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Distribution and composition of the epibenthic megafauna north of Svalbard (Arctic)

M. Sswat · B. Gulliksen · I. Menn · A. K. Sweetman · D. Piepenburg

Abstract Benthic communities north of Svalbard are less investigated than in other Arctic shelf regions, as this area was covered by sea-ice during most of the year. Improving our knowledge on this region is timely, however, since climate change is strongly evident there, particularly with regard to the extent of sea-ice decline and its huge ecological impact on all marine biota, including the benthos. Moreover, longer ice-free periods will certainly lead to an increase in human activity levels in the area, including bottom trawling. In two adjacent shelf and slope regions off northern Svalbard, we studied the composition of epibenthic megafauna and seafloor habitat structures by analyzing seabed images taken with both still and video cameras. In addition, we also used an Agassiz trawl to catch epibenthic organisms for ground-truthing seabed-image information. A wide variety of mostly sessile organisms 141 epibenthic taxa were identified in the images. The brittle star *Ophiura sarsii* and the soft coral *Gersemia rubiformis* were the most common species. At all stations >300 m in depth, evidence of trawling activities was detected at the seabed. The distribution of the benthic fauna in the study area exhibited a clear depth zonation, mainly reflecting depth-related differences in seabed composition. We conclude that natural factors determining the composition of the seafloor mostly affect the distribution and composition of epibenthic assemblages. Anthropogenic impact indicated by the trawl scours found is likely also important at smaller spatial scales.

Keywords Arctic · Svalbard · Epibenthic megafauna · Depth · Zonation · Community structure · Trawling

M. Sswat (✉) · D. Piepenburg
Department of Polar Ecology, Institute for Ecosystem Research, University of Kiel, 24118 Kiel, Germany
e-mail: michaelsswat@gmail.com

Present Address:
M. Sswat
GEOMAR, Helmholtz Centre for Ocean Research Kiel, Kiel, Germany

B. Gulliksen
Faculty of Biosciences, Fisheries and Economics, University of Tromsö, 9037 Tromsö, Norway

I. Menn
Greenpeace Germany, 20457 Hamburg, Germany

A. K. Sweetman
International Research Institute of Stavanger, 4070 Randaberg, Norway

D. Piepenburg
Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, 27570 Bremerhaven, Germany

Introduction

The knowledge on Arctic benthic ecosystems, their functioning and drivers has strongly increased in the past two decades (Piepenburg 2005), especially for the regions off Svalbard and the northern Barents Sea (Piepenburg et al. 2011). The majority of the studies focused on the structure of benthic communities in the fjords of Spitsbergen (Holte and Gulliksen 1998; Wlodarska-Kowalczuk et al. 1998; Hop et al. 2002; Kendall et al. 2003; Wlodarska-Kowalczuk and Pearson 2004; Renaud et al. 2007), off the western coast of Spitsbergen (Blacker 1957, 1965), and on the shelf break of the Fram Strait (Weslawski et al. 2003;

Wlodarska-Kowalczuk and Pearson 2004). The deep-sea benthos of the eastern Fram Strait have been intensively investigated in the course of the long-term HAUSGAR-TEN project (Soltwedel et al. 2005, 2009; Hoste et al. 2007; Budaeva et al. 2008; Bergmann et al. 2009, 2011; van Oevelen et al. 2011). Other benthic studies have concentrated on the Barents Sea (Zenkevich 1963; Antipova 1975; Carroll et al. 2008; Cochrane et al. 2009). In comparison, the waters north of Svalbard have been much less investigated, since this region was covered by sea-ice during most of the year before the onset of the general sea-ice decline in the Arctic (ACIA 2004).

Improving our knowledge on the area north of Svalbard is timely, however, since it belongs to the Arctic sea regions where climate change is strongly evident (IPCC 2007), particularly with regard to the extent of sea-ice decline (Onarheim et al. 2014) and its huge ecological impact on all marine biota, including the benthos (Piepenburg 2005). Moreover, longer ice-free periods will certainly lead to an increase in human activity levels, in Arctic seas in general and the waters north of Svalbard in particular, including bottom trawling (ACIA 2004). This development will exert additional anthropogenic pressure on the marine ecosystems by either direct top–down effects of the fishery or indirect bottom–up effects by subsequent changes in trophic relationships or, most likely, the combination of both (Renaud et al. 2008; Perry et al. 2010). To document such direct anthropogenic impact on the benthos, field studies are necessary to document the current status of the threatened habitats.

The largely sessile mode of life and relatively long life spans of macro- and megabenthic fauna are biological traits that make these animals, at a scale of either organisms or communities, useful for detection of time-integrated responses to alterations in environmental conditions (Pearson and Barnett 1987; Underwood 1996). Therefore, the composition, diversity, abundance and biomass of macro- and megabenthic benthic communities have often been used as sensitive indicators of natural decadal-scale environmental change (e.g., Reise and Schubert 1987; Kröncke 1995; Kröncke et al. 1998, 2001; Tunberg and Nelson 1998; Gröger and Rumohr 2006) and of the ecological impacts of human activities like fishing and eutrophication (e.g., Pearson and Rosenberg 1978; Underwood 1996; Pearson and Mannvik 1998; Beukema et al. 2002; Carroll et al. 2003; Kaiser et al. 2006).

The main objective of our field study was to provide a qualitative and quantitative inventory of the epibenthic megafauna communities of the shelf and upper slope north of Svalbard. In addition, we elucidated the influence of environmental factors (water depth, seabed properties) on the faunal distribution and composition. Moreover, we investigated the evidence of trawling activities in the study area. Our study was aimed to provide baseline information on the current status of the benthos in the target area that can be used to detect the effects of future anthropogenic and natural impacts in the Arctic.

