orbiculata* is an abundant bivalve, which was presently found already at 5 m. However, this thyasirid bivalve increased its density towards deeper stations. Hence, it was also recorded on soft bottoms of Kongsfjorden between 50 and 70 m (Wlodarska-Kowalczyk et al. 1998) and characterises the species association transitional between the glacial bay community impacted strongly through inorganic sedimentation and the associations inhabiting the central basin and experiencing low levels of sedimentation (Wlodarska-Kowalczyk and Pearson 2004; Wlodarska-Kowalczyk et al. 2005).

The present abundances of the polychaetes *C. setosa* and Paraonidae indet. at 25 m (781 and 10 individuals m^{-2}) are in agreement with abundances of 739 and 11 individuals m^{-2} , respectively, recorded in the deeper study (Wlodarska-Kowalczyk et al. 1998). The former polychaete species was the most abundant taxon in the shallow water dredging survey (Kaczmarek et al. 2005) but ranked after *D. quadrilobata*, *S. armiger* and *S. armata* only in fourth position in the present study. It can be found throughout the fjord with increasing dominance towards the glaciers (Wlodarska-Kowalczyk and Pearson 2004; Wlodarska-Kowalczyk et al. 2005) and has been identified as typical in open coastal glacial bays and fjords of Spitsbergen (Kenall and Aschan 1993, Wlodarska-Kowalczyk et al. 1998; Wlodarska-Kowalczyk and Pearson 2004). The bivalves *Macoma* sp. and *Liocyma fluctuosa* were only found in the present and previous shallow sub-tidal Kongsfjorden study located further away from the main glacier outflows (Kaczmarek et al. 2005). They were also recorded in Julibukta, Skoddebukta and Bettybukta (Wlodarska-Kowalczyk et al. 1998) but not in the Kongsfjorden survey carried out up to 1 nautical mile (nm) from the glacier fringe. The distance of the sampling location in relation to the glacier front may explain this pattern: both bivalves require coarser sediments (Ockelmann 1958) and less turbid

waters (Kaczmarek et al. 2005) and thus sites, where they were observed are located at greater distance from the glaciers (Brandal is ~ 8.5 nm off the glacier). Svendsen et al. (2002) detected maximum fluxes of particulate inorganic matter (PIM, $800 \text{ g m}^{-2} \text{ day}^{-1}$) in front of the Kongsbreen glacier fringe during a study conducted along Kongsfjorden. The sediment load dropped steadily with distance and was lower than $20 \text{ g m}^{-2} \text{ day}^{-1}$ at 5.5 nm from the glacier margin. Sedimentation has been shown to have a structuring effect on the distribution of macrobenthic communities (Gorlich et al. 1987; Wlodarska-Kowalczyk and Pearson 2004; Wlodarska-Kowalczyk et al. 2005) and especially on bivalves as inorganic material is particularly stressful to most suspension feeders. It affects their feeding and respiration by clogging the filtering organs and may hinder settlement of larvae (e.g. Moore 1977). Similarly the polychaete worms *Ophelina* sp. and *Maldanidae* 1 indet (unfortunately only parts of the animals were available for taxonomy but most likely they belong to *Praxillella praetermissa*, A. Bick, personal communication) were abundant in the present Kongsfjorden study and also occurred in fjords sampled at a distance of at least 1.7 nm from the glacier front (Wlodarska-Kowalczyk et al. 1998). This is in line with the observed decrease in species richness along the Kongsfjorden axis towards the glacial sediment source (Kaczmarek et al. 2005). Similar patterns were found on the way to the glacial margins or glaciofluvial outflows in Arctic fjords both for soft and hard bottom communities (Farrow et al. 1983; Kendall 1994; Holte et al. 1996; Wlodarska et al. 1996) and for benthic decapods off the South Patagonian Icefield (Mutschke and Gorny 1999). Likewise, in Potter Cove (King George Island, South Shetlands), where a large amount of PIM is washed from a glacier into the bay (Kl oser et al. 1994), an ascidian dominated community is substituting the high Antarctic sponge community, as the former active filter feeders are able to irrigate their filtration unit by mantel contraction in contrast to sponges, which cannot effectively clean their filtering chambers (Sahade et al. 1998).

