RESEARCH/REVIEW ARTICLE

Diversity of hard-bottom fauna relative to environmental gradients in Kongsfjorden, Svalbard

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Abstract

A baseline study of hard-bottom zoobenthos in relation to environmental gradients in Kongsfjorden, a glacial fjord in Svalbard, is presented, based on collections from 1996 to 1998. The total species richness in 62 samples from 0 to 30 m depth along five transects was 403 species. Because 32 taxa could not be identified to species level and because 11 species are probably new to science, the total number of identified species was 360. Of these, 47 species are new for Svalbard waters. Bryozoa was the most diverse group. Biogeographic composition revealed features of both Arctic and sub-Arctic properties of the fauna. Species richness, frequency of species occurrence, mean abundance and biomass generally decreased towards the tidal glaciers in inner Kongsfjorden. Among eight environmental factors, depth was most important for explaining variance in the composition of the zoobenthos. The diversity was consistently low at shallow depths, whereas the non-linear patterns of species composition of deeper samples indicated a transitional zone between surface and deeper water masses at 15–20 m depth. Groups of "colonial" and "non-colonial" species differed in diversity, biogeographic composition and distribution by location and depth as well as in relation to other environmental factors. "Non-colonial" species made a greater contribution than "colonial" species to total species richness, total occurrence and biomass in samples, and were more influenced by the depth gradient. Biogeographic composition was sensitive to variation of zoobenthic characteristics over the studied depth range. A list of recorded species and a description of sampling sites are presented.

To access the supplementary material for this article, please see supplementary files under Article Tools online.

Fjords are typically ecosystems that contain a complexity of habitats and, often, strong environmental gradients. Studying marine habitats along a fjord's axis gives an opportunity to estimate the patterns of diversity variation within a limited area. Patterns of zoobenthic diversity in fjords have been the topic of many studies (e.g., Derjugin 1915; Soot-Ryen 1924; Brattegard 1966; Gulliksen et al. 1985; Buhl-Mortensen & Høisæter 1993; Kendall 1994; Holte 1998; Chenelot et al. 2011). However, most of them have been conducted on soft-bottom or on inter-tidal hard-bottom. Hard-bottom subtidal habitats, where rock or gravel substrata dominate, are still relatively poorly studied. Hard-bottom habitats are most common in coastal shallow habitats, precluding the extensive use of dredges and other types of surface-operated sampling gear from larger research vessels. Ecological studies of hard-bottom benthos before the era of SCUBA diving are therefore fragmentary (Spärck 1933; Thorson 1933, 1934; Madsen 1936).

Hard-bottom habitats are usually complex and heterogeneous environments. The angle of the bottom and substratum characteristics may vary considerably within

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a small geographical area. Abiotic substrata range from sand or gravel to solid bedrock and examples of biotic substrata are macroalgae, crustose coralline algae, and shells of molluscs and barnacles. The identification of fauna down to species level usually involves several taxonomic specialists, and the complex data set, distinguishing colonial from solitary (non-colonial) organisms, needs to be analysed using multivariate statistical techniques to achieve estimates of biodiversity. For these reasons, only a limited number of complex faunistic surveys of the composition of hard-bottom fauna in the Arctic have been published (Propp 1971; Gulliksen 1978, 1979; Gulliksen et al. 1980; Averintzev 1992; Golikov et al. 1993; Jørgensen & Gulliksen 2001).

The aim of this paper is to present detailed background information on biodiversity by describing the composition of the hard-bottom zoobenthos within a depth range from the tidal zone (ca. 0 m depth) to 30 m depth in Kongsfjorden, Svalbard. Hard substrata are widely distributed along the main axis of Kongsfjorden, from the innermost parts at the glacier fronts to outer parts close to the open sea. In some localities, especially in the outer part of the fjord, hard substrata extend to 30 m depth or even deeper. Spatial gradients in environmental factors were determined in order to explain observed patterns in biodiversity. Based on the geographical location, it is expected that the biota in this fjord is influenced by Arctic environmental conditions such as low temperature and large seasonal fluctuations in light intensity and sea-ice cover. At the same time, Kongsfjorden is assumed to have some characteristics of a sub-Arctic fjord due to the strong influence of the northern branch of the North Atlantic warm current, the West Spitsbergen Current.

We present biodiversity as species composition, including data on abundance and biomass. Zoogeographic analyses in relation to environmental conditions, as presented in this study, are rarely published. We found no published data relating "colonial" and "non-colonial" taxa to different environmental conditions. How the distinction between "colonial" and "non-colonial" species is meaningful ecologically is a question that is still not resolved. The detailed information collected on benthic biodiversity during the study reported here will serve as a basis for further investigations, including comparative biodiversity studies, aut- and synecological studies and studies related to climate change.

Material and methods

Benthic fauna from hard substrata in Kongsfjorden was collected during expeditions organized by the Norwegian Polar Institute in August–September 1996 and 1998. In this context, the hard-bottom is recognized as bedrock, rock or coarse gravel, including pockets or thin layers of softer sediments often found on the surface of rocky substrata. Sampling sites were located near Kapp Mitra (abbreviated to MITR), Kapp Guissez (GUIS), Hansneset (HANS), Juttaholmen (JUTT) and Colletthøgda (OSSI), which is near the mountain Ossian Sarsfjellet (Fig. 1). These sites were selected on the basis of the topography given in sea charts, the type of substratum in the tidal zone and observations made during exploratory dives before sampling was carried out.

Environmental gradients are described in accordance with the classification presented in Table 1. Environmental gradients considered were: distance from the Kronebreen glacier, depth, and the main character and composition of the substratum. The gradients in the amount of silt on substratum, substratum angle, currents and wave activity were described as relative characteristics, without precise measurements, using method and in accordance to the classification presented in Table 1. Substratum types are distinguished according to a classification that has been used to describe the marine ecosystem of Kongsfjorden (Hop et al. 2002).

Benthic flora and fauna were collected by SCUBA divers from inside square frames with a size of 0.25 m^2 along transects from 0 (littoral zone), 2.5, 5, 10, 15, 20, 25 and 30 m depths. Hard substrata deeper than 30 m were not sampled in this study due to dive limits. Macrobenthic organisms were handpicked from the hard surfaces. Algae and organisms attached to the surface were cut loose with a diver's knife. Animals attached to algae were included and all macroalgae attached to the bottom within the sampling frame were removed and collected. Collected material was, often together with parts of the substratum, placed into divers' sampling bags with a mesh size of 1 mm. Small motile and sessile organisms were collected using an underwater suction pump (Lønne 1988). Compared to transects from the outer part of the fjord, transects from the inner part of the fjord were shorter because the hard substrata diminished at 15 m depth for JUTT and 5 m depth for OSSI. Along each transect, two 0.25 m^2 samples were taken at each depth, resulting in a total of 62 samples, each of which was treated as a separate sample in the statistical analyses. Digital video recording of each transect was conducted along a line from the surface to the maximum sampling depth. Sampling depths are within ± 0.5 m due to variation in tide.

Benthic animals were taxonomically sorted in the laboratory to phylum and preserved in 4% formaldehyde or 75% alcohol. Organisms were later identified to the
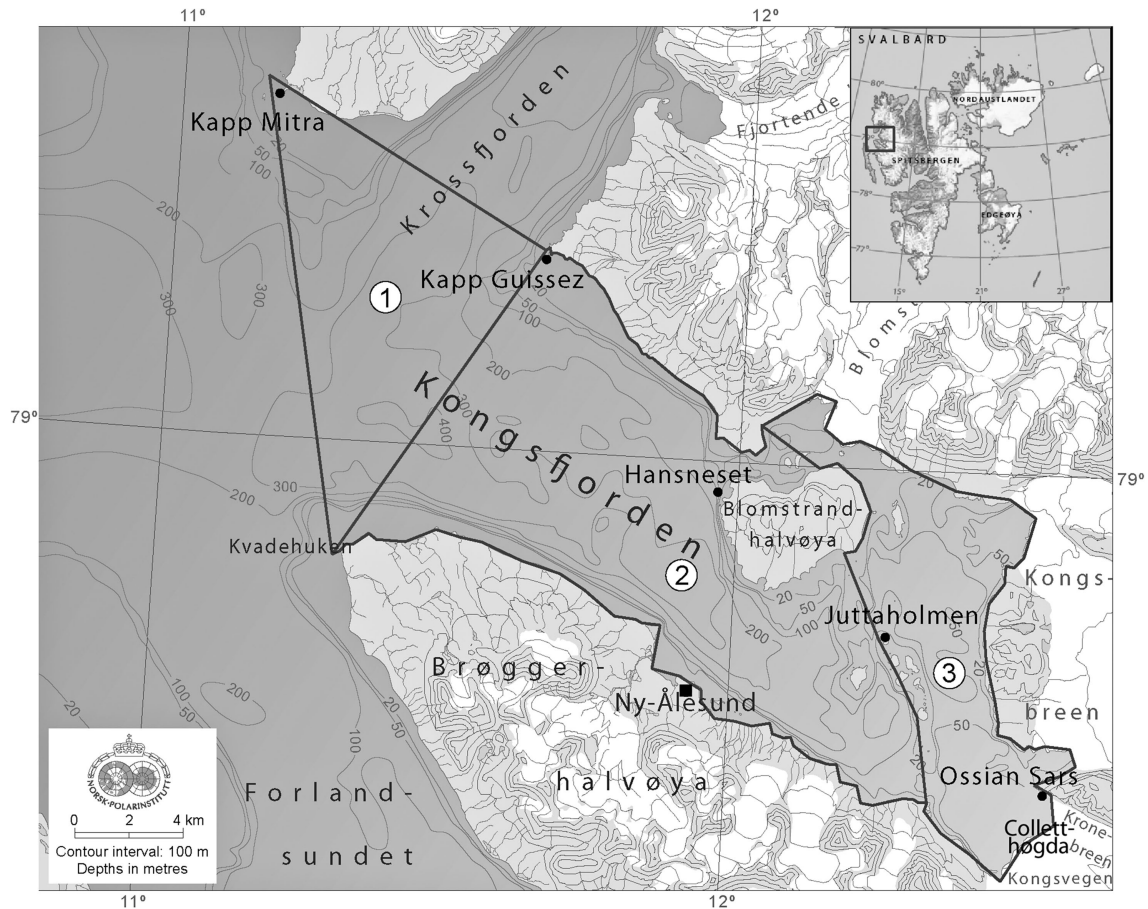
Fig. 1 Locations of sampling transects (black dots) in Kongsfjorden, Svalbard. Black lines limit outer (1), middle (2) and inner (3) parts of the fjord (modified from Hop et al. 2002).

lowest possible taxa by specialists on different taxonomic groups (see Acknowledgements). All identified species, with taxonomic authorities and year for descriptions, are presented in Supplementary Table S1. Additional data recorded included the number of individuals and the weight of each taxon in each sample. Biomass (g m^{-2}) was estimated as the wet weight of whole individuals or colonies. Hard parts, such as shells, were included in the wet biomass. The weight of encrusting bryozoan species was estimated as a colony's size multiplied by the weight of 1 mm^2 of colony. Comparisons were done mainly based on species richness (SR), average occurrence (AO) and frequency of species occurrence (FO) in the samples. SR was determined as the total number of species in a sample or in a group of samples. The AO for a set of samples was the total number of species records averaged per sample. FO was the number of species records expressed as a percentage of all species records in a set of samples. The coefficient of variation applied is the ratio

of the standard deviation to the mean. Biogeographic types of species were defined based on the distribution patterns for shelf species found in the Eurasian Arctic seas (Sirenko et al. 2009). To adequately describe the fauna, it is necessary to consider different scales of diversity measures (Gray 2000). We present an analysis of the data on the hard-bottom zoobenthos in Kongsfjorden at the sample level and in terms of combined data for transects and depths, as well as presenting general features of diversity in the fjord as a sum of data from the transects and depths we investigated. Using diversity indices directly based on abundance data is difficult for hard-bottom samples due to the frequent occurrence of colonial animals. Differences in the number of samples from transects and depths limit the statistical treatment of combined data. The data were treated by univariate and multivariate statistics using the statistical packages Primer 5.2.1 (Clarke & Warwick 2001; Clarke & Gorley 2001) and CANOCO 4.5 (ter Braak & Smilauer 2002).

Table 1 Environmental characteristics of hard-bottom sampling locations in Kongsfjorden, Svalbard. Double numbers indicate that data are available from two different samples; single numbers indicate that data are available from a single sample.