## Materials and methods

Study area

The study was carried out in the region north of Svalbard, which features the continental shelf, deep shelf troughs and the upper continental slope (Fig. 1). It is characterized by the close juxtaposition of different water masses. Water of Atlantic origin, transported northward with the Spitsbergen Current and sinking on its way eastward below the sea surface, influences the northwestern region, while Arctic waters prevail in the southeastern region (Fig. 1). This, together with the complex shelf geomorphology and the seasonal dynamics of sea-ice cover, results in diverse environmental conditions (Carroll et al. 2008). Moreover, this area is affected by a particularly profound decrease in sea-ice cover. The decline is evident over the entire year but is most pronounced in winter, in contrast to the summer melts in the central Arctic Ocean (Onarheim et al. 2014). The region is part of the northern Barents Sea shelf, which is generally characterized by a relatively high average productivity of 93 g C m^2 $year^{-1}$, accounting for 49 % of the total Arctic shelf primary production (Sakshaug 2004; Wassmann et al. 2006). Gulliksen et al. (1999) reported a total of 363 species of marine benthic macro-organisms to occur in the study area.

Field sampling

Epibenthic megafauna communities were investigated during the Greenpeace Arctic Expedition of MS "Esperanza" in June 2010. A sonde equipped with both a video and a still camera was lowered vertically from the drifting ship (Table 1) at a total of 22 stations along bottom transects with lengths ranging from 0.22 to 2.97 nautical miles (mean: 1.2 nm) at water depths between 50 and 450 m (Fig. 1). Continuous video footage was obtained by the sonde's standard-definition composite PAL video camera (576i; 576 interlaced lines), towed 1 m above the ground and looking at the seabed at an approximate angle of 45°. In addition, high-resolution still pictures were taken by the operator using an oblique-mounted still camera (17-mm lens, 10.5 Mega Pixel) fixed above the video camera, whenever interesting organisms or habitat features were detected in the real-time video footage.

In September 2011, additional seabed still photographs were taken by means of another drop-camera system

Fig. 1 Location of sampling stations off northern Svalbard visited in 2010 and 2011. Lengths of video/photograph transects are indicated by *red lines*. (Color figure online)
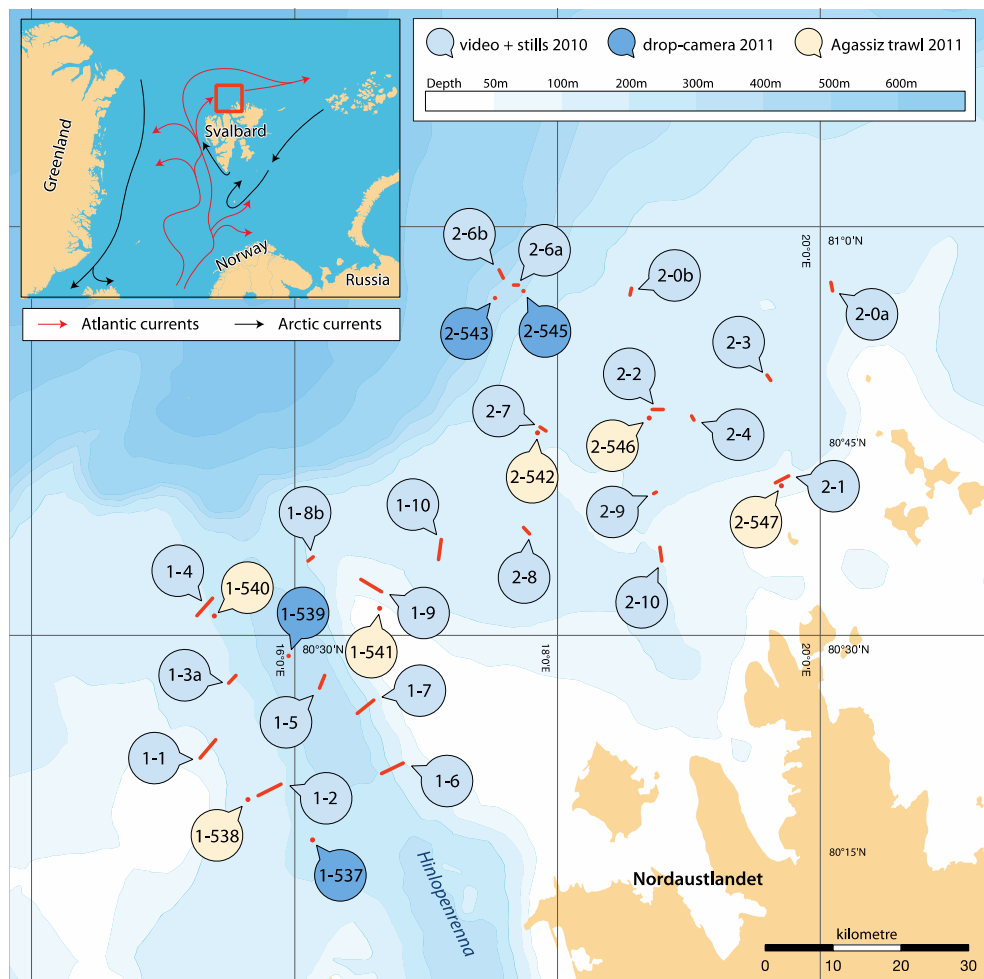
during the cruise of the Norwegian RV "Helmer Hanssen" to northern Svalbard at four stations, using the approach described by Sweetman and Chapman (2011).

In addition, Agassiz trawl (AGT) samples were collected in September 2011 at six selected stations (Fig. 1; Table 1), to aid the taxonomic identification of organisms visible in the seabed images. These stations were chosen to be as close as possible to the imaging stations visited in 2010, which were most diverse in terms of the composition of epibenthic taxa (stations 1-2, 1-4, 1-9, 2-1, 2-2, and 2-7). The width of the AGT frame was 2 m, and the mesh size of the net was 2 cm. All AGT hauls lasted 25 min (time of trawling over the bottom).