The soft bottom fauna was dominated by polychaetes and molluscs, both in species number (28 and 18) and individuals (4,544 and 820 individuals m^{-2}). Crustaceans inhabited the sediment only in lesser numbers (ten species, 78 individuals m^{-2}) revealing a proportion of annelids : molluscs : crustaceans = 8:5:2.9. In contrast to our results and that of Gorlich et al. (1987) who also discovered low percentages of crustaceans in glacier-impacted parts of Hornsund, as did Holte et al. (1996) in Gronfjord and Adventfjord, Kaczmarek et al. (2005) recorded a much higher percentage of crustaceans during their dredging survey in Kongsfjorden. The latter sampled indeed a much larger area and reached 50 m depth. For scarce and highly mobile species like crustaceans, dredging might be an

appropriate tool (Syvitsky et al. 1989; Wlodarska et al. 1996; Kaczmarek et al. 2005). The shortcomings of this method are, however, that it does not sample quantitatively and the gear does not penetrate deeply enough into the sediment to collect the majority of the burrowing animals (Holme 1964). This is apparent through the observation that although the sampling area exceeded the present one by two magnitudes, the total number of all 11 common polychaete species collected during the dredging-survey is much lower compared to the present survey. The airlift system operated by scientific divers as used during this study may be a more adequate quantitative method compared to grab-sampling. The latter method revealed even lower proportions of crustaceans, though at deeper bottoms (annelids : molluscs : crustaceans = 8:5:1; Wlodarska-Kowalczyk et al. 1998) and did not sample any necrophagous amphipods (Wlodarska-Kowalczyk and Pearson 2004), although they were collected in the same area by dredging (Kaczmarek et al. 2005).

The soft-sediment fauna is dominated by detritivorous and suspension feeding polychaetes (*D. quadrilobata*, *S. armata* and *E. analis*) and the sub-surface detritivorous polychaete *S. armiger*, which was also the numerically dominating species in a nearby intertidal and sub-tidal habitat (Bick and Arlt 2005). Furthermore the surface detritivorous and carnivorous amphipod *C. crassicornis* showed high individual abundances. While $\sim 73\%$ of the fauna collected in the inner basin (38–83 m) was deposit feeding and sub-surface detritivorous (Wlodarska-Kowalczyk et al. 2005), this fraction diminished to 36% at the present site, but at shallower depth (5–30 m) (Fig. 5). Furthermore, suspension feeders became more dominant (from 20.5%, Wlodarska-Kowalczyk et al. 2005 to 27%, present study), which may reflect the reduced impact of PIM sedimentation compared to the areas near the glacier front. This observation is consistent with the common trend that deposit feeders become more prominent with a declining distance to the glacier fringe and intensified glacier activity (Farrow et al.

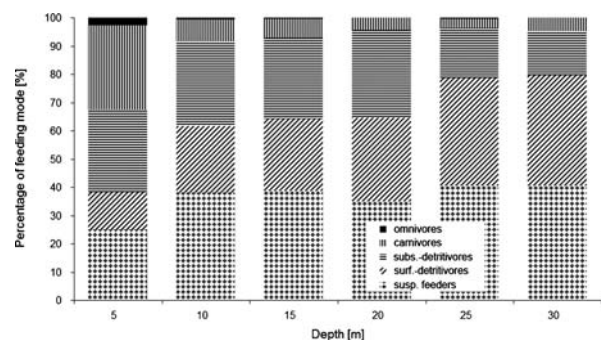


Fig. 5 Percentage of feeding modes of soft bottom macrobenthos at six different depths (5–30 m) at Brandal (Kongsfjorden, Spitsbergen)

1983; Syvitski et al. 1989; Wlodarska-Kowalczyk and Pearson 2004).