Location	Distance from glacier front (km)	Substratum type	Depth (m)	Exposure to tidal waves[a]	Seabed feature[b]	Angle of substratum inclination in sample frame	Water current flow[c]	Amount of silt on substratum surface[d]
MITR	33	Subtidal rock	2.5	6; 6	2; 2	65; 45	3; 3	1; 1
79°06′N			5	6; 5	2; 2	25; 65	3; 3	1; 1
11°08′E			10	5; 5	1; 2	5; 30	3; 4	1; 1
			15	5; 5	1; 2	0; 10	3; 3	1; 1
			20	4	1	5	3	1
		Subtidal gravel	20	4	1	0	3	1
			25	4; 4	1; 1	0; 0	3; 3	1; 1
			30	4; 4	1; 1	0; 0	4; 4	1; 1
GUIS	27	Intertidal rock	0	6; 6	2; 2	25; 15	3; 3	1; 1
79°03′N		Subtidal rock	2.5	6; 6	2; 2	30; 25	3; 3	1; 1
11°37′E			5	6; 5	2; 2	0; 20	3; 3	1; 1
			10	5; 5	1; 2	15; 15	3; 3	1; 1
			15	4	2	25	3	1
		Subtidal gravel	15	5	1	0	3	1
			20	5; 4	1; 1	0; 0	3; 3	1; 1
			25	3; 3	1; 1	10; 5	3; 3	1; 1
			30	4; 3	1; 1	5; 0	2; 3	2; 2
HANS	16	Intertidal rock	0	6; 6	2; 2	35; 5	3; 3	1; 1
78°59′N		Subtidal rock	2.5	6; 6	2; 2	15; 30	3; 3	1; 1
11°57′E			5	5; 5	1; 2	10; 15	3; 3	1; 1
			10	5; 4	2; 2	60; 60	3; 3	1; 2
			15	6; 4	1; 2	30; 30	2; 3	4; 1
			20	4	2	45	1	4
			25	3	2	15	3	4
			30	4; 3	2; 2	30; 50	2; 3	4; 4
		Subtidal gravel	20	4	1	40	3	4
			25	4	1	40	2	4
JUTT	14	Intertidal rock	0	4; 6	2; 2	45; 75	2; 3	1; 1
78°56′N		Subtidal rock	2.5	4; 4	1; 2	40; 15	2; 3	4; 1
12°18′E			5	4; 3	2; 2	45; 90	3; 2	4; 3
		Subtidal muddy gravel	5	3	1	30	2	4
			10	3; 3	1; 1	40; 30	2; 3	5; 5
			15	2	1	10	2	5
OSSI	7	Intertidal rock	0	5; 5	2; 2	0; 60	1; 1	1; 1
78°56′N		Subtidal rock	2.5	4	1	0	1	4
12°25′E		Subtidal muddy gravel	2.5	4	1	0	2	4
			5	3; 1	1; 1	10; 15	2; 2	5; 5

[a]1=extremely sheltered; 2=very sheltered; 3=sheltered; 4=semi-exposed; 5=exposed; 6=very exposed.
[b]1=gentle slope; 2=steep rock.
[c]1=ca. 0 m sec^{-1}; 2=0.1–0.5 m sec^{-1}; 3=0.6–1 m sec^{-1}; 4=> ca. 1 m sec^{-1}.
[d]1=no mud/silt; 2=only some sediments; 3=very thin layer on rocks; 4=thin flocculent layer; 5=thick cover.

Physical environment of Kongsfjorden

General topography

Kongsfjorden is a glacial fjord 32 km in length (Fig. 1). For the purposes of this study, we include Krossfjorden as part of Kongsfjorden because these two fjords share an opening to the sea and belong to the same fjord system (Svendsen et al. 2002). The width across the shared opening (between Kvadehuken and Kapp Mitra) is about 17 km. Within Kongsfjorden proper, the width varies from 4 km at Kronebreen to 13 km between Kvadehuken and Kapp Guissez. A distinguishing feature of outer Kongsfjorden is the absence of a sill between the main fjord basin and the Spitsbergen shelf. This allows relatively warm and saline Atlantic water to penetrate into the fjord system, forming distinctive circulation patterns (Cottier et al. 2005; Willis et al. 2006). Another important

feature is the presence of one big island (Blomstrandhal-vøya) and a number of small islands (Lovènøyane) in the inner part of the fjord. The inner islands are connected to shallow (<20 m) sills that mark the outer boundary of the inner zone of Kongsfjorden (see the classification by Hop et al. [2002]). The islands and sills divide the fjord into a shallow inner part with a depth less than 100 m and a middle/outer part with depth down to 430 m. The sills prevent larger icebergs from passing from the glacier fronts to the middle fjord and thereby influence benthic habitats through scouring. Two sampling transects—JUTT and OSSI—are located in the inner part of the fjord, between the glacier fronts and the sill. GUIS and HANS are in the middle part of the fjord, while MITR is located in the outer fjord.

Transect MITR was situated close to Kapp Mitra to the west of a small island outside this cape. The distance was approximately 33 km from the innermost transect, OSSI. The bottom transect at MITR included a gentle slope, with a contour declining from 0 to 30 m depth about 270 m from the shore, giving a mean inclination of 6.3° (the angle of a horizontal bottom was <5°, while that of a vertical rocky face was >70°). MITR, like the two transects in the middle fjord (GUIS and HANS), was characterized by step-like terraces interrupted by steep walls. At MITR, samples from 0 m depth were not taken due to extremely strong wave exposure. Transect GUIS was situated on the west side of a small island off Kapp Guissez. The total length of this transect from the shore to 30 m depth was 230 m, giving a mean angle of inclination of 7.3°. Transect HANS was to the west of the most southern rocky island, near Hansneset on Blomstrandhalvøya, at a distance of about 16 km from the glacial front of Kronebreen in inner Kongsfjorden. The distance from the shore to 30 m depth was 74 m, giving a mean angle of inclination of 23.2°. The transect JUTT was located on the north-west front of the steep rock wall on the island Juttaholmen. JUTT was not sampled below 15 m depth because the hard substratum was covered by layers of silt below a depth of 10–15 m. The length from the shore to 15 m depth was about 55 m, giving a mean angle of inclination of 28.6°. The innermost transect OSSI was located in front of the steepest part of Colletthøgda, near the mountain Ossian Sarsfjellet. Hard-bottom occurred from the shore to 5 m depth, and the length of this transect was 35 m, with a mean inclination of 8.1°. The angle of inclination was measured for all samples. Most (87%) of the samples were taken at substratum angles in the range of 0–45° while 13% had angles between 50 and 90°. Most habitats had steep shallow parts (at 0–10 m depth) and relatively flat terraces with steep inclines below. The deepest locations (>20 m)

were generally flat at GUIS and MITR, but not at HANS, where the steep slope continued below 30 m depth.

Distance from the glacier front, depth and angle of inclination influence the amount of sediment accumulated on the bottom. Generally, most sediment accumulates at the innermost localities (Svendsen et al. 2002). The outer transects, MITR and GUIS, have little accumulated silt on the hard-bottom even in the deepest samples at 30 m depth (Table 1), although some silt could be found between rocks and in pockets. The HANS transect had silt on the rock bottom from 15 m down to 30 m, even when the substratum had an angle of 30–50°. Along the two innermost transects, JUTT and OSSI, silt was recorded on the rocks at all depths below the tidal zone (Table 1).

Oceanography

The composition of the water masses in Kongsfjorden is highly dependent upon the influx of water from the north-going West Spitsbergen Current and the run-off of freshwater from land surrounding the fjord. There are four main sources for freshwater run-off to Kongsfjorden, namely glacier ablation, snowmelt, rivers and ice calving (Svendsen et al. 2002). Glacier melting is the main source of freshwater run-off (Hagen & Lefauconnier 1995). Tidewater glaciers release freshwater both in summer and winter time, although the flow is much reduced in the period of winter to spring.

The circulation system in the fjord is highly dependent on the influx of Atlantic water via the West Spitsbergen Current, directed by the Coriolis effect of rotational dynamics as well as local winds (Ingvaldsen et al. 2001). This results in an inflow of water along the fjord's southern coast and an outflow along the northern coast, as well as the appearance of fresher and colder water on the northern side of Kongsfjorden, where our sampling stations were located. Thus, our sampling transects were placed in an increasing gradient of salinity from the front of Kronebreen (transect OSSI) to the fjord's outlet (MITR). Surface salinities below 28 psu can be recorded near the glacial front in the summer and salinities near the surface in the inner basin are generally below 30. Surface water salinity in the middle of the fjord, north-west of Blomstrandhalvøya, is around 33, increasing to greater than 34 at the opening of Kongsfjorden. A local source of fresh and cold water from the glacier Blomstrandbreen in the middle of the fjord, which may influence the HANS transect, must also be taken into consideration. Freshwater run-off may temporarily induce stratification, which again may influence benthic habitats in Kongsfjorden. The stratification is relatively stable during summer, whereas it is less stable during

autumn and winter due to reduced run-off, increased wind mixing and cooling of the water masses.

The upper water layers (0–50 m), which are most relevant for this study, may include surface water, intermediate water and local water. Surface water is characterized by a temperature above 1°C and salinity below 34, intermediate water has a temperature above 1°C and salinity between 34 and 34.65, and local water has a temperature between −0.5 and 1°C and salinity between 34.30 and 34.85 (Svendsen et al. 2002; Basedow et al. 2004; Cottier et al. 2005). The thickness of the different water layers is not stable at temporal and spatial scales. According to Ingvaldsen et al. (2001), surface water seems to be limited to the upper 5–6 m in the central and outer parts of the fjord. The main pycnocline (border between surface and intermediate waters) in the middle part of fjord, near Blomstrandhalvøya and close to the HANS transect, was found at 7–12 m depth during summer/autumn (A. Beszczynska-Møller, pers. comm.) and at 12–17 m in the vicinity of Ny-Ålesund in July 1997 (Walkusz et al. 2007). In August–September 1996 and 1998, we observed water temperatures close to negative values at depth of 25–30 m on northern side of the fjord. Kang et al. (2003) reported an increasing temperature gradient in surface water during August 2002 from 2.5°C in front of Kronebreen to more than 6°C close to the MITR transect.

Warm and saline Atlantic Water (>3°C, salinity >34.65) may enter the fjords at the west coast of Spitsbergen and induce biological effects. An example is the reappearance of the blue mussel (*Mytilus edulis* L., 1758) in Isfjorden, Svalbard, at a depth of 4–7 m (Berge et al. 2005). Zooplankton fauna in Kongsfjorden, which is comprised of both boreal and Arctic species, has been found to respond to shifts in the influence of warm Atlantic Water brought by the West Spitsbergen Current and cold water conveyed by the coastal East Spitsbergen Current (Willis et al. 2006; Willis et al. 2008). Atlantic Water may influence the composition of benthic communities along MITR and GUIS, particularly organisms with pelagic larvae.

Currents and waves

The currents in Kongsfjorden are influenced by both tides and wind and are therefore variable. Although the tide gauge in Ny-Ålesund indicates a tidal maximum of about 2 m (Ito & Kudoh 1997), the tide in Kongsfjorden is generally less than 1 m and the tidal amplitude outside the fjord is 0.5 m (Svendsen et al. 2002). There are persistent tidal currents along the southern shore of outer Kongsfjorden, but our stations were located in the northern part of the fjord, where the tidal current is weaker and has a direction out of the fjord. Precise current measurements were not taken but were estimated subjectively by divers based on their experience swimming against currents (Table 1). The average current velocity is usually less in the inner fjord compared to the outer fjord. Waves have an impact on zoobenthos, but the impact is reduced with depth. The wave exposure extended to 15–20 m depth on the MITR, GUIS and HANS transects (Table 1). Sheltered habitats were found at depths below 20 m on the middle-fjord transects and below 2.5 m on the inner-fjord transects. Waves generally do not allow sediments to remain on hard surfaces, but in subtidal habitats exposed to wave action, sediments may be found in pockets and crevices in the hard substrata.

Suspended and sedimented particulate matter

The concentration of suspended particulate matter in Kongsfjorden is mainly a reflection of the activity of glaciers (Beszczynska-Møller et al. 1997). There are four tidewater glaciers in the inner part of the fjord: Conwaybreen, Kongsbreen, Pedersenbreen and, in the middle of the fjord, Blomstrandbreen. Most important for the fjord's water environment is Kronebreen because this glacier has a negative net balance and is fast flowing (Lefauconnier et al. 1999). Rates of silt and clay sedimentation at the ice front are more than 10 cm y^{-1} (Svendsen et al. 2002). Observations carried out on suspended solids along the main axis of Kongsfjorden in 1996 (M. Zajaczkowski, pers. comm.) revealed maximum concentrations of particulate inorganic matter in areas close to the front of the glacier Kronebreen (up to 373.5 mg L^{-1} in the upper 5 m at a distance of 1.4 km from the front of the glacier). Decreasing markedly with depth, the concentration was less than 14–17 mg L^{-1} at 30–60 m depth. The concentration also decreased rapidly in a horizontal direction towards the mouth of fjord. Concentrations in the 0–30 m layer close to the OSSI and JUTT transects were 20–40 mg L^{-1}, around HANS it was 5–19 mg L^{-1}, and close to GUIS the concentration was 5–14 mg L^{-1}. Particulate organic matter was found to show similar tendencies. The concentration of particulate organic matter decreased gradually from 4.3–12.5 mg L^{-1} at the front of Kronebreen to 4.3–8.6 mg L^{-1} at OSSI and JUTT, 1.7–3.0 mg L^{-1} at HANS and 2.9–4.3 mg L^{-1} at GUIS. Distributions of the concentrations of particulate organic carbon and particulate organic nitrogen were patchy, with local peaks observed at variable depths in different parts of the fjord.

During most of the year, the highest water transparency is at the mouth of the fjord. According to Keck et al. (1999), the lower limit of the euphotic zone in Kongsfjorden was 33.5 m, and it was 24 m in the vicinity of MITR in May 2006 (E.N. Hegseth, pers. comm.). In the inner part of the fjord among the small islands of Lovènøyane, the euphotic zone varied from 6 to 25 m (8.5–14.5 m according to Hegseth's data). Close to the Kronebreen glacier front, the euphotic zone is limited to less than 0.3 m. The intensity of turbidity is highly dependent on the season (Hanelt et al. 2001). During the high melt season in April 2006, the euphotic zone was less than 9.5 m in all parts of the fjord, including the outermost parts of the fjord system.