Image analysis

All epibenthic megafauna visible in the seabed images and collected from AGT catches were identified to the lowest possible taxonomic level, using various references (Gulliksen et al. 1999; Gulliksen and Svensen 2004; Moen and Svensen 2004; Appeltans et al. 2012; Palomares and Pauly 2014; http://

hercules.kgs.ku.edu/hexacoral/anemone2/index.cfm). Furthermore, taxonomic specialists were consulted for expert advice (personal communication: J. Berge, T. Brattegard, S. Cochrane, P. Kuklinski, A. Plotkin, P. Renaud, A.H. Tandberg, M. Włodarska-Kowalczuk).

Based on the height over ground and the field of vision of the obliquely oriented video camera, each frame shot approximately depicts a rectangular seabed area with a baseline of 1 m and a "depth" (in drift direction) of 1.2 m. The latter was estimated using the drift speed of the sonde (grand average across all stations: 0.6 ± 0.4 m s^{-1} SD, range: 0.1 to 1.8 m s^{-1}) and the time needed to cross the area imaged in a frame shot, which was taken from the video frame time stamps. Therefore, each frame shot depicted a seabed area of approximately 1.2 m^2. A subset of frame shots was randomly chosen for each station for further image analysis to gain for quantitative information on the abundances of ten higher taxa that could be unequivocally identified in the frame shots: poriferans, soft corals (mainly of *Gersemia rubiformis*), actiniarians, decapod crustaceans (mostly *Pandalus borealis*), crinoids,

Table 1 Information on stations where seabed images and Agassiz trawl catches were taken in 2010 and 2011

Station			Mean depth in m	Depth range in m	Zone	Transect length in nautical miles	Number of stills	Number of video frame shots analyzed
Photograph /video sonde casts (2010)	Start of transect	End of transect						
1-1	80°20.723′N 15°16.764′E	80°22.125′N 15°24.120′E	94	81–110	Shallow	2.97	52	45
1-8b	80°35.640′N 16°06.231′E	80°35.876′N 16°08.432′E	56	51–60	Shallow	0.95	54	19
1-9	80°33.256′N 16°39.688′E	80°34.201′N 16°30.270′E	56	50–65	Shallow	1.92	56	50
2-1	80°40.098′N 19°41.817′E	80°40.609′N 19°47.894′E	73	51–87	Shallow	1.12	29	29
2-2	80°46.764′N 18°43.116′E	80°46.797′N 18°48.271′E	87	84–90	Shallow	0.83	30	31
2-3	80°49.280′N 19°35.563′E	80°48.886′N 19°37.158′E	123	136–109	Shallow	0.80	20	19
2-4	80°46.251′N 19°01.321′E	80°46.031′N 19°02.183′E	89	87–90	Shallow	0.80	37	30
2-7	80°45.468′N 17°52.023′E	80°45.206′ 17°54.672′	113	111–114	Shallow	0.67	37	31
2-8	80°38.118′N 17°44.412′E	80°37.577′N 17°47.339′E	138	132–144	Shallow	0.74	9	30
2-9	80°40.600′ 18°43.900′E	80°40.700′ 18°45.100′E	90	90	Shallow	0.22	24	31
2-10	80°36.612′N 18°46.681′E	80°35.586′N 18°47.541′E	58	55–60	Shallow	1.31	26	30
1-2	80°17.804′N 15°43.429′E	80°18.668′N 15°53.746′E	176	163–193	Intermediate	1.94	39	46
1-3a	80°26.434′N 15°28.855′E	80°26.992′N 15°33.335′E	180	170–190	Intermediate	0.93	68	48
1-4	80°32.846′N 15°22.637′E	80°31.543′N 15°15.405′E	193	160–251	Intermediate	1.77	41	40
1-10	80°37.222′N 17°06.948′E	80°35.664′N 17°05.777′E	161	150–176	Intermediate	1.59	32	40
2-0a	80°55.972′N 20°04.843′E	80°55.365′N 20°05.516′E	112	150–174	Intermediate	0.65	13	25
2-0b	80°55.650′N 18°33.766′E	80°55.112′N 18°33.198′E	169	165–176	Intermediate	0.59	40	31
2-6a	80°55.845′N 17°42.126′E	80°55.782′N 17°39.914′E	238	238	Intermediate	0.48	20	11
1-5	80°26.965′N 16°13.746′E	80°26.027′N 16°11.269′E	398	366–446	Deep	1.03	10	43
2-6b	80°56.919′N 17°33.431′E	80°56.328′N 17°35.323′E	386	368–405	Deep	0.66	9	18
1-6	80°19.477′N 16°39.785′E	80°20.294′N 16°49.505′E	193	87–277	Transition	1.90	63	46
1-7	80°24.123′N 16°28.468′E	80°25.141′N 16°36.176′E	202	90–330	Transition	1.64	58	46

Table 1 continued

Station		Mean depth in m	Depth range in m	Zone	Transect length in nautical miles	Number of stills	Number of video frame shots analyzed
Drop-camera casts (2011)	Position						
2-545	80°55.140′N	192	192	Intermediate		44	
	17°55.236′E						
1-537	80°14.939′N	286	285	Deep		3	
	16°08.108′E						
1-539	80°29.989′N	350	349	Deep		8	
	15°58.301′E						
2-543	80°54.132′N	361	360	Deep		12	
	17°27.431′E						
Agassiz trawl hauls (2011)	Position						
1-541	80°33.180′N	56	56	Shallow			
	16°38.811′E						
2-542	80°44.670′N	104	104	Shallow			
	17°51.107′E						
2-546	80°45.832′N	95	95	Shallow			
	18°43.705′E						
2-547	80°39.893′N	81	81	Shallow			
	19°43.391′E						
1-538	80°17.392′N	164	164	Intermediate			
	15°44.515′E						
1-540	80°32.312′N	215	215	Intermediate			
	15°21.697′E						