Biomass was significantly higher compared to estimates of Wlodarska-Kowalczyk et al. (1998) from their deeper sampling (50–70 m), which was additionally closer to the glacier front (51 and 248 g m⁻² wet mass and 3.5 and 25.0 g m⁻² AFDM: this study; 6 and 11 g m⁻² wet formalin mass: former study). This again supports the observation that effects of sedimentation structure the faunal community. Additionally, decreasing biomasses near the glacial sediment source have also been related to a shortage of food available to the sub-surface detritivorous fauna since primary production is decreased and the proportion of organic matter in the sediment reduced due to a high sedimentation rate (Görlich et al. 1987). The distinctive sampling method (van Veen grab in the former study) and a very small number of samples ($N = 2$) were also mentioned by Kowalczyk et al. (1998) as possible reasons for underestimations. However, biomass estimates of the study including 23 cores reaching 380 m revealed an even lower mean biomass (4.34 ± 3.77 SD g m⁻² wet formalin mass; Wlodarska-Kowalczyk et al. 2005). The present shallow-water soft bottom biomass values are, however, about one order of magnitude lower than estimates from hard bottom fauna of Kongsfjorden (380–2,300 g m⁻² wet mass; Jørgensen and Gulliksen 2001), which is to be expected since the soft bottom species are relatively small sized.

Shannon diversity ranged between 1.85 and 2.19. Lowest diversity was found in shallow areas and this value is in agreement with 1.64 estimated for even shallower macrofaunal communities (<1 m depth, A. Bick personal communication) analysed by Bick and Arlt (2005). Our highest values were estimated at 10 m. These results are in the range of the dredging survey of Kongsfjorden (Kaczmarek et al. 2005) and very compatible with estimates reported from different Spitsbergen glacial or glaciofluvial bays (Table 2). Dissimilarities in diversity of analogous habitats have been explained again with variable inorganic sedimentation rates (Kendall and Aschan 1993; Wlodarska et al. 1996). However, differences detected during the present study along the depth range between 5 and 30 m must be the consequence of other factors since the maximum distance between the two outer transects was less than 100 m. Thus, differences in sedimentation levels should be negligible and the present observations are somehow related to water depth. Species richness (for 508 species pooled) of the soft bottom fauna from the deeper Norwegian continental shelf is not correlated with water depth or median grain size (Ellingsen 2002) and regression analyses indicated that patterns of change in the macrofauna of Kongsfjorden were unrelated to depth (38–380 m) (Wlodarska-Kowalczyk et al. 2005). It is not clear if this result can be applied to shallow water, because it is impossible to discriminate

Table 2 Ranges of Shannon index (H' , Log e), from different glacial or glaciofluvial Spitsbergen bays at sampling depths ranging from 2 to 80 m, modified from Wlodarska-Kowalczyk et al. (1998)

Site	Depth	H'
Kongsfjord (present study)	5–30	1.85–2.19
Kongsfjord ^b	50–70	1.49
Kongsfjord ^c	5–50	0.57–2.84
Skoddebukta ^b	30–75	1.49–2.54
Yoldiabukta ^b	57–75	1.26–1.48
Julibukta ^b	30–50	2.22–2.30
Ekmanfjord ^b	30–55	2.22–2.31
Tempelfjord ^b	40–80	1.85–2.01
Bettybukta ^b	40–80	0.43–2.11
Sassenfjord ^d	30–95	2.6–2.9
Hornsund at Hyrnebreen ^e	5–53	0.7–1.38 ^a
Hornsund at Storbreen ^e	18–37	1.2–2.07 ^a
Skoddebukta ^f	2–60	0.38–2.49
Van Mijenfjord ^g	25–75	2–2.5 ^a
Raudfjord ^g	25–75	2.7–3.2 ^a
Adventfjord ^h	26–52	1.38–1.79