Deposition rates of suspended particles in 1996 were maximum at 15 m depth in front of Kronebreen (about 893 g m^{-2} d^{-1}), decreasing gradually to 4–15 g m^{-2} d^{-1} close to transect GUIS (M. Zajaczkowski, pers. comm.). A similar tendency was apparent for deposition rates of particulate organic matter and particulate organic carbon. These data were collected using a sediment trap. Actual deposition rates to benthic habitats in the upper layers in the middle and outer parts of fjord are likely to be less because of the presence of strong currents and the influence of surf waves.

Phytobenthos

The benthic flora of the fjord is a depauperated North Atlantic flora with four endemic Arctic species (Hop et al. 2002; Hop et al. 2012). A total of 62 macroalgal species have been recorded at HANS in the middle part of Kongsfjorden (Wiencke et al. 2004; Hop et al. 2012). The shallow subtidal phytobenthos was represented mainly by *Chordaria flagelliformis* on transects from the outer and middle parts of the fjord and by *Fucus distichus* and *Pilayella littoralis* in sheltered areas of the inner fjord. From 2.5 to 10 m depth, dominant species included *Laminaria digitata, L. saccharina* and *Alaria esculenta*. Between 10 and 15 m depth, *Alaria esculenta* was the most conspicuous species, followed by *A. grandifolia*. *Saccorhiza dermatodea* was present at all depths within the kelp belt on transects from outer and middle parts of the fjord, but had less biomass than the species mentioned above. The endemic Arctic species *Laminaria solidungula* was present at 2.5–10 m depth on transects JUTT and GUIS. No kelp was recorded below 20 m depth. The red algae *Phycodrys rubens* and *Ptilota gunneri* were abundant at 10–30 m depth. *Desmarestia aculeata* was one of the most important non-kelp species within 2.5–15 m depth. The major biomasses of this species occurred in the inner part of the fjord at shallow depths and in the

middle part of the fjord at greater depths. At 20–25 m depth, *Desmarestia aculeata* was replaced by *D. viridis*. Crustose algae covering rock, stones and mollusc shells were abundant on all transects and depths where hard substrata occurred. The exception was the deepest part (5 m depth) of the location close to the Kronebreen glacier, where hard substrata were covered by a layer of silt.

Results

Zoobenthic composition

In our Kongsfjorden samples, 360 species were identified. In addition, samples contained 32 taxa that lacked identification features and could not be identified to species level but should be considered as separate species. Eleven species are new or probably new to science (nine species of Bryozoa, one species of Scyphozoa and one species of Nemertea). The total SR of our samples was around 403 species (Supplementary Table S1). The cumulative species count curve (Clarke & Warwick 2001) is not asymptotic, which implies that total SR has the potential to rise with increased sampling effort.

Species represented 11 phyla of animals (Table 2). Among important taxa, bryozoans showed the highest SR (Table 2, Fig. 2). Comprising 29.1% of the total number of zoobenthic species, 118 bryozoan species were identified. Polychaetes, amphipods, molluscs, hydroids, ascidians and sponges were less diverse (sum total 56.1%). The remaining 16 taxa comprised 14.8% of the total number of identified species.

Polychaeta and Gastropoda species and, to an even larger extent, Bryozoa, Amphipoda and Bivalvia showed not only the greatest SR, but also occurred most frequently in samples. In contrast, ascidians, sponges and hydroids were less frequent in samples (7.5% of total number of identifications) though they represented relatively high SR across the whole collection (12.8% of the total number of species).

Bryozoans predominated among species that were most widely distributed at the collection sites. Of the 10 most widely distributed species in our samples, eight were bryozoans. For example, *Hippothoa hyalina*, *Tegella arctica* and *Tricellaria ternata* occurred, respectively, at 51, 48 and 41 stations of 62 (Supplementary Table S1). Among the most frequently occurring species from other taxa were: the molluscs *Hiatella arctica*, *Margarites helicina* and *Tonicella marmorea* (in 48, 39 and 37 samples), the crustaceans *Caprella septentrionalis*, *Balanus balanus* and *Ischyrocerus anguipes* (in 34, 32 and 30 samples), the sponge *Scypha utriculus*, the brittle star *Ophiopholis aculeata* and the annelid *Nereis zonata* (in 31, 28 and 27 samples).

Table 2 Number of species of main zoobenthic taxa from hard substrata in Kongsfjorden, Svalbard, in comparison with data in the published literature. "Varia" comprises groups not recorded in our samples: Hirudinea, Echiura, Leptostraca, Tanaidacea, Aplacophora, Scaphopoda, Brachiopoda, Phoronida, Pogonophora, Crinoidea and Enteropneusta. Data for benthic animals do not include fishes and meiofaunal Foraminifera, Ostracoda, Nematoda and Oligochaeta.

Phylum	Junior taxon	No. of species in hard-bottom samples, own data	New for Svalbard waters from own data	No. of species (Palerud et al. 2004)	No. of species from Barents Sea (Sirenko 2001)	No. of species from Eurasian Arctic seas (Sirenko 2001)
Porifera		12	5	146	137	163
Cnidaria	Class Anthozoa	6		42	45	55
	Class Hydrozoa	23	3	106	138	156
	Class Scyphozoa	4		7	6	7
Plathelmintes		1		0	105	134
Nemertea		5	1	10	36	79
Sipuncula		4		5	12	12
Annelida	Class Polychaeta	72	6	253	347	469
Articulata	Order Amphipoda	48	1	270	343	562
	Order Decapoda	6		22	39	69
	Order Cirripedia	3		14	7	13
	Order Isopoda	6	3	35	43	102
	Order Cumacea	2		30	38	59
	Order Mysidacea	1		16	21	33
	Class Pycnogonida	5	3	25	31	39
Mollusca	Class Polyplacophora	3		5	6	8
	Class Bivalvia	21		75	96	140
	Class Gastropoda	34	6	160	258	304
Echinodermata	Class Asteroidea	2		28	37	79
	Class Holothurioidea	4		14	21	26
	Class Echinoidea	2		5	9	11
	Class Ophiuroidea	3		16	24	30
Tentaculata	Class Bryozoa	118	17	182	273	325
Chordata	Class Ascidiacea	18	2	51	45	57
Varia		0		34	60	78
Total		403	47	1551	2177	3010

About half of the species (47.1%) were rare and were represented in only one to three samples of 62.

"Colonial" versus "non-colonial" species

Zoobenthic communities in Kongsfjorden are composed of "colonial" and "non-colonial" (or "solitary") organisms. Among the "colonial" organisms we counted all Porifera species, all Cnidaria Hydroidea Thecaphora species, and a major proportion of Cnidaria Hydroidea Athecata species, all Bryozoa species, all Ascidiacea Aplousobranchia species and a minor proportion of Ascidiacea Stolidobranchia species. All other benthic animals were regarded as "solitary" organisms. Some of them, like barnacles, can form colonial populations. Such species, however, have a lower level of cognate relations and integration of individuals within a colony: individuals are relatively large and can be clearly separated and counted.

"Non-colonial" species made a larger contribution to total SR, total occurrence in samples and total biomass.

A total of 156 species (38.7% of total SR) were specified as "colonial", whereas 247 were classified as "solitary". The mean occurrence of "colonial" species in samples was 21.8, or 43.3% of the total number of identifications, whereas 28.6 species per station were "solitary", which was 56.7% of the total number of identifications. Thus, "non-colonial" species were more widely distributed in samples. However, with regard to SR values, "colonial"
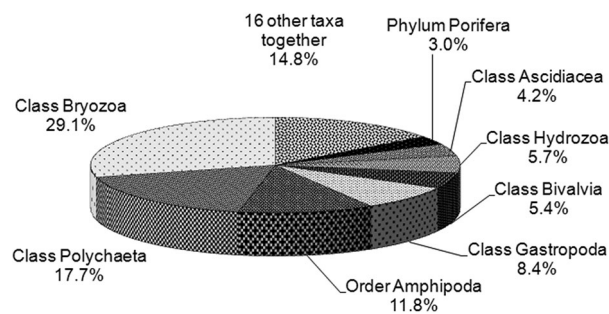

Fig. 2 Contribution (%) of different taxa to total species richness in 62 samples from hard substrata in Kongsfjorden, Svalbard.

species occurred in samples relatively more frequently than did "solitary" species.

"Colonial" organisms contributed 18.6% to total biomass, with a mean biomass per sample of 191.5 g m^{-2}. The total biomass of "solitary" organisms was 4.4 times greater, with an average of 835.8 g m^{-2} per sample. Because of the co-occurrence of both "colonial" and "non-colonial" organisms in samples, abundance data cannot characterize appropriately the pattern of zoobenthic diversity on hard substrata.

Polychaeta was the most abundant "non-colonial" group, with 81.9% of total abundance. Within polychaetes, 98.9% were worms in the order Sabellida. Small polychaetes from the families Sabellidae, Serpulidae and Spirorbidae form calcareous tubes on the surface of different biogenic and abiogenic substrata and are often considered as "fouling" organisms rather than "proper macrobenthos." All other "non-colonial" groups contributed 18.1% to total abundance. With the exclusion of Polychaeta Sabellida, more than half of the rest (59.4%) were Crustacea (of which 79.8% were in the order Amphipoda) and 30.8% were molluscs (Bivalvia 16.7%, Gastropoda 10.2% and Polyplacophora 3.9%). Echinodermata (2.8%), the rest of Polychaeta (4.5%) and all other "non-colonial" groups together made up the remaining 9.8%.

Polychaeta Sabellida reached 7208 individuals per square metre (ind. m^{-2}) on average per sample (Supplementary Table S1). Most abundant species on hard substrata were the barnacle Balanus balanus (179 ind. m^{-2}), amphipods Ischyrocerus anguipes, Gammarus setosus, Gammarellus homari and Caprella septentrionalis, molluscs Hiatella arctica, Margarites helicina, Musculus discors, M. laevigatus, Tonicella marmorea and T. rubra (25–132 ind. m^{-2}). The most abundant echinoderm was Ophiopholis aculeata (30 ind. m^{-2}). The highest abundance for the above-mentioned species is closely tied to the wide distribution of these species in the samples. The exception was Gammarus setosus, a species with high abundance (1171 ind. m^{-2}) that was found in only 10 samples of 62. This was the only species with a coefficient of variation as high as 30.8%; it was considerably less for all other species. Therefore, we consider the dominance of the species mentioned above (except for G. setosus) as characteristic for the hard-bottom communities of Kongsfjorden in August–September.

All samples except for three contained "colonial" forms. Samples without "colonial" species were situated on different transects at 0 m depth, on the border between the littoral and sublittoral zones. It is most likely that these rock wall locations were also inhabited by some, although not numerous, bryozoans, which could not be properly sampled. The separate colonies of some "colonial" species were not included in the abundance analysis, but should also be mentioned here. Average abundance of colonies of encrusting bryozoans in samples was 678 colonies per square metre (col. m^{-2}). The most abundant were: Lichenopora sp., Tegella arctica (mean 100 col. m^{-2} each), Hippothoa hyalina and Harmeria scutulata (60 col. m^{-2} and 57 col. m^{-2}, respectively). The sponge Scypha utriculus (28 col. m^{-2}) can also be regarded among the important species that make a considerable contribution to the cycling of biogenic elements in the fjord's ecosystem.

Bryozoa Cheilostomata formed 68.6% of the total biomass of colonial organisms at the stations. However, large biomass was only recorded for a small number of species. Three species (out of 96) represented most of the biomass. Branched colonies of Tricellaria ternata, Eucratea loricata and Dendrobeania murrayana made up 77.6% of the total biomass of branched and encrusting colonies of Bryozoa Cheilostomata. Important biomasses were also formed by Synoicum sp. (Ascidiacea Aplousobranchia), Haliclona aqueductus and Halichondria panicea (Porifera Demospongia), and Symplectoscyphus tricuspidatus var. acuminatus (Cnidaria Hydroidea).

Biogeographic composition

Biogeographic characteristics are known for 362 species of 403 (89.8%). In the biogeographic analysis, 81.8% of the total number of identifications was used, with the remaining part summed up from the identifications to the supraspecific levels. Species were distributed into seven categories (Fig. 3). About half (51.4%) of the species had a boreal–Arctic distribution (185 species). Species with even wider distribution ranges—subtropical–Arctic, subtropical–Boreal and pan-ocean species—included 7.2% in total (26 species). Of the species with more narrow distributional ranges, Arctic, high-boreal–Arctic and boreal species represented 150 species (41.4%).