ophiuroids, asteroids, echinoids, ascidians and fishes. The number of selected frame shots depended on the total length of the video transect and hence overall area imaged, of each station. It was chosen to represent approximately 1/60 (~ 2 %) of the overall station transect length. Using this approach, eleven to 51 separate "frame shots" (depending on the video transect length) were randomly selected for each station based on the time stamps of the first frame in the sequence (Table 1). The selected 902 frame shots from 26 stations were processed by means of Adobe Photoshop CS5 to enhance overall image quality with regard to brightness, contrast, resolution, hue, etc. Photoshop's count tool was used to enumerate the numbers of benthic specimens visible in each frame shot. In case of colonial organisms (sponges, soft corals and ascidians), we counted the number of colonies. All counts were standardized to numbers m^{-2}.

In addition, the still photographs taken in 2011 were analyzed quantitatively for abundances of epibenthic organisms visible in the images. In contrast to the video frame shots, the seabed area depicted by each photograph could be assessed with high precision due to the presence of 2 lasers mounted 26 cm apart from each other, providing a scale in each photograph (Sweetman and Chapman 2011). The outer margins of the photographs were not considered in the analysis to avoid systematic errors possibly introduced by any peripheral image bias. We did not quantitatively analyze the still photographs taken in 2010 because they were not taken at random. Their "qualitative" analysis, however, provided presence–absence data for each station at a much finer taxonomic, often "putative-species," level than the quantitative data gained in the video image analysis.

Finally, the type of seabed substrate was determined in each frame shot and photograph, using a modified classification scheme proposed by Hiscock (1996). It is based on the presence–absence of different substrate types: gravel, sand, mud, and—as structuring substrates—boulders (larger than 50 cm), stones (15–50 cm size) and pebbles (<15 cm in size). Since usually more than one substrate type occurred in a single picture, the frequencies of each substrate type across all frame shots and still photographs from 2011 were calculated for each station.

Data analysis

The faunistic analyses of video and still images yielded two biotic datasets. The first one was based on the analysis of still pictures taken in 2010 and contains qualitative presence–absence data at a fine taxonomic level. The second set was produced through the analysis of video frame shots, as well as still photographs from 2011, and features the quantitative abundance values at a coarser taxonomic level (see above). Information on abiotic seabed substrate composition, which contained frequencies of substrate types for each station, was stored in a third dataset.

These three datasets were subjected to multivariate statistical analysis, using the software package PRIMER v6 (Clarke and Gorley 2006). The stations were a priori allocated to three depth zones to study depth-related shifts in benthic community and habitat structure: "Shallow" (50–150 m), "Intermediate" (150 and 250 m) and "Deep" (250–450 m). Two stations, which encompassed a within-station depth range of 90 to 330 m (thus covering all three depth zones), were excluded from the statistical analysis and were only used for the compilation of the overall taxa list.

Bray-Curtis similarities between all stations were calculated for both biotic datasets. For the quantitative dataset, abundance values were square root transformed prior to the computation of similarities to downscale the effect of very abundant taxa in the analysis. For the abiotic dataset, Euclidean distances were computed as resemblance measures. For both the qualitative and quantitative biotic dataset, analysis of similarities (ANOSIM) was used to test

for significant differences ($p \leq 0.05$) among depth zones. RELATE tests were applied to test whether there was a significant correlation between the among-station variation in faunal community composition and seabed structure. BEST analysis was performed to identify the set of abiotic seabed features that are most correlated with—and thus very likely best explains—the spatial pattern of epibenthic composition. The qualitative biotic dataset was analyzed by means of SIMPER analysis to determine those taxa that could be used as indicator organisms for a given depth zone.

Results

Seabed characteristics

The composition of the seabed did not differ markedly among stations at shallow and intermediate depths, where it was likewise characterized by a dominance of sandy sediments, with occasional boulders and stones lying at the surface (Fig. 2). Exceptions were shallow station 2-3 and intermediate stations 2-0a, 2-0b, 2-545, which primarily featured muddy sediments. The two transition stations showed a mixture of the other zones, but the seabed at station 1-7 largely consisted of mud. Deep stations were generally characterized by a muddy seafloor surface, with only very few stones. Overall, the among-zone differences in seabed composition are statistically significant (Global ANOSIM R: 0.424; $p = 0.001$). In the MDS plot visualizing the among-station resemblance pattern in terms of
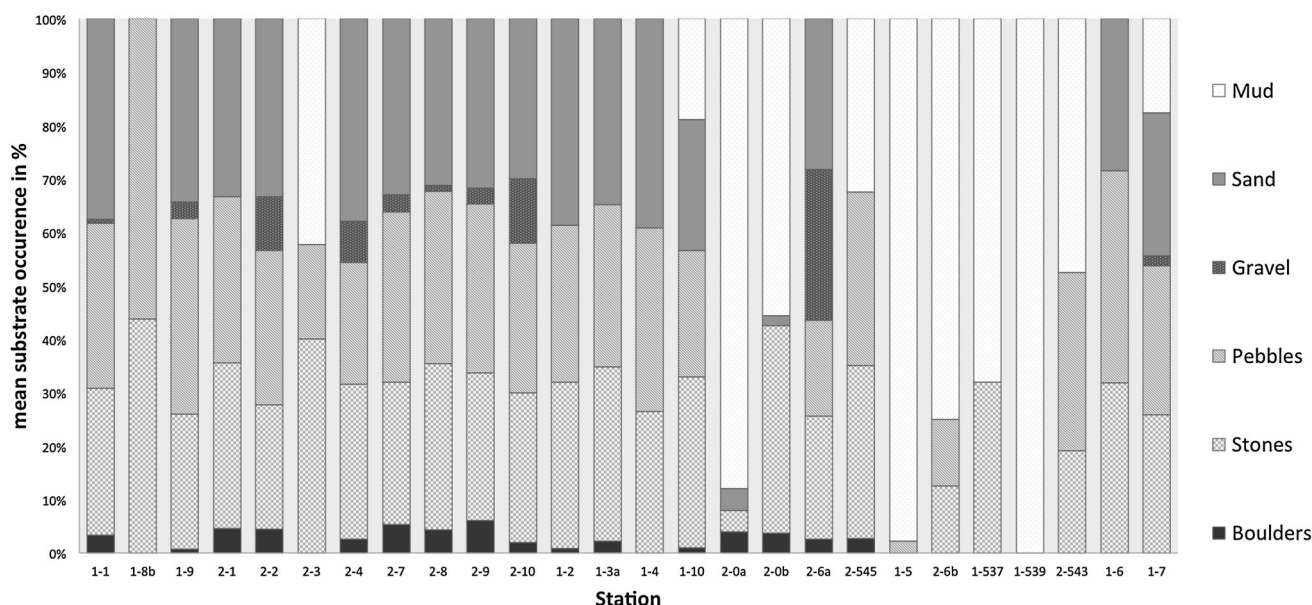