^a Values taken from graphs

^b Wlodarska-Kowalczyk et al. (1998)

^c Kaczmarek et al. (2005)

^d Kendall and Aschan (1993)

^e Gromisz (1983)

^f Wlodarska et al. (1996)

^g Gulliksen et al. (1984)

^h Holte et al. (1996)

between water depth and the frequency and level of disturbance caused by iceberg scouring (which is irrevocably correlated with water depth). Large scratches where the benthos is gouged by grounded ice can be commonly observed in the shallow part of the study site (personal observation). Besides the erasure of the benthos, ice scour also modulates the seafloor topography and bottom current flow, changes the sediment characteristics and yields in resuspension followed by sediment transport (Woodworth-Lynas et al. 1991; Peck et al. 1999; Gutt 2001). Biological ramifications are the drop out of benthic biomass, changes in abundance and diversity patterns, and modified community structure and function (Conlan et al. 1998; Gutt 2001; Conlan and Kvitek 2005). The probability for an iceberg to ground can be indirectly estimated from the relationship of its freeboard and given assumptions regarding the shape and density of the respective iceberg. For our study area Dowdeswell and Forsberg (1992) observed along their transect “A” (Fig. 1) that the percentage of icebergs with a freeboard high enough to scour the ground at 5 m was 17%, while 4% could plough the ground at 10–15 m depth and only 0.5% could scour below 21 m (values taken from their

Fig. 3). Although the scouring frequency was only estimated indirectly it is highly correlated with depth, consequently shallow zones are more frequently disturbed by scouring than deeper areas.

The observed patterns of species richness (Fig. 6) support the ‘intermediate disturbance hypothesis’ (Connell 1978; Huston 1979). Figure 7 illustrates the distribution of the observed total species numbers with scouring probability calculated from Dowdeswell and Forsberg (1992). All three parameters of the superimposed polynomial function fitted to the data of the six depth zones are significant ($P < 0.02$). This supports our hypothesis that zones scarcely impacted by scouring show low species richness (SR_S sensu Gray 2000), which may be caused by competitive

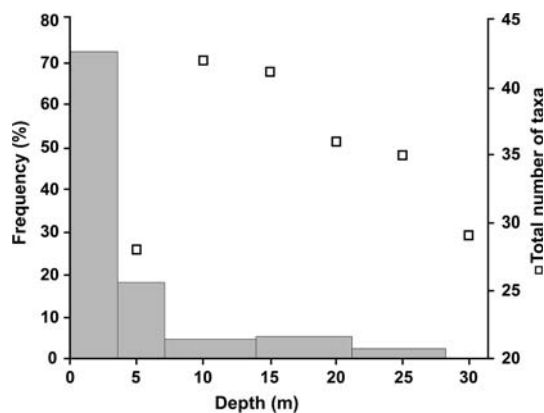


Fig. 6 Iceberg depth-frequencies (grey bars, calculated from Dowdeswell and Forsberg 1992, their Fig. 3) and total number of soft bottom taxa (open square) from Brandal