Species with boreal–Arctic, boreal and subtropical–Arctic distribution showed higher percentages in total species occurrence (74.9%) than in total SR (64.9%). Groups of "colonial" and "non-colonial" species showed some differences in biogeographic patterns. Arctic species contributed more to "colonial" forms than to "non-colonial" forms (29.6% vs. 5.8%). Species with northern distribution in the "non-colonial" group are represented more by high-boreal–Arctic than by Arctic species (17.6% vs. 4.0% in the "colonial" group). The proportion of species with subtropical–Arctic, subtropical–Boreal and pan-ocean distribution was also higher for "non-colonial" forms (11.4% vs. 3.8% in the "colonial" group).
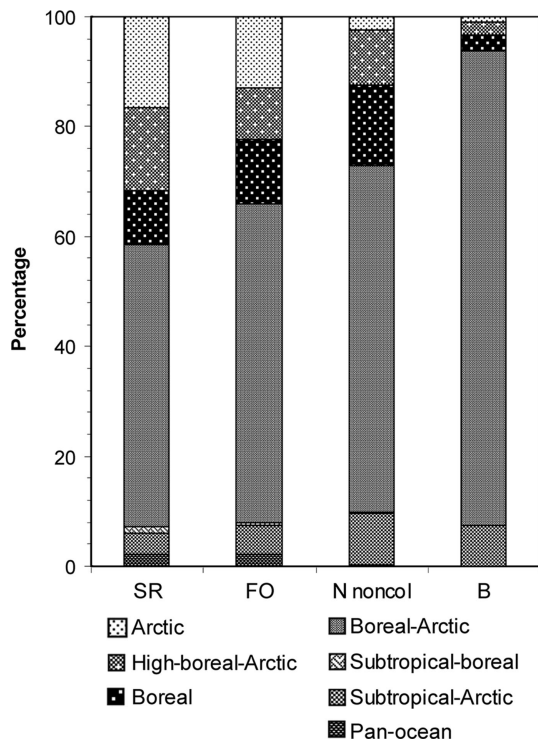
Fig. 3 Relative importance (%) of species with different biogeographic characteristics on hard substrata in Kongsfjorden, Svalbard. Total species richness is abbreviated to SR, frequency of species occurrence in samples to FO, total abundance of "non-colonial" species to N noncol and total biomass to B.

There were more boreal species in the "non-colonial" group (11.2% vs. 7.5% in the "colonial" group). The proportion of boreal–Arctic species was more than 54% in both groups. Thus, "colonial" species found on the hard-bottom of Kongsfjorden generally had narrower and more northern distributional ranges.

Boreal–Arctic species contributed 86.2% to the total biomass in the samples and were responsible for 63.2% of the total abundance of "non-colonial" species (Fig. 3). This proportion was similar for "colonial" and "non-colonial" species. Geographical distributions of the remaining "non-colonial" species were subtropical–Arctic and, for the "colonial" group, boreal and Arctic. There were no Arctic species with very high abundance; the most abundant were species with boreal–Arctic and boreal distributional ranges. Thus, the upper 30 m of the hard-bottom environment of Kongsfjorden was inhabited by a fauna largely comprised of warm-water species.

Zoobenthos distribution along fjord's axis and with depth

SR varied within the fjord and was highest along transects from the outer and middle parts of fjord. Similar

SR was found along the MITR, GUIS and HANS transects (298, 299 and 293 species, respectively). Hard substrata along transects JUTT and OSSI were not as species-rich (217 and 63 species, respectively). The number of species in samples varied broadly from 2 to 136, and often also varied considerably among samples from the same transect and depth. This resulted in high variance when averaging species richness data by transects and depths.

Generally, the mean number of species per sample was reduced on transects close to the Kronebreen glacier compared to transects further away (Fig. 4a). However, "colonial" and "non-colonial" species showed some differences in distribution along the fjord's axis. SR for "colonial" species and the occurrence of "colonial" species were relatively low on the GUIS transect. In general, the low SR for "colonial" species at GUIS was compensated by the high SR of "non-colonial" species, so the total SR was almost the same as at MITR and HANS. Relatively low occurrence in samples from GUIS was characteristic for all "colonial" groups—Bryozoa, Ascidiacea, Cnidaria and Porifera. However, the scarcity of Cnidaria Hydroidea accounted for most of this deficiency. The relative SR for this group at GUIS was intermediate between MITR and HANS, but the FO was much less (3.7% vs. 8.3% and 6.5% in MITR and HANS, respectively).

The composition of zoobenthos varied with depth. SR was minimal at 0 m depth, comprising 11.7% of the total number of species recorded for hard-bottom habitats (42 species of 360). The samples from 5 m depth contained 78.3% of the species from the total list (282 species of 360; Fig. 4b). The patterns of zoobenthic response to the depth gradient were generally similar for SR and occurrence and appeared to be non-linear. The lowest values were from habitats right below low-tide level, on the border between the littoral and sublittoral zones (i.e., <5 m depth). The values increased markedly with increasing depth and reached a maximum at 5 m depth, followed by a decrease to 15–20 m depth and an increase to 30 m depth. The mean number of species per sample was largest at 10 m depth, although the species composition was less rich. Samples from the same depth sometimes contained very different numbers of species (especially samples from 15 m depth) since the heterogeneous hard-bottom habitat harboured zoobenthic communities of different types. The non-linear pattern of species composition in relation to the depth gradient may be attributed to the stratified hydrographical structures of the upper 30 m water layer, with a transitional zone between surface and deeper water masses at 15–20 m depth.

Bray-Curtis similarity values were calculated for each pair of transects based on the presence/absence of species
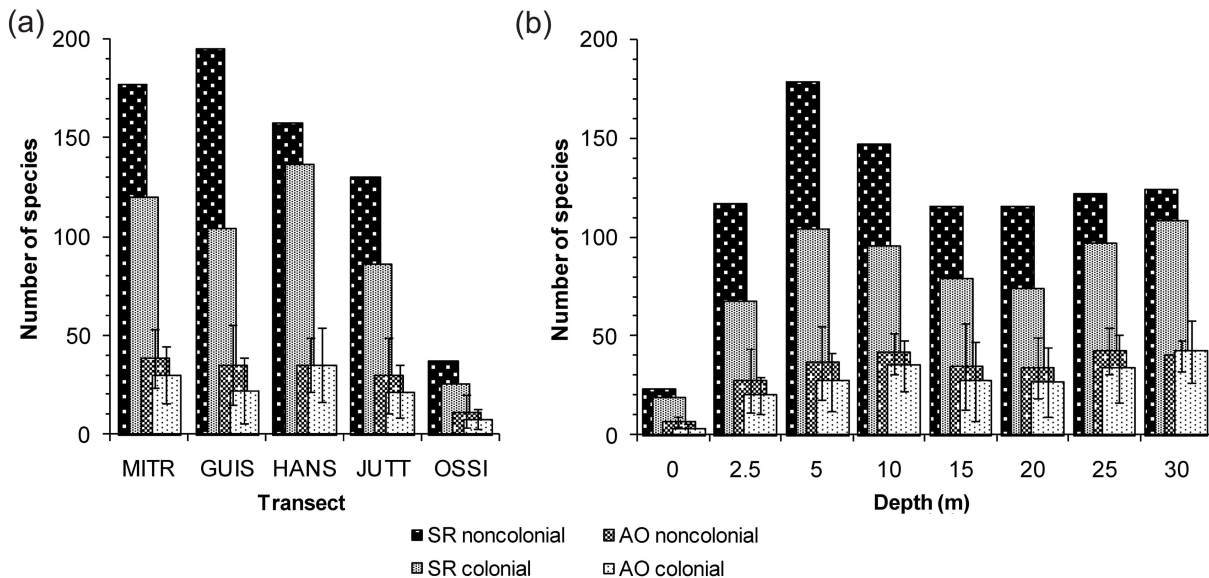
Fig. 4 Zoobenthic species richness and average species occurrence in samples from (a) different transects and (b) depths on hard substrata in Kongsfjorden, Svalbard. "Non-colonial" species richness is abbreviated to SR noncolonial, "colonial" species richness to SR colonial, mean number of "non-colonial" species per sample ($\pm$SD) to AO noncolonial and mean number of "colonial" species per sample ($\pm$SD) to AO colonial.

and standardized occurrence of species in samples on transects. The similarity coefficients varied broadly, from 71.3% between MITR and HANS to 23.3% between OSSI and MITR. Fisher's F-test indicated that for SR and FO the differences were not statistically significant for samples from the MITR, GUIS and HANS transects. Differences in species composition between the JUTT and OSSI transects were significant ($P < 0.05$) and they differed significantly from other transects as well. Transects further from the glaciers were more similar to one another in terms of species composition than were transects closer to the glaciers. Along transects in the inner part of the fjord, distance from the glacier had a strong influence on SR and AO. Despite the long distances between MITR, GUIS and HANS, the similarity in SR among them was relatively high (Fig. 5a). The species that made the main contribution to the similarity of MITR, GUIS and HANS transects were not widely distributed in samples. That is the reason why

Fig. 5 Multidimensional scaling plot of similarity in species composition (Bray-Curtis, presence/absence) among transects on hard substrata in Kongsfjorden, Svalbard, for (a) transects and (b) depths.

these three transects are much closer to each other on the multidimensional scaling (MDS) plot for species occurrence in the samples. When comparing species composition at different depths, it is clear that the highest singularity occurs in the list of species from 0 m depth. Bray-Curtis similarity coefficients for SR ranged from 9.9 to 28.3. Samples from 15 m depth were most similar to the samples from all other depths (19.5–71.6%). Patterns for SR and FO were similar in general. The MDS plot based on Bray-Curtis similarity illustrated greater differences in species composition with increasing separation in depth (Fig. 5b).

The similarity between sets of samples is a function of the differences in the total number of species and the number of common and uncommon species. The percentage of "common" species for transects (i.e., species which were found on 4–5 transects) increased on transects along gradients of environmental conditions from outer to inner fjord (Fig. 6a). This implies that most species from the innermost transects were also found on all other transects. The percentages of "unique" species for transects, i.e., species that were found on a single transect only, showed little difference from transect to transect, with no clear tendency. The differences and tendencies were more evident when "rare" and "unique" species (i.e., species found on a single transect or on two transects out of five) were considered together. The proportion of "rare" and "unique" species for transects decreased from outer to inner transects, from 37.5% on transect MITR to 28.2% and 21.6% on transects JUTT and OSSI, respectively.
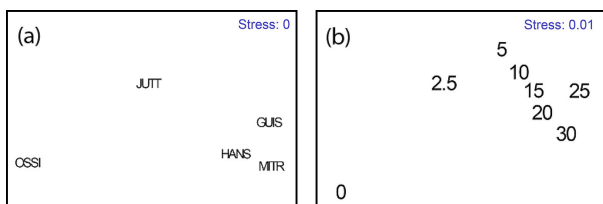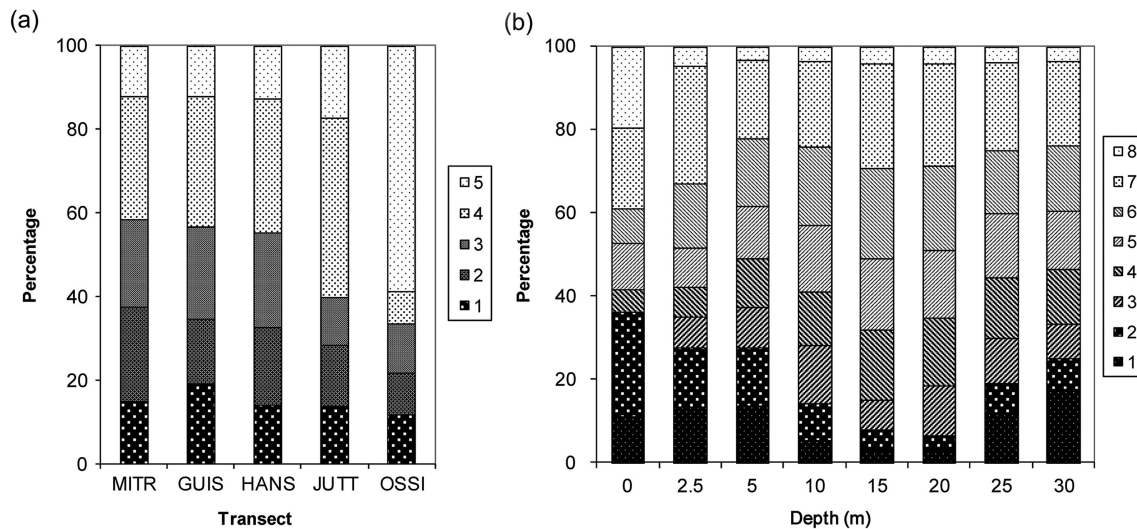
Fig. 6 Percentages of rare to widely distributed species by transects and depths. (a) Numbers 1–5 correspond to the percentage of species found on one to five transects. (b) Numbers 1–8 correspond to the percentage of species found at one to eight depths.

If the differences in biodiversity indices were mainly connected with qualitative differences in species lists, the tendency would be contrary: an increase in the proportion of "rare" and "unique" species towards the inner part of the fjord would be expected. However, the overall faunal depletion toward the inner part of the fjord was not accompanied by more pronounced faunal peculiarity.

Different species in samples had different ranges of distribution by depth ranging from detection at a single depth to detection at eight studied depths. We classified species found in the range of one to two depths as "stenobathic". We regarded species found in the range of seven to eight depths as "eurybathic", and species were considered "intermediate" if detected at three to six consecutive depths. The eurybathic species comprised 19.9% of total SR. With a total of 54.2%, eurybathic species occurred in samples more frequently than steno-bathic species, which had an FO of only 8.2%, although such species represented 42.5% of the total species list. Intermediate species contributed 37.6% both in total SR and FO in samples. Stenobathic species could be also referred to as "rare" species (found at one or two depths). The percentage of "rare" species (as well as most "common") was high at 0 m and low at 15–20 m depth (Fig. 6b). Therefore, decreased values of SR at 0 m were accompanied with uniqueness of species composition. In contrast, the decreased SR values at depths of 15 m and 20 m were not accompanied by peculiarity of species composition. This was similar to the feature described for the species-poor transects JUTT and OSSI (Fig. 6a).