Fig. 2 Seabed composition in seabed images taken off northern Svalbard in 2010 and 2011, according to percentage frequencies of substrate types determined using a modified classification scheme proposed by Hiscock (1996)
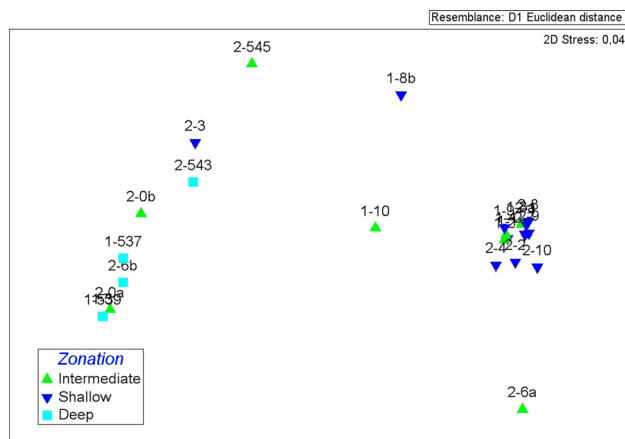
Fig. 3 MDS plot visualizing the resemblances (quantified as Euclidean distances) among stations in terms of the composition of the seabed analyzed in images taken off northern Svalbard in 2010 and 2011

seabed features (Fig. 3), pronounced variations among depth zones are also detectable: A well-defined group of deep stations is clearly separated from the shallow stations, while intermediate stations are widely distributed across the plot, indicating that they are much more heterogeneous in seabed composition than the stations in the other depth zones.

Faunal composition

Seabed images

A total of 141 taxa (including 26 poriferans, 31 cnidarians, 14 mollusks, one brachiopod, seven bryozoans, five polychaetes, one nemertine, eight arthropods, 23 echinoderms, eight ascidians and 17 fishes) were identified in the seabed images taken at 26 stations off northern Svalbard (Online Resource 1). The number of taxa recorded per station ranged from three at station 1-537 to 68 at station 1-3a, with an average of 32 ± 19 SD (Online Resource 1). The brittle star *Ophiura sarsii* was the most common species, being present in 21 stations, followed by the soft coral *G. rubiformis* that was found at 19 stations (Table 2). The two commercially utilized invertebrates, the prawn *P. borealis* and the scallop *Chlamys islandica*, occurred at depths of 87–405 and 50–277 m, respectively (Online Resource 1). A total of 31 taxa were recorded at only a single station (Online Resource 1).

More than one-third of the 141 taxa detected in the seabed images were found at the most diverse shallow stations (Figs. 4a, 5a), and up to roughly half of them at intermediate stations (Figs. 4b, 5b). In comparison, the deep stations were clearly less diverse, featuring <10 % of all taxa found in all three depth zones (Figs. 4c, 5c).

The composition of epibenthic megafauna differed significantly among depth zones (ANOSIM Global R: 0.545; $p = 0.001$) (Fig. 6). Pairwise ANOSIM tests indicated that shallow and intermediate stations were comparatively similar in composition, while deep stations were clearly different from the other zones. SIMPER analysis revealed that in the shallow zone, *O. sarsii*, *Strongylocentrotus* sp., *G. rubiformis* and *Hydroides norvegicus* were most frequent, whereas in the intermediate zone, *G. rubiformis*, *Hornera* sp. and *Ophiopholis aculeata* prevailed; the deep zone was characterized by *P. borealis* as well as *O. sarsii* (Table 3). The biotic distribution pattern, based on presence–absence data, was significantly related to the among-station variation in abiotic seabed composition (RELATE test $r = 0.518$; $p = 0.001$). According to the BEST analysis, it was explained best by the presence of stones and pebbles (BEST analysis correlation = 0.581).

Agassiz trawl catches

A total of 107 taxa were identified in the AGT catches (Online Resource 1). Of these, 50 taxa were also found in seabed images and 41 of these taxa at the same stations. Ten taxa were present at more than three AGT stations. The brittle star *O. aculeata* and the sea urchin *Strongylocentrotus* sp. were present at all six stations, and the bryozoan *Myriapora* sp. occurred at five stations. The highest numbers of taxa (>40) were recorded at AGT stations 540 (corresponding to seabed-image station 1-4) and 541 (corresponding to seabed-image station 1-9), while the lowest number of taxa (16) was collected at AGT station 542 (corresponding to seabed-image station 2-7) (Fig. 7a; Online Resource 1). Porifera dominated the AGT catches at stations 538 and 540, while station 541 was characterized by more equally distributed numbers of Cnidaria, Mollusca, Arthropoda and Echinodermata (Fig. 7a). Cnidaria dominated Station 542, Echinodermata station 546, and fairly equal proportions of Porifera, Cnidaria, Arthropoda and Echinodermata were recorded at station 547 (Fig. 7a). Overall, the coarse-level taxonomic composition of the fauna recorded in AGT catches was quite similar to that identified in the seabed images (Fig. 7b).