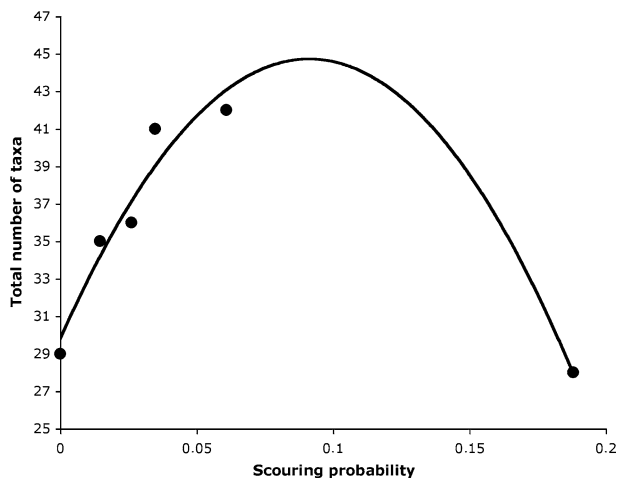


Fig. 7 Distribution of observed total species number with scouring probability calculated from Dowdeswell and Forsberg (1992). Superimposed is the polynomial function fitted to the data ($x =$ scouring probability and $y =$ total species number): $y = 35.01 + 133.65x - 1794.23(x - 0.05)^2$; $R^2 = 0.96$ following an idea of Brey and Gerdes (1997), all three parameters are significant ($P < 0.02$)

exclusion of species, explaining the lower total number of taxa at 30 m (29 species). With a rising, moderate intensity and rate of scouring in intermediate water depths the competition is relaxed and recolonization, first of species with lecithotrophic or planktotrophic larvae (Bick and Arlt 2005) takes place, which is reflected in higher species richness (intermediate depth zones: 35–42 species) and more diverse living strategies. In frequently disturbed areas—most icebergs ground in shallower areas, since the freeboard of the majority of icebergs is small—species start to be eliminated by stress (5 m: 28 species) resulting again in declining diversity and biomass (minimal biomass was 3.5 g m^{-2} AFDM at 5 m). The latter pattern is often observed in areas severely disturbed (glacial sedimentation: Włodarska-Kowalczyk et al. 2005; fluvial sedimentation: Aller and Stupakoff 1996; organic enrichment: Pearson and Rosenberg 1978; fish trawling: Jennings et al. 2001; deep-sea nodule mining: Ingole et al. 2001). Therefore, species richness of the Kongsfjorden soft bottom community is highest at intermediate levels of scouring impact assuming that at medium depth the competition for space and food (Wilson 1991) of dominating species is moderated by the disturbance, which reduces the depression of sub-ordinate species. Thus, species of a lower level in the competitive hierarchy would reemerge (Valdivia et al. 2005). This hypothesis is supported by observations from Barrow Strait along the exposed coast of Cornwallis Island (high Arctic Canada): Conlan and Kvitek (2005) analysed benthic communities of a chronically, although infrequently scoured, area and an ice-protected community comparatively and revealed that the former was more species-rich, abundant and massive. However, early and late colonists co-existed throughout the 9 years of monitoring suggesting that the higher recruitment rate of opportunists counterbalances the enhanced competitive powers of later colonists (Reice 1994). The significant correlation of these community parameters with the time elapsed after the disturbance ($1.1 \text{ events km}^{-1} \text{ year}^{-1}$) also supports the intermediate disturbance hypothesis, whereby succession occurs as the period passed since the disturbance took place, creating high diversity over all scours of different ages combined (Conlan and Kvitek 2005).

Antarctic icebergs are much larger and scouring activity reaches bottoms down to 400 m depths. The biological consequences are nevertheless similar as in the high Antarctic, too, communities belonging to a variety of simultaneous stages of recolonization inhabit the impacted grounds and thus beta-diversity increases on a larger scale (Gutt and Piepenburg 2003). At Signy Island for example nearshore diversity is greatest where scour frequency is moderate, i.e. about once every 10 years (Barnes 1999).

Further chronic glacier related disturbances to the benthic realm are natural glacial sedimentation accompanied by

low input levels of organic material. Along Kongsfjorden Włodarska-Kowalczyk et al. (2005) showed that the number of species was highest in the zone, which was moderately impacted. Here the faunal community consists of small, disturbance-tolerant species and larger long-living species preferably inhabiting undisturbed bottoms, a pattern which is also consistent with the predictions of the intermediate disturbance hypothesis.

Future work should comprise sampling sites along a larger depth scale and include the direct quantification of disturbance resulting from scouring icebergs calved from tidewater glaciers, before generality can be attached to our results.

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