Eurybathic species were usually "common" at different depths (found at seven or eight depths). Some of the species found at two to three depths were also regarded as eurybathic, but there were more "rare" stenobathic species at these depths. Thus, the majority of species had narrow ecological niches in the studied habitats.

Taxonomic diversity on transects and at depths

The contribution of the main zoobenthic taxa to SR (Fig. 2) was consistent among the MITR, GUIS and HANS transects. There were no significant differences between these three transects and the JUTT transect with regard to richness of higher taxa despite a considerably lower total number of species at JUTT. This similarity in the number of supraspecific taxa applied to levels from phyla to order (Fig. 7a). Transect OSSI, which was the transect closest to a glacier, was much poorer in SR and in number of supraspecific taxa, with only six phyla of 11. There were no tunicates, nemerteans, plathelminthes, sponges or sipunculids. Coelenterates were represented by hydroids only and echinoderms by one species of holothurians. Molluscs were much less diverse than on transects further out, and Polyplacophora was absent. The phylum Articulata was represented mainly by amphipods (13 species of 15). Barnacles, one of the most important groups in Kongsfjorden zoobenthic communities, were not recorded at all on the OSSI transect.

Samples taken at 0 m depth (Figs. 5b, 6b) exhibited taxonomic uniqueness not only at the species level but also at higher taxonomic levels. This depth had large contributions of Crustacea and Coelenterata species (Fig. 8). However, a high percentage of these taxa in the total SR was not accompanied by high SR of
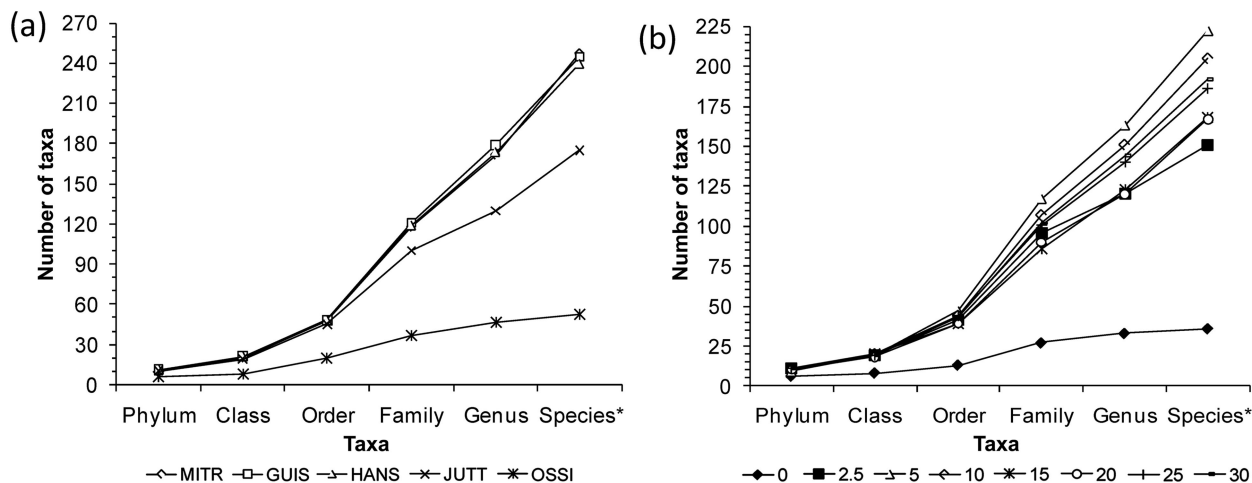
Fig. 7 Number of taxa (a) on transects and (b) at depths in Kongsfjorden, Svalbard. Asterisks indicate organisms identified to species level only.

crustaceans (16 species of Amphipoda) and coelenterates (six species of Hydroidea). At other depths, average values of SR for Crustacea and Coelenterata were 31 and 10 species, respectively. Polychaeta, Mollusca Bivalvia, Echinodermata and Ascidiacea were not found at 0 m depth. The number of Bryozoa species was low (eight species) at 0 m depth, in contrast to an average of 58 Bryozoa species recorded at other depths. At 2.5–30 m depth, all the main taxa were presented, and there were no considerable differences in the number of supraspecific taxa from phylum to order. The differences were chiefly seen at the family to species levels (Fig. 7b), with some tendencies for a change of taxonomical groups with depth. The percentage of coelenterates generally

decreased, whereas bryozoans and bivalve molluscs increased, with increasing depth (Fig. 8). These tendencies were also seen for FO in the samples.

Abundance on transects and at depths

For "non-colonial" species, the mean abundance in samples was highest in the outer part of the fjord and decreased toward the inner glaciers (Fig. 9a). Polychaeta Sabellida contributed most to the decrease in mean abundance. For the second important group, Amphipoda Gammaridea, its relative contribution to total abundance on transects generally increased towards the inner-fjord glaciers. Joint abundance of other "non-colonial" animals
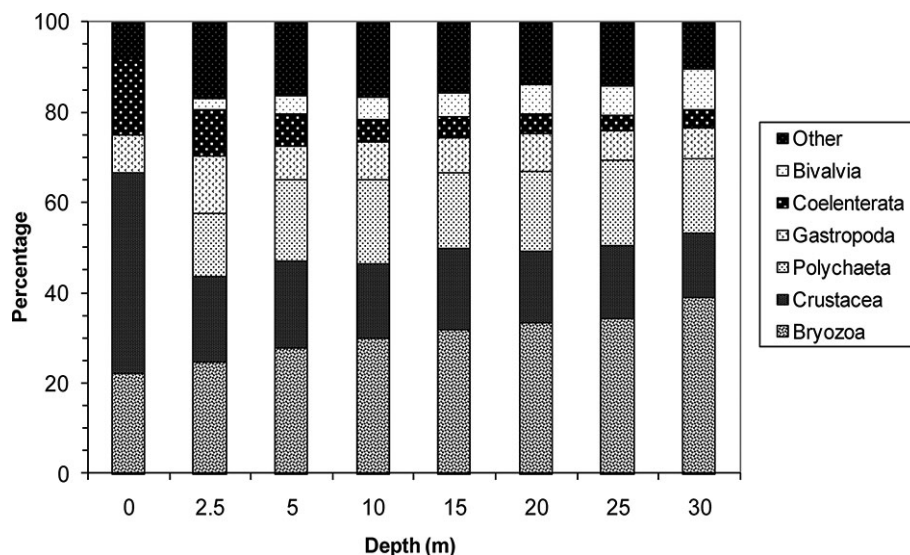

Fig. 8 Percentage of different taxa with regard to species richness at studied depths in Kongsfjorden, Svalbard.

showed a tendency to decrease towards the inner part of the fjord. The four outer transects were more or less similar in the composition of taxa with regard to total abundance. In addition to Polychaeta Sabellida and Crustacea Amphipoda, Crustacea Cirripedia and Mollusca Bivalvia and Gastropoda should also be mentioned (Fig. 9a). The OSSI transect was special since the abundances of Polychaeta Sabellida and Bivalvia were negligible and Cirripedia was absent. Most of the abundance (85.9%) involved amphipods (73.6% as a single species, *Gammarus setosus*). Other groups apparent for total abundance on OSSI were Polychaeta Spionida, Mollusca Gastropoda and Crustacea Cumacea and Caprellida.

K-dominance curves, with cumulative ranked abundances or biomasses plotted against species rank (Clarke & Warwick 2001), were used for estimating the relative dominance in samples on transects and depths. More elevated curves illustrate relatively lower diversity. For transects on the chart (not shown here) for accumulated abundances that include data on Polychaeta Sabellida the curves cross each other and differences in elevation were not clear. The same chart without Polychaeta Sabellida shows relatively low diversity of "non-colonial" species for the OSSI transect (Fig. 10). The highest relative diversity was apparent for the JUTT and GUIS transects, whereas the diversity was intermediate at MITR and HANS, and lowest at OSSI. The most dominant species at MITR and HANS were *Ischyrocerus anguipes, Balanus balanus* and *Hiatella arctica*. They were much more abundant on MITR and HANS than on JUTT and GUIS. When the importance of these three species was removed using a partial type of dominance curves, the elevation of

curves (not shown here) for the four transects became similar.

The abundance of "non-colonial" organisms at different depths varied significantly (Fig. 9b). Mean abundance was minimal in samples from 0 m depth (2582 ind. m^{-2}), and increased with depth, resembling patterns described for SR and AO for the whole material (Fig. 4b). The maximum abundance per sample was 18695 ind. m^{-2} at 10 m depth. In contrast to SR and AO, there was no increase in abundance values at 25–30 m depth. Thus, the decrease in relative abundance was gradual from 5 to 30 m depth if we consider the relation of mean abundance to AO. The deepest habitats contained more species compared to 15–20 m depth, but in the deepest habitats the species present were less abundant. When fouling Polychaeta Sabellida was excluded from consideration, the mean abundance decreased with increasing depth from 0 to 30 m (Fig. 9b). High abundance at shallow depth mainly involved Amphipoda Gammaridea. The abundance of remaining "non-colonial" macrobenthos increased from 0 to 5 m depth and then gradually decreased to 30 m depth. Depths from 5 to 30 m were similar in the composition of dominant supraspecific taxa with regard to total abundance: Mollusca Bivalvia, Polyplacophora and Gastropoda Pectinibranchia, Crustacea Cirripedia, and Ophiuroidea. Species and higher taxa composition at 0 and 2.5 m depth were significantly different. The most important taxa included Gastropoda Pectinibranchia, Amphipoda Caprellidea and Nemertea Enopla.

The composition of dominant species with regard to abundance changed with depth. At 0 m depth, *Ischyrocerus anguipes, Gammarus setosus, Gammarellus homari* and
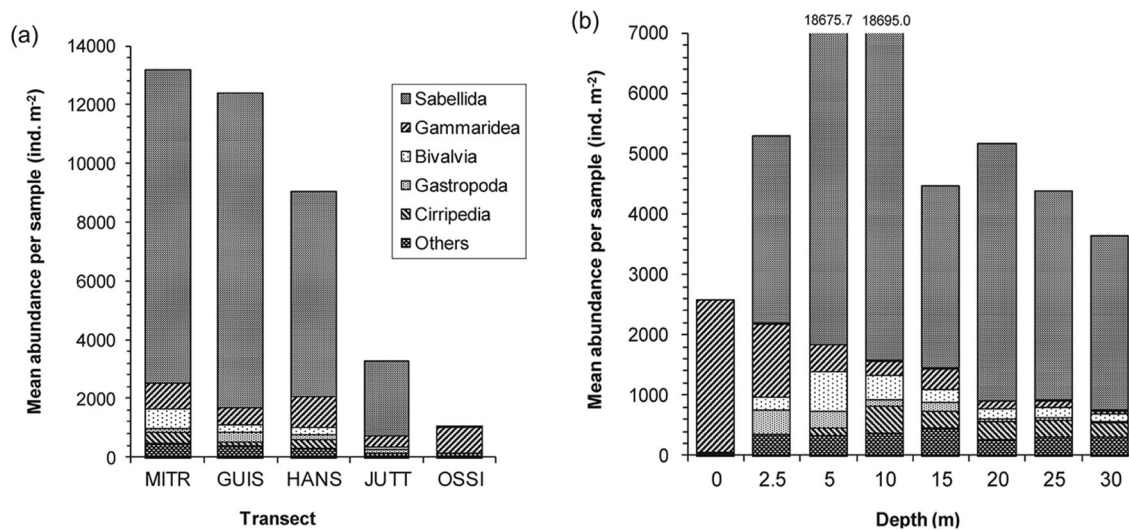

Fig. 9 Mean abundance of main "non-colonial" taxa in samples from (a) transects and (b) depths in Kongsfjorden, Svalbard.
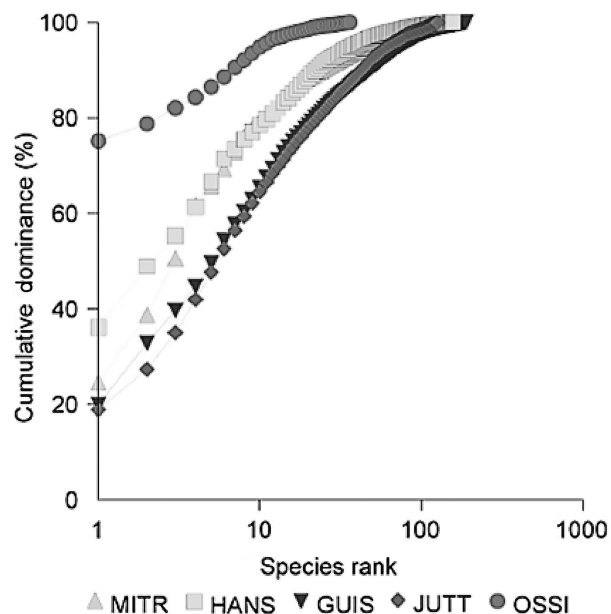
Fig. 10 Cumulative K-dominance curves for abundance of ''non-colonial'' species, without Polychaeta Sabellida, on transects in Kongsfjorden, Svalbard.

Caprella septentrionalis dominated. From 2.5 m depth and deeper, Spirorbidae g. spp. and crustaceans were most abundant in samples. The dominance of molluscs *Margarites helicina*, *Hiatella arctica* and *Musculus* spp. became evident at 2.5 m, but even more so at 5 m depth. From 10 m and deeper, most abundant after Spirorbidae g. spp. were *Balanus balanus*, *Hiatella arctica* and *Tonicella* spp. Partial K-dominance curves after removal of the five to seven most dominant species appeared elevated for 0 and 2.5 m depths showing decreased diversity of abundance characteristics.