Faunal abundance

Ophiuroids were most abundant at all seabed-image stations, together with ascidians, which showed higher variations in abundance than the ophiuroids (both with up to almost 40 ind m^{-2}; Table 4). Crinoids, actinians, poriferans and echinoids were also abundant (up to 4.8 and 8.0 ind m^{-2}); 1.8–1.4 ind m^{-2} were the highest abundances for shrimps and soft corals, while asteroids and

Table 2 Presence–absence data of all megabenthic taxa, which were present in seabed images and Agassiz trawl catches taken north of Svalbard in 2010 and 2011 at more than ten stations

Depth zone	Station	*Lafoeina maxima*	*Gersemia rubiformis*	*Ptychogastria polaris*	*Hormathia* sp.	*Urticina* sp.	*Hydroides norvegica*	*Sabellida* indet.	*Lebbeus* cf. *polaris*	*Balanus* cf. *balanus*
Shallow	1-1	1	1	0	1	1	1	1	0	1
	1-8b	1	1	0	1	1	1	1	1	1
	1-9	1	1	0	0	1	1	1	1	1
	2-1	1	1	1	1	1	1	1	1	1
	2-2	1	1	1	1	0	1	1	1	1
	2-3	1	1	1	1	0	1	0	0	0
	2-4	0	1	1	1	0	1	0	1	0
	2-7	1	1	1	1	1	1	1	1	0
	2-8	0	0	1	0	0	0	0	0	1
	2-9	1	1	1	1	1	1	0	1	1
	2-10	0	1	1	1	1	1	0	1	1
Intermediate	1-2	0	1	1	1	1	1	1	0	0
	1-3a	1	1	1	1	1	1	1	1	1
	1-4	1	1	0	0	0	1	1	0	1
	1-10	1	1	1	1	1	0	0	0	0
	2-0a	0	1	1	1	1	0	0	0	0
	2-0b	0	1	0	1	1	1	1	1	1
	2-6a	0	1	0	0	0	1	0	1	1
	2-545	0	1	1	1	1	1	1	0	0
Deep	1-5	0	1	0	0	0	0	1	0	0
	2-6b	0	0	1	0	0	0	1	0	0
	1-537	0	0	0	0	0	0	0	0	0
	1-539	0	0	0	0	0	0	0	0	0
	2-543	0	0	1	1	0	0	0	0	0
Transition	1-6	1	1	1	1	1	1	1	1	1
	1-7	1	1	1	1	1	1	1	1	1
All	Sum	11	19	15	16	13	16	13	11	12

Depth zone	Station	*Strongylocentrotus* sp.	*Ophiopholis aculeata*	*Ophiura sarsii*	*Gorgonocephalus* sp.	*Heliometra glacialis*	*Botryllus* sp.	Ascidiacea indet. 1	*Leptoclinus maculatus*
Shallow	1-1	1	1	1	1	1	1	1	1
	1-8b	1	1	1	1	1	1	0	0
	1-9	1	1	1	1	1	1	1	1
	2-1	1	1	1	1	1	1	0	0
	2-2	1	1	1	1	1	1	0	1
	2-3	1	0	1	1	1	0	0	0
	2-4	0	1	1	1	1	1	1	1
	2-7	1	1	1	0	1	1	1	0
	2-8	1	0	1	0	0	1	0	0
	2-9	1	1	1	1	1	1	0	0
	2-10	1	1	1	1	0	0	1	0
Intermediate	1-2	1	1	1	0	0	0	1	1
	1-3a	0	1	1	1	1	1	1	0
	1-4	0	1	1	0	0	1	1	0
	1-10	1	1	1	0	0	1	1	1
	2-0a	0	0	0	1	1	0	0	1
	2-0b	0	1	0	1	1	0	1	1
	2-6a	1	1	0	0	0	1	0	0

Table 2 continued

Depth zone	Station	*Strongylocentrotus* sp.	*Ophiopholis aculeata*	*Ophiura sarsii*	*Gorgonocephalus* sp.	*Heliometra glacialis*	*Botryllus* sp.	Ascidiacea indet. 1	*Leptoclinus maculatus*
	2-545	1	1	1	0	1	1	1	1
Deep	1-5	0	0	1	0	1	0	0	0
	2-6b	0	0	1	0	0	0	0	0
	1-537	0	0	1	0	0	0	0	0
	1-539	0	0	1	0	0	0	0	1
	2-543	0	0	1	0	0	0	0	1
Transition	1-6	1	1	1	1	1	1	1	0
	1-7	1	1	1	1	1	1	0	1
All	Sum	14	16	21	12	14	14	11	11
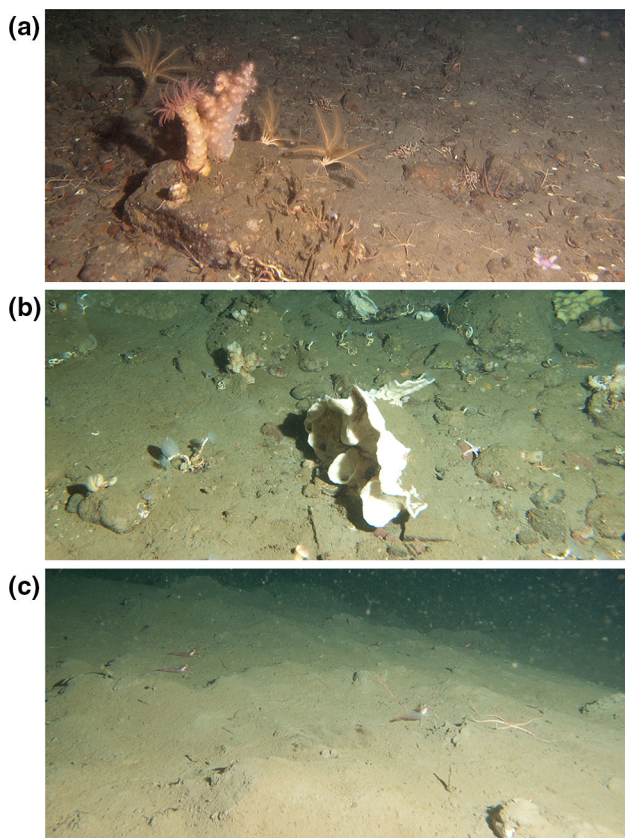
Fig. 4 Sample images taken off northern Svalbard in 2010, showing the seabed at **a** a shallow station (1-1, 80–110 m), **b** an intermediate station (1-2, 163–193 m) and **c** a deep station (1-5, 366–446 m)

fishes reached a maximum abundance of 0.2–0.1 ind m^{-2}, respectively. The quantitative faunal composition varied pronouncedly among stations, even at coarse taxonomic level. Ophiuroids and ascidians, for example, were dominant at some stations but absent at other stations.

The spatial pattern in the abundance data was very similar to that visible in the presence–absence data, except that three intermediate stations were clearly different from both one another and all other stations (Fig. 8). Again, there was a significant overall difference among the three depth zones (ANOSIM Global R: 0.448; $p = 0.001$). Pairwise ANOSIM tests showed the shallow and intermediate depth zones to be more similar to one another than to the deep zone. Furthermore, as also in case for presence–absence data (see above), the abundance-based biotic distribution pattern was significantly related to the among-station variation in abiotic seabed composition, even though the correlation was clearly weaker (RELATE test $r = 0.245$; $p = 0.012$). The presence of stones, gravel and sand best explained the variations in faunal abundance (BEST analysis correlation = 0.388).

Other findings

Coralline red algae were found at a number of stations down to a water depth of 90 m, mostly covering stones and shells (Table 5). A large amount of bivalve shells were found at station 2-10, covered with coralline red algae (Table 5).

At each station deeper than 286 m, pronounced dents of approximately 50 cm width were recorded at the seafloor (Table 5). These marks (Fig. 9a) differed between stations in conspicuousness. They were often also characterized by excavated infaunal bottom fauna, mainly polychaetes (Fig. 9b).

Discussion

Our inventory of the epibenthic megafauna north of Svalbard extends the knowledge on the distribution and

Fig. 5 Number of epibenthic megafauna taxa and faunal composition (at a coarse taxonomic level) in seabed images taken of northern Svalbard in 2010 and 2011, in three depth zones: **a** shallow, **b** intermediate and **c** deep
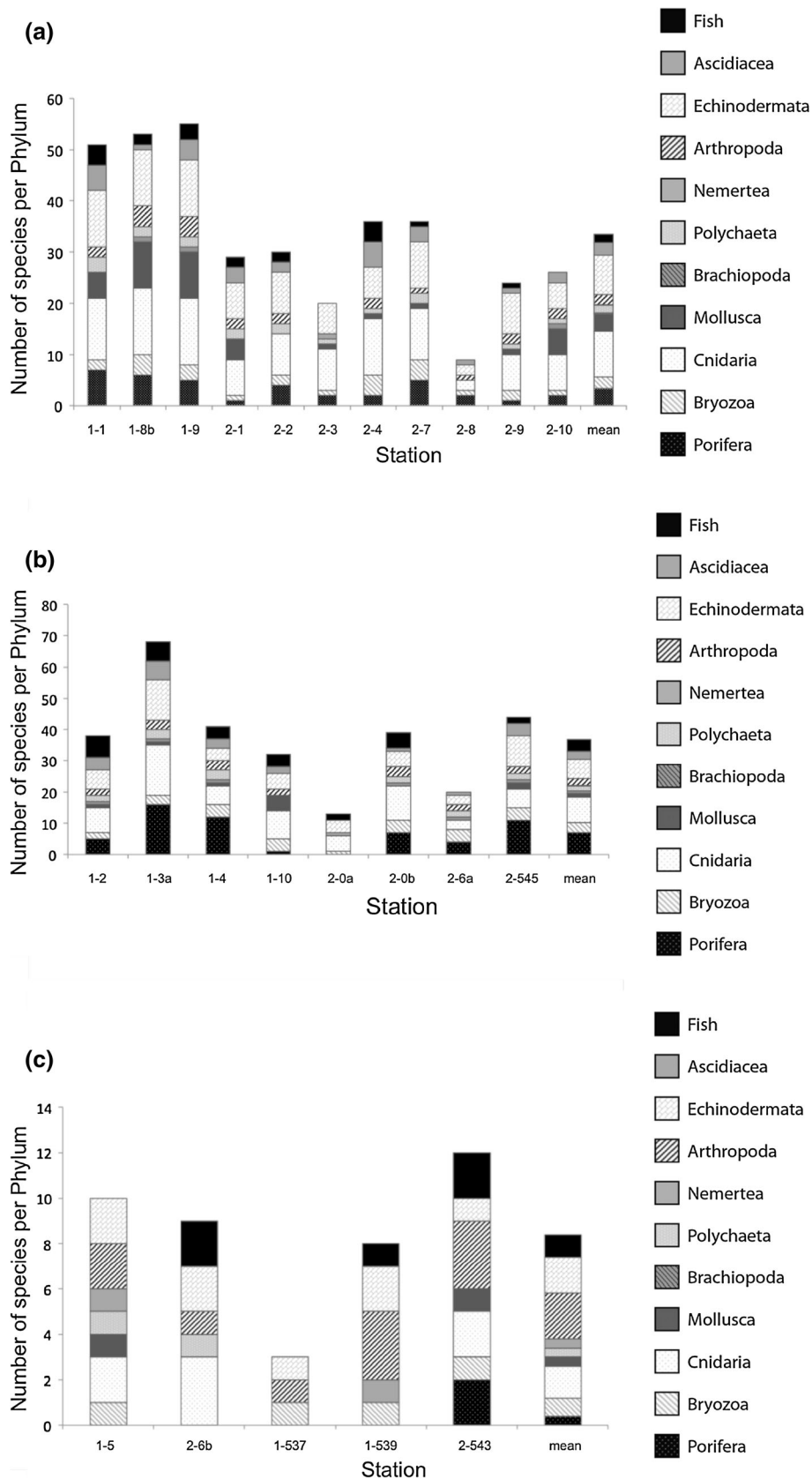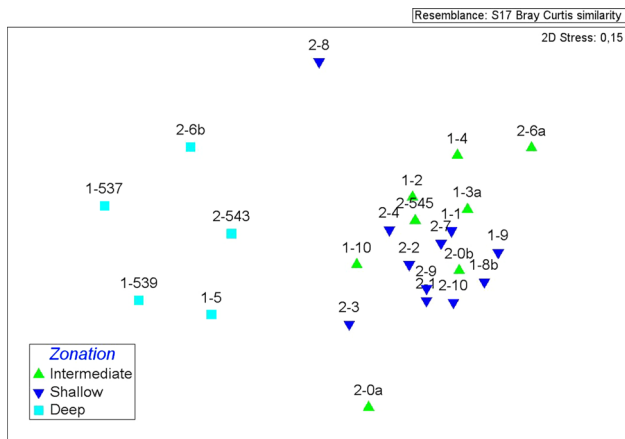
Fig. 6 MDS plot visualizing the pattern of Bray–Curtis resemblances among stations, computed using presence–absence data of epibenthic taxa recorded in seabed images taken off northern Svalbard in 2010 and 2011