Biomass on transects and at depths

Crustaceans formed more than a half of the total biomass (53.7%) in hard-bottom samples from Kongsfjorden. Most (96.8%) crustaceans comprised barnacles *Balanus* and *Semibalanus* (soft parts together with their massive calcareous shell). All other crustaceans (Amphipoda, Decapoda, Cumacea, Isopoda and Mysidacea) represented only 1.7% of total zoobenthic biomass. Bryozoa (13.3%), Echinodermata (12.0%), Bivalvia (8.9%) and Ascidiacea (3.9%) contributed 38.1% of the total biomass, whereas other taxa were up 8.2%. The weight of zoobenthos in samples fluctuated widely, from 0.7 g m^{-2} at 0 m depth on the inner transect OSSI to 10554.9 g m^{-2} at 10 m depth on the outer transect MITR. The variation was high because of high patchiness in community distribution even on the same transect and at the same

depth. The total coefficient of variation for all samples was 162.8%.

Dominance, estimated by elevation of biomass cumulative curves, was biggest for the HANS transect. For the total species list, dominance further decreased in this order: MITR, GUIS, OSSI, JUTT. The most dominant species, which were similar for the three outermost transects, included: the barnacle *Balanus balanus*, sea urchins *Strongylocentrotus droebachiensis* and *S. pallidus*, the mollusc *Hiatella arctica*, branched bryozoans *Tricellaria ternata* and *Eucratea loricata*, the colonial ascidian *Synoicum* sp. and the sponge *Haliclona aqueductus*. Collectively, these species amounted to a much larger biomass than the other species on the MITR and HANS transects, but less so on GUIS. The inner transects OSSI and JUTT had a different set of species with high biomass. Most important were: *Halichondria panacea*, *Hormathia digitata*, *Chlamys islandica*, *Styela rustica* and *Gammarus setosus*. The level of their dominance was less than on the outer transects. However, partial dominance curves, which remove the importance of the most dominant species, showed that the relative diversity of zoobenthos estimated by biomass values was lower on transects close to Kronebreen glacier. The dominance in biomass of "colonial" species was lower than of "non-colonial" species, and, correspondingly, the relative diversity of "colonial" species in terms of their biomass should be considered as higher.

The biomass of organisms was considerably lower in the inner part of the fjord (Fig. 11a). This decrease was characteristic for both "colonial" and "non-colonial" components of the zoobenthos, but the decrease was more pronounced in the "non-colonial" case. The mean biomass per sample on the MITR transect was 2317.2 g m^{-2}, whereas at OSSI it was reduced to 12.3 g m^{-2}. The change in mean biomass towards the inner part of the fjord was not gradual, and the low biomass at GUIS was a consequence of the limited distribution of *Balanus balanus* (Crustacea Cirripedia) aggregations (Fig. 12a). This, in turn, accounted for the low abundance and biomass of the bivalve *Hiatella arctica*, which is closely associated with *Balanus balanus* aggregations, and the low biomass of "colonial" species. The mean biomass of "non-colonial" organisms, with the exception of Crustacea Cirripedia, gradually decreased towards the glaciers.

The mean biomass in samples increased steeply from 0 to 10–15 m depth and then decreased gradually to 30 m (Fig. 11b). The dominant species with regard to biomass at 0 m depth included the amphipods *Gammarellus homari*, *Ischyrocerus anguipes* and *Gammarus setosus*. At 2.5 m, amphipods gave way to the molluscs *Hiatella arctica*, *Margarites helicina* and *Buccinum glaciale*. At greater depths
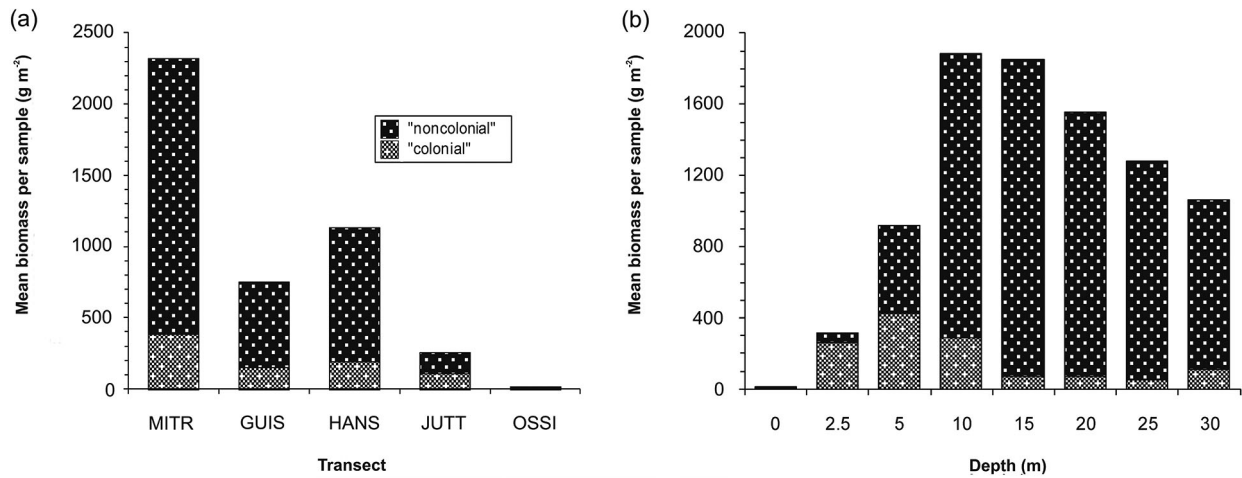
Fig. 11 Mean biomass of "colonial" and "non-colonial" species in samples from (a) transects and (b) depths in Kongsfjorden, Svalbard.

(5–30 m), *Balanus balanus*, *Hiatella arctica* and *Strongylo-centrotus* spp. were most dominant by biomass.

The largest biomasses of "colonial" species (up to 1776.7 g m^{-2}) were skewed to more shallow depths compared to "non-colonials". Depths of 2.5–10 m were optimal for branched colonies of Bryozoa Cheilostomata (mainly *Tricellaria ternata* and *Eucratea loricata*), which contributed most to the biomass of "colonial" species in Kongsfjorden (Fig. 12b). "Non-colonial" species formed the largest biomasses deeper, at 10–20 m depth. A high contribution to biomass was made by motile sea urchins *Strongylocentrotus* spp. However, their distribution by depth may vary seasonally (Agatsuma et al. 2000). Considering "non-colonial" species, with the exclusion of *Strongylocentrotus* spp., mean biomass per sample was largest at 10 m depth and gradually decreased to 30 m depth. This pattern did not completely coincide with the

pattern of average abundance distribution (Fig. 9b), since low mean abundance at 15 m depth was accompanied by high biomass. Low abundance associated with high diversity is often evidence of a "healthy" or "undisturbed" benthic community (Warwick 1986). However, in our case, the zoobenthos at 15–20 m depth had less diversity, in terms of species composition, compared to both shallower and greater depths, which can be interpreted a sign of the "disturbed" state of the biota (Fig. 4b). The disagreement between—on the one hand—the reduced diversity shown by SR and AO data and—on the other hand—high levels of abundance in relation to biomass, which can be interpreted as indicating that the habitat is undisturbed, can be explained by the less pronounced dominance (in terms of abundance) of Polychaeta Sabellida g. spp. at 15 m depth. Sabellida abundance was probably underestimated because of the
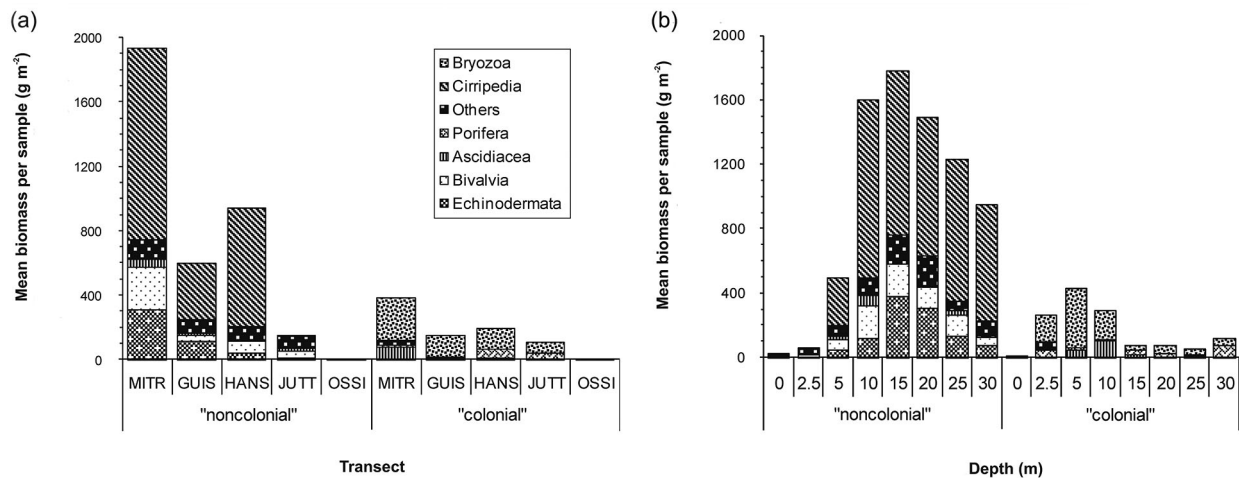

Fig. 12 Taxa biomass distribution in samples from (a) transects and (b) depths in Kongsfjorden, Svalbard.

impossibility of collecting all these little worms from the surface of the bedrock.

Biogeographic characteristics of transects and depths

Considerable differences in zoobenthic composition were not reflected in the main biogeographic groups (Fig. 3) represented on transects along the fjord's axis for joint data on "colonial" and "non-colonial" species. The percentages did not differ significantly among transects. An exception was the increased percentage of species with Arctic distribution on the innermost transect OSSI. The values were 22.9% and 20.7% for SR and AO, respectively, which was higher than for other transects (means 14.6% and 12.3%). The Arctic component was larger on OSSI for both "colonial" and "non-colonial" species. This increase was accompanied by a decrease in high-boreal–Arctic species. The combined values for Arctic and high-boreal–Arctic species were similar for all transects.

Arctic environmental conditions in the inner part of the fjord have consequences for hard-bottom zoobenthic biomass. Species with a boreal–Arctic distributional range contributed considerably to the total biomass on each of the transects. However, their contribution to the biomass found on the innermost transect OSSI was much less compared to the other transects (Fig. 13a). Species with more northern distributional ranges formed almost half (44.6%) of the total biomass on OSSI. The Arctic species on OSSI were mostly "colonial" species, whereas the high-boreal–Arctic species were mainly "solitary." Arctic species also made a relatively high contribution to the total biomass on the JUTT transect in the inner part of the fjord.

The exact contributions of species with different distributional ranges to the total abundance of "non-colonial" species varied among transects, but for all of them, except OSSI, the proportions were generally similar to the combined pattern (Fig. 3). The OSSI transect differed from the other transects in terms of the proportion of high-boreal–Arctic species (80.6% vs. <6.5% on other transects). *Gammarus setosus* contributed most to the very large high-boreal–Arctic component at OSSI. This species was not evenly abundant in samples, and when its extremely high value was down-weighted, the ratio of biogeographic groups detected on OSSI did not differ significantly from other transects. The abundance analysis here did not include data on Polychaeta Sabellida g. spp.

Data on SR, FO, total biomass and abundance showed that species with different latitudinal preferences were distributed unevenly by depth. The proportion of boreal species generally decreased with increasing depth (Fig. 13b). There was a corresponding increase in the percentage of boreal–Arctic species with depth, whereas other groups showed no clear tendencies. We also noted a decrease in the percentage of groups with narrow distributional ranges (Arctic, high-boreal–Arctic and boreal) with increasing depth. FO patterns were similar to SR except for the increased percentage of Arctic species in terms of SR at shallow depths. The "non-colonial" species accounted for the decrease with depth in the occurrence of boreal species, and the concomitant increase with depth in species with wider distribution ranges. In terms of their biogeographic composition, "colonial" species showed fewer changes with respect to the depth gradient. Shallow habitats, especially the shallowest (0 m depth), have singularity in terms of zoobenthos biogeographic composition. A contrast in biogeographic composition between the shallowest depths and the 5–30 m depth range was also apparent for relative biomass (Fig. 13c). A decrease in the percentage of boreal species and an increase in the percentage of species with the widest distributional ranges from 2.5 m depth and deeper were due to the abundance of "non-colonial" organisms (Fig. 13d). Making up a large proportion of the high-boreal–Arctic species was the great abundance of *Gammarus setosus* on the innermost transect OSSI. As noted above, the occurrence of this species in samples was highly variable. The biogeographic composition of hard-bottom zoobenthos is likely sensitive to the presence of separate water layer(s) at shallow depths. However, as described earlier, the decrease in species diversity at 15–20 m depth was not reflected in the biogeographic composition.

Relative importance of different factors

Canonical correspondence analysis (CCA) based on species composition data, together with Monte-Carlo permutation tests (ter Braak & Smilauer 2002), were used to estimate the relative importance and correlation of environmental factors (Table 1) with regard to species. Depth was most important for explaining the variance in zoobenthos composition in samples from hard substrata in Kongsfjorden (Table 3). Depth was positively correlated with the type of substratum (bedrock, gravel to muddy gravel) and negatively correlated with the substratum inclination and seabed feature (gentle slope to steep rock) as well as to exposure to waves (Fig. 14a). The factor of distance from the Kronebreen glacier showed a stronger positive relation to water currents than did the factor of depth. The relation to the amount of silt on the substratum surface was negative for the factor of distance
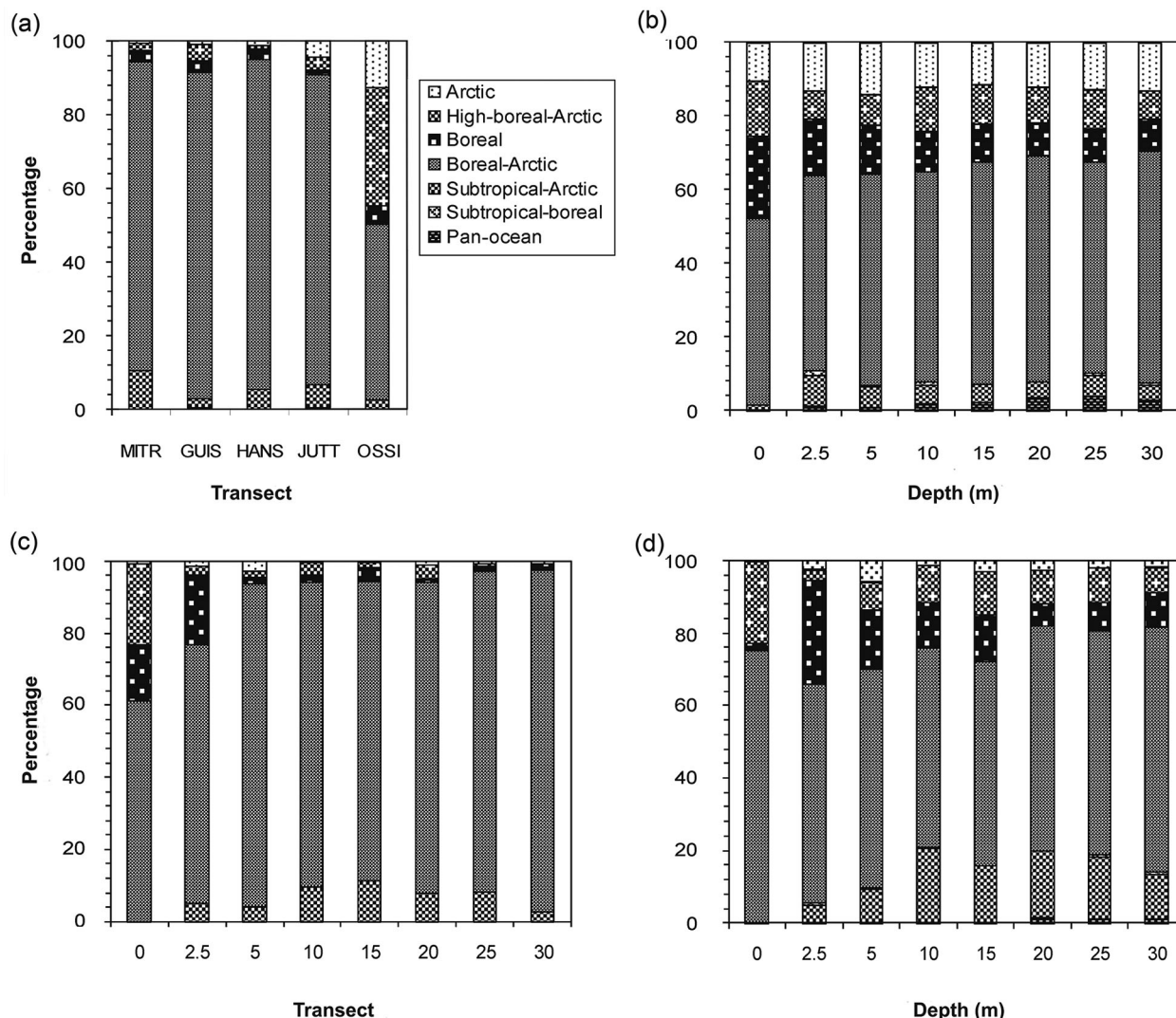
Fig. 13 Percentages of species with different biogeographic characteristics (%) in (a) total biomass on transects for depths combined, (b) frequency of species occurrence, (c) total biomass and (d) abundance of "non-colonial" organisms for transects combined at depths in Kongsfjorden, Svalbard.

from glacier and this relation was also stronger than for the factor of depth.

Depth and distance from the glacier, together with substratum type and amount of silt on the substratum surface, explained most of the variation in the presence of different species, biomass and the abundance of "non-colonial" species. Factors of water movement, i.e., exposure to waves and strength of water currents, as well as substratum inclination, i.e., angle of substratum inclination and seabed feature (gentle slope to steep rock), had little impact on zoobenthos distribution compared to depth, distance from the glacier, substratum type and amount of silt. For the total biomass and the total species occurrence in the samples, these four factors displayed a high level of significance. The "non-colonial" part of the fauna, which dominated over the "colonial"

species, was similarly linked to these four factors. The "colonial" component was somewhat peculiar insofar as its species composition was more strongly linked to distance from the glacier and angle of substratum than to the primary substratum type and the amount of silt on the rock surface. "Colonial" organisms were more diverse in the outer part of the fjord and in habitats with steep relief. The variation in "colonial" biomass distribution along the fjord's axis was not significantly connected to the distance from glacier (Table 3).

The CCA plot joined the patterns of species distributions in the samples and showed their relation to different factors. The 38 most important species for hard-bottom habitats were selected from a total number of 403 species using the similarity percentages (SIMPER) procedure (Clarke & Gorley 2001). Species that contributed most

Table 3 Significance levels from the Monte Carlo permutation test for factors which affected species composition, biomass and abundance of zoobenthos on hard substrata in Kongsfjorden, Svalbard. *P* values at the 95% confidence level are marked with asterisks.

Factor	Species composition			Biomass			Abundance
	"Colonial"	"Non-colonial"	Total	"Colonial"	"Non-colonial"	Total	"Non-colonial"
Depth (m)	0.002*	0.002*	0.002*	0.002*	0.002*	0.002*	0.002*
Substratum type	0.092	0.002*	0.002*	0.002*	0.012*	0.004*	0.008*
Amount of silt on substratum surface[a]	0.356	0.004*	0.004*	0.002*	0.002*	0.020*	0.026*
Distance from glacier front (km)	0.002*	0.002*	0.002*	0.360	0.024*	0.002*	0.418
Exposure to tidal waves[b]	0.166	0.090	0.162	0.138	0.272	0.238	0.002*
Angle of substratum inclination in sample frame	0.028*	0.162	0.164	0.516	0.392	0.312	0.290
Water current flow[c]	0.316	0.384	0.482	0.456	0.262	0.668	0.044*
Seabed feature[d]	0.570	0.418	0.590	0.612	0.322	0.454	0.450

[a] 1 =no mud/silt; 2 =only some sediments; 3 =very thin layer on rocks; 4 =thin flocculent layer; 5 =thick cover.
[b] 1 =extremely sheltered; 2 =very sheltered; 3 =sheltered; 4 =semi-exposed; 5 =exposed; 6 =very exposed.
[c] 1 =ca. 0 m sec^{-1}; 2 =0.1–.5 m sec^{-1}; 3 =0.6–1 m sec^{-1}; 4 =>ca. 1 m sec^{-1}.
[d] 1 =gentle slope; 2 =steep rock.

to the occurrence, abundance and biomass dissimilarity among samples were, as a rule, the most widely distributed in the studied habitats and/or they had the highest abundance/biomass in the samples. The resulting chart (Fig. 14b) is especially interesting in the context of closely related species whose statuses as distinct species are currently being discussed. For example, the closely related bivalves *Musculus discors* and *Musculus laevigatus* showed major variation in distribution related to distance from the glacier, but not to depth. *M. laevigatus* is likely more tolerant to the turbid conditions in the inner part of the fjord, than *M. discors* (Fig. 14b). The sea urchins *Strongylocentrotus droebachiensis* and *S. pallidus*, on the other hand, showed major variation in distribution in
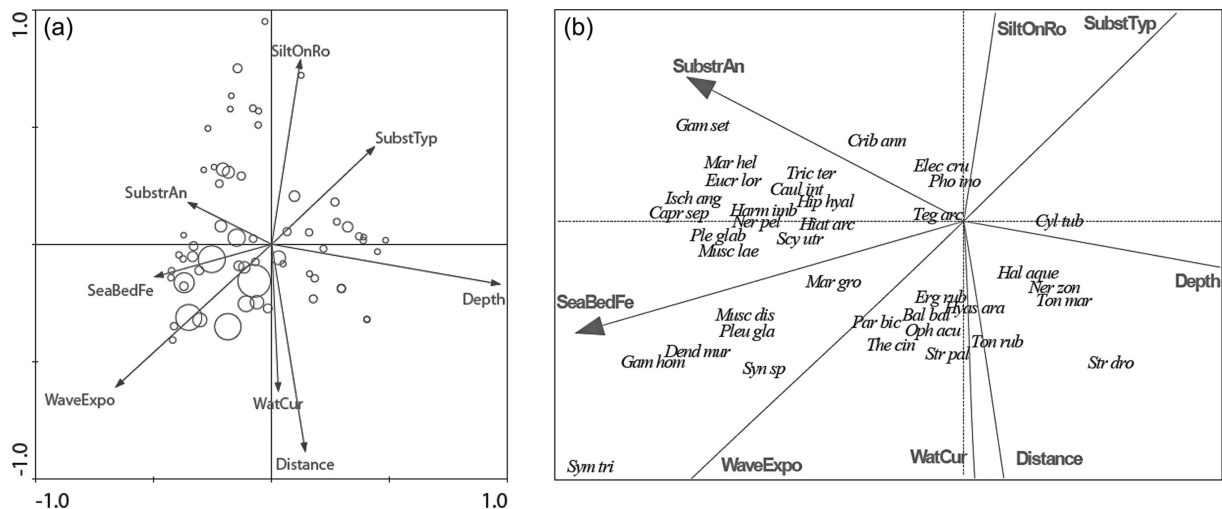

Fig. 14 Canonical correspondence analysis plots for zoobenthos on hard substrata in Kongsfjorden, Svalbard. (a) Biplot samples/factors (data on presence/absence of 403 species in samples, focus on inter-species distances, square root transformation). In (a), the size of the circles corresponds to the total biomass of each sample. Factors designations as in Table 1. (b) Biplot species/factors (data on presence/absence of 403 species in samples, focus on inter-species distances, square root transformation). The biplot is zoomed to show 38 species, which are the most widely distributed in studied habitats and (or) with the greatest abundance/biomass in samples. Species are abbreviated as follows: *Balanus balanus* Bal bal; *Caprella septentrionalis* Capr sep; *Cauloramphus intermedius* Caul int; *Cribrilina annulata* Crib ann; *Cylindroporella tubulosa* Cyl tub; *Dendrobeania murrayana* Dend mur; *Electra crustulenta arctica* Elec cru; *Erginus rubella* Erg rub; *Eucratea loricata* Eucr lor; *Gammarellus homari* Gam hom; *Gammarus setosus* Gam set; *Haliclona aqueductus* Hal aque; *Harmothoe imbricata* Harm imb; *Hiatella arctica* Hiat arc; *Hippothoa hyalina* Hip hyal; *Hyas araneus* Hyas ara; *Ischyrocerus anguipes* Isch ang; *Margarites groenlandica* var. *groenlandica* Mar gro; *Margarites helicina* Mar hel; *Musculus discors* Musc dis; *Musculus laevigatus* Musc lae; *Nereis pelagica* Ner pel; *Nereis zonata* Ner zon; *Ophiopholis aculeata* Oph acu; *Parapleustes bicuspis* Par bic; *Pholoe inornata* Pho ino; *Pleusymtes glabroides* Ple glab; *Pleusymtes glaber* Pleu gla; *Scypha utriculus* Scy utr; *Strongylocentrotus droebachiensis* Str dro; *Strongylocentrotus pallidus* Str pal; *Symplectoscyphus tricuspidatus* var. *acuminatus* Sym tri; *Synoicum* sp. Syn sp; *Tegella arctica* Teg arc; *Thelepus cincinnatus* The cin; *Tonicella marmorea* Ton mar; *Tonicella rubra* Ton rub; *Tricellaria ternata* Tric ter.

relation to depth, with *S. droebachiensis* distributed in deeper habitats than *S. pallidus.* Samples with the largest biomass came from steep rock habitats at intermediate depths in the fjord's outer reaches, which are exposed to waves and currents and, correspondingly, have little sedimentation (Fig. 14a).

Discussion

Investigations of the hard-bottom zoobenthos in Kongsfjorden were started in 1962. The French Recherche Coopérative sur Programme 42 expedition collected quite extensive data from different transects and points in Krossfjorden, Kongsfjorden and the Forlandsundet area (Lagardere 1968). Some of the samples were collected by SCUBA divers. Among sampling locations were those in the vicinity of Kapp Mitra, Kapp Guissez and Juttaholmen. Using SCUBA equipment allows for making more detailed description of hard-bottom habitats. Unfortunately, most of data collected by the expedition remain unpublished. The only published work estimates the diversity of Crustacea in the fjord at a depth range of 5 to 40 m. Lagardere (1968) rated the fauna of the fjord as a composition of well-known species with little original peculiarity. However, showing a certain distinctness of Kongsfjorden's ecosystem, he described four new species and one new genus of Amphipoda, in addition to finding 32 known crustacean species. Our samples are less extensive than samples collected by the French expedition in 1962, but our list of crustaceans contains more species (65). This suggests that modern collecting equipment and methods of processing samples are important for accurately estimating diversity.

After 1962, the macrobenthos of Kongsfjorden was not thoroughly investigated for approximately 20 years. The development of national and international research programmes (e.g., Swerpel & Weslawski 1989; Warwick et al. 2003), better logistic infrastructure and the establishment of the Kings Bay Marine Laboratory (2005) resulted in considerable increase of research activity in Kongsfjorden. Several works containing zoobenthic species lists were published (Ambrose & Leinaas 1988; Hansen & Haugen 1989; Wlodarska-Kowalczuk et al. 1998; Jørgensen & Gulliksen 2001; Lippert et al. 2001; Kendall et al. 2003; Weslawski et al. 2003; Laudien et al. 2004; Lippert 2004; Sahade et al. 2004; Wessels et al. 2004; Wlodarska-Kowalczuk & Pearson 2004; Bick & Arlt 2005; Kaczmarek et al. 2005; McMahon et al. 2006; Weslawski et al. 2006; Wessels et al. 2006; Carlsen et al. 2007; Beuchel & Gulliksen 2008; Kedra et al. 2011).

Special attention has been paid to specific benthic taxa: benthic Foraminifera (Elverhøi et al. 1980); Porifera

(Assmann 2004); Hydrozoa (Ronowicz 2007; Ronowicz et al. 2008; Voronkov et al. 2010); Mollusca (Wlodarska-Kowalczuk 2007); Crustacea (Blazewicz-Paszkowycz & Sekulska-Nalewajko 2004); Bryozoa (Gontar et al. 2001; Kuklinski 2002, 2005; Kuklinski & Barnes 2005a, b; Kuklinski et al. 2005, 2006; Kuklinski & Bader 2007); and Sipuncula (Kedra & Murina 2007; Kedra & Wlodarska-Kowalczuk 2008). The composition and distribution of other groups need to be described more thoroughly and the inventory of the fauna cannot be considered as complete. This is evident from our samples, for which the species accumulation curve was not asymptotic even with 62 samples.

The contribution of this study to the inventory of Svalbard fauna was estimated using the list of the marine macro-organisms in Svalbard waters published by Palerud et al. (2004) and its previous version in Gulliksen et al. (1999), which also includes the waters around the island Jan Mayen and contains some synonyms. Our samples contained 25.9% of the total number of species of zoobenthic invertebrate macroorganisms recorded to date in Svalbard waters (Table 2). The majority of species have been reported previously for the Svalbard area. Forty-seven species from our samples should probably be considered new for the area (Supplementary Table S1). For eight species from our list, which are not mentioned in Palerud et al. (2004) but are in Gulliksen et al. (1999), it is possible to extend the limits of their distribution from Jan Mayen or Bjørnøya (Bear Island) to Spitsbergen in the Svalbard Archipelago.

For the majority of supraspecific taxa, the number of species was less than 50% of the total number of species recorded in specific taxa in the Svalbard or Barents Sea area (Table 2), except for Bryozoa and some taxa with low SR. This suggests that more extensive sampling will reduce the underestimation of diversity on hard substrata, as indicated by the cumulative species count (Clarke & Warwick 2001).

Our data on species composition showed good correspondence with estimations made by other authors in similar habitats and depth ranges. For example, the number of bryozoans identified down to the species level in our Kongsfjorden samples was 106 (excluding new species). Kuklinski et al. (2005) reported an asymptotic species accumulation curve with the detection of 108 bryozoan species. This could suggest that the estimation of species composition is somewhat complete for this group. However, the diversity of other groups, such as Echinodermata, seems to be underestimated in our survey. Our sampling design, which used standard double 0.25 m^2 square frames at each depth on the transects, lowers the chance of recording large rare individuals. It also makes

accounting of periphyton more difficult. A sampling design that includes more frames of different sizes $(0.25 - 0.01 \text{ m}^2)$, together with recordings of large rare individuals or colonies along transects, may yield a more complete inventory of species (e.g., Skarlato et al. 1967).

Despite several studies on the soft-bottom fauna in Kongsfjorden (e.g., Kendall et al. 2003; Laudien et al. 2004; Wlodarska-Kowalczuk & Pearson 2004; Kaczmarek et al. 2005), there is still no complete published list of soft-bottom species. Comparing soft- and hard-bottom fauna in terms of diversity is therefore difficult. It is known that biodiversity is generally higher on coasts compared to offshore areas (Gray 1997), although the magnitude of difference may vary depending on scale and geographic position. Based on dredged samples from a single expedition, Kaczmarek et al. (2005) reported the presence of 123 taxa in a soft-bottom association at depths ranging from 5 to 50 m. This is 3.3 times less than the number of species we found on the hard-bottom in our study.

Decreased diversity in inner parts of fjords has been demonstrated by many studies of the soft-bottom (e.g., Schmid & Piepenburg 1993; Kendall 1994; Wlodarska-Kowalczuk & Pearson 2004; Kaczmarek et al. 2005) and intertidal habitats (Brattegard 1966). Our data also show decreased SR and FO in the inner part of the fjord. However, the decrease was not gradual. Lower diversity on the GUIS transect compared to HANS was probably related to less abundant *Balanus balanus* associations at GUIS. The reason for such limited distribution of this highly important habitat-forming species is not clear, but could also reflect patchiness in the hard-bottom environment. Decreased diversity on the hard bottom in the inner part of the fjord was associated with a high percentage of species widely distributed on the transects. These species are common and can resist chronic natural disturbance connected with glacier run-off to inner fjord habitats (Wlodarska-Kowalczuk et al. 2005). Similarly, 15–20 m depth showed a high percentage of species that are common at different depths, i.e., "eurybathic" species, which could be evidence of some natural disturbance. Species compositions at 5–10 m depth were quite different from those at 25–30 m depth, which leads us to propose the presence of unstable transitional water masses or layers at the "intermediate" depth of 15–20 m. Hydrographical studies in the upper 30 m depth layer in near-shore areas in the fjord are a topical problem, given that there is no consensus regarding the structure of the upper 30 m water layer. Such studies could support or undermine the hypothesis that the decreased diversity at 15–20 m depth is the result of unstable conditions. This depth also represents the lower

limit for the kelp zone, where brown algae terminate and only red algae continue to depth of at least 30 m (Hop et al. 2012). Relating zoobenthos to macroalgae distribution could elucidate this transitional zone. Another possible explanation of the lower diversity at 25–30 m depth could be related to the slope angle, which tends to be less steep at depth below 20 m. Gravel patches and pockets of sediments start to appear below this depth. This results in some diversification of habitats, with a corresponding increase of species diversity. Iceberg scour is unlikely to occur at 15–20 m depth. Big icebergs strand on the sills between the inner and middle parts of the fjord, around Lovénøyane and Blomstrandhalvøya (Svendsen et al. 2002), where the depth is usually less than 20 m.

We found that the shallowest habitats (0–2.5 m) also had reduced species diversity. However, the pattern was different from that mentioned above. There was a high percentage of species that were found only at this depth and the neighbouring depth. This indicates that decreased diversity in the shallowest habitats is caused by factors other than those that account for the decreased diversity in the inner part of the fjord and at 15–25 m depth. The "specialization" of species in relation to conditions at shallow depth in Kongsfjorden is more pronounced than in relation to glaciomarine conditions. However, high peculiarity at this depth is accompanied by a high percentage of "eurybathic" species. This emphasizes the high natural disturbance in this habitat.

According to Kaczmarek et al. (2005), the composition of soft- and hard-bottom faunal associations in Kongsfjorden is primarily dependent on the bottom type, with the depth gradient having no effect. However, our data provide evidence that the main factor structuring diversity of the benthos on hard substrata is depth. The type of substratum, which is correlated with depth, is also important, but less so than the depth. Glacier-induced sedimentation is often mentioned as a main reason for the decrease of diversity of soft-bottom fauna in inner parts of Arctic and sub-Arctic fjords (Holte et al. 1996; Kaczmarek et al. 2005; Wlodarska-Kowalczuk et al. 2005). Our data support this. The impact of the amount of silt on the rock surface is high for species composition, abundance and biomass.

The angle of the hard substratum surface may also be of great importance for faunal composition (Jørgensen & Gulliksen 2001). Our data indicate that the factor of substratum inclination is not very important, but the sampling site used by Jørgensen & Gulliksen (2001) included steeper rock walls with overhangs. The only significant influence the substratum angle had in our study was on the composition of "colonial" species, with

higher diversity in steep relief habitats. Dividing the zoobenthos into "colonial" and "non-colonial" species is somewhat subjective, given that the degree of integration of cells or individuals into colonies varies. However, such a division may have promise in the study of zoobenthic features in relation to environmental change. Based on the different compositions and distribution of "colonial" and "non-colonial" species, we propose that these two groups of species will show different responses to environmental change and, consequently, their relative part in carbon cycling in the fjord's ecosystem may vary. A review of the literature shows that there has been little effort to describe the relation of "colonial" and "non-colonial" species in different habitats and conditions. Further investigations could help to clarify whether the differences described in this paper are connected to the integration of specimens into colonies or whether they have other causes.

Different researchers use different systems to analyse the biogeographic composition of the fauna, and the sampling ranges and habitats also vary. This makes it difficult to compare results. In spite of this, we can estimate the position of Kongsfjorden as intermediate between boreal and Arctic fjord environments. Golikov et al. (1985) estimated that boreal species comprise 33–38% of species on hard substrata, and Arctic species as 1–2%, in different parts of the Chupa Inlet of the White Sea. The percentage of boreal species in High-Arctic shallow habitats (0–36 m) in Franz Josef Land was 1–3% (Golikov & Averincev 1977) and Arctic species comprised 14–19%. In our Kongsfjorden study, boreal species represented 9.7% and Arctic species 16.6%. The relatively high contribution of boreal species is because of the influence of the warm West Spitsbergen Current. This influence does not, however, prevent the existence of Arctic species, and the relatively high percentage of Arctic species is a feature of the Arctic location of the fjord. The relative importance of Arctic and high-boreal–Arctic biogeographic groups was higher in the inner part of Kongsfjorden, indicating that the inner part of this fjord is more Arctic, whereas the outer part is more boreal or sub-Arctic. This was most notable at the OSSI transect, which lay closest to the Kronebreen glacier. The biogeographic composition at the other transects was rather similar in spite of differences in species composition. This illustrates the similarity of Kongsfjorden, which has sub-Arctic characteristics on account of transformed Atlantic water advected into the fjord (Hop et al. 2002; Svendsen et al. 2002), with eastern Atlantic fjords, where the increased percentage of species with northern distributional ranges in the innermost parts is a common feature (Brattegard 1966). This differs from the western Pacific boreal

gulfs and bays, where continental climatic conditions support the dominance of warm-water species in inner parts (Golikov & Skarlato 1965, 1967, 1968; Skarlato et al. 1967). The absence of significant differences in biogeographic composition in the four more outer transects could indicate that limits of zoobenthic species resistance are broad and that along-fjord gradients in environmental conditions are not strong enough to structure the hard-bottom benthos. From a benthic point of view, the North Atlantic water influence is relatively similar for outer and middle parts of the fjord, including habitats on the border between middle and inner parts of the fjord (transect JUTT).

In a study by Golikov & Averincev (1977), the authors stated that at sites with High-Arctic conditions the proportion of widespread boreal–Arctic species was larger compared to localities with moderate Arctic conditions. Arctic environmental conditions predominate in the inner part of Kongsfjorden, but we did not record a larger proportion of boreal–Arctic species. In our samples, boreal–Arctic species contributed more to total biomass in the outer part of the fjord, whereas the percentage of Arctic and high-boreal–Arctic species was more pronounced in the inner fjord's basin. The tendency of the percentage of boreal species on hard substrata to decrease with increasing depth has been described for Chupa Inlet in the White Sea (Golikov et al. 1985) and for Ramfjorden in mainland Norway (Soot-Ryen 1924), and this was also valid for our Kongsfjorden transects.

Our biomass data do not allow the direct estimation of differences in the content of organic carbon in samples. Species have different fractions of organic carbon content in relation to biomass. Combining data on these fractions and data on weights distribution could allow the estimation of organic carbon budgets in different parts of the fjord and at different depths.

It is necessary to note that the properties of the hard-bottom communities of the fjord, as described here, are valid for August–September. Seasonality is a characteristic feature of Svalbard fjords (Weslawski et al. 1988; Kedra et al. 2011). Even though benthic communities are more stable seasonally than pelagic communities, seasonal migrations and presence/absence of juveniles in samples may change some diversity patterns. To clarify this it necessary to include a seasonal aspect in the hard-bottom ecosystem studies in Kongsfjorden. In addition, there are interannual variations that only can be addressed in long-term monitoring studies (Beuchel et al. 2006). Our study represents a detailed species inventory of hard-bottom benthos, with identification of the main physical factors influencing species diversity and community composition. Climate-related changes in

benthic fauna can only be addressed if one knows the diversity relative to environmental gradients. Repeating some of these quantitative recordings in future studies could elucidate the effects of climate change, such as the potential expansion of boreal species and invasions of new species.

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