composition of the benthos in this area, which was described the last time by Gulliksen et al. (1999) who summarized findings from many sources, including peer-reviewed literature, cruise reports and personal observations. For our study area, they reported a total of 363 macro-organisms. Caution is advised when comparing our findings with these previous reports, since differences in sampling methods may lead to bias. First, the numbers published by Gulliksen et al. (1999) are based on many surveys, using a variety of sampling gear, and do not only include epibenthic organisms but also infaunal species. Our survey of epibenthic megafauna, however, was primarily

based on seabed imaging. This sampling approach has clear advantages to conventional benthic sampling techniques, but there are also some important constraints that have to be considered in the interpretation of the results (Smith and Rumohr 2005). To begin with, image-based inventories are confined to the epibenthos. Moreover, rare species may not be represented in the data, due to limitations in sampling effort (here: number of images). Species accumulation curves constructed for the three depth zones (Fig. 10) illustrate diversity differences among depth zones and also suggest that 75 % of the epibenthic taxa occurring in a zone would have been recorded by analyzing 63, 49 and 60 images taken in the shallow, intermediate and deep zone, respectively.

From the 163 epibenthic taxa we identified in seabed images and AGT catches, almost half were identified to genus level. Out of these 84 identified genera, a total of 28 that we report in this survey (Table 6) were not recorded before in the study area (Gulliksen et al. 1999). For some taxa, such as Porifera, the mismatch can be explained by difficulties in identification, but also shifts in distribution ranges must be taken into account (Renaud et al. 2008). In some cases, it is evident that our findings add to the growing list of benthic species that extend their distribution boundaries northward. For instance, we identified the coralline red algae *Lithothamnion* sp. at two stations, in both AGT catches and seabed stills, at 80°33′N and 80°39′N, respectively. This is the northernmost finding of these algae. Gulliksen et al. (1999) did not record it in our area but Teichert et al. (2012) reported it in the Nordkappbukta (Nordaustlandet, Svalbard) at 80°31′N. Furthermore, one

Table 3 SIMPER analysis of presence–absences of megabenthic epifauna taxa in seabed images taken off northern Svalbard in 2010 and 2011 in three depth zones

	Av. Abund (ind m^{-2})	Av. Sim (%)	Contrib. %	Cum. %
Shallow				
Ophiura sarsii	1.00	3.23	7.46	7.46
Strongylocentrotus sp.	0.91	2.69	6.21	13.67
Gersemia rubiformis	0.91	2.37	5.47	19.15
Hydroides norvergica	0.91	2.37	5.47	24.62
Ptychogastria polaris	0.73	2.03	4.69	29.30
Intermediate				
Gersemia rubiformis	1.00	2.93	7.67	7.67
Hornera sp.	0.88	1.94	5.07	12.74
Ophiopholis aculeata	0.88	1.94	5.07	17.81
Hormathia sp.	0.75	1.47	3.84	21.65
Urticina sp.	0.75	1.47	3.84	25.50
Deep				
Pandalus borealis	1.00	12.56	36.76	36.76
Ophiura sarsii	1.00	12.56	36.76	73.52
Exidmonea sp.	0.6	3.02	8.84	82.36
Nemertea indet.	0.4	1.11	3.25	85.62
Sabellida indet.	0.4	1.05	3.08	88.70

Av. Abund, Average Abundance; Av. Sim, Average Similarity; Contrib. %: contributed percentage; Cum. %: cumulative contribution

Fig. 7 a Number of taxa collected from Agassiz trawl catches and **b** match to taxa recorded in both seabed images and Agassiz trawl (AGT) catches taken off northern Svalbard in 2010 and 2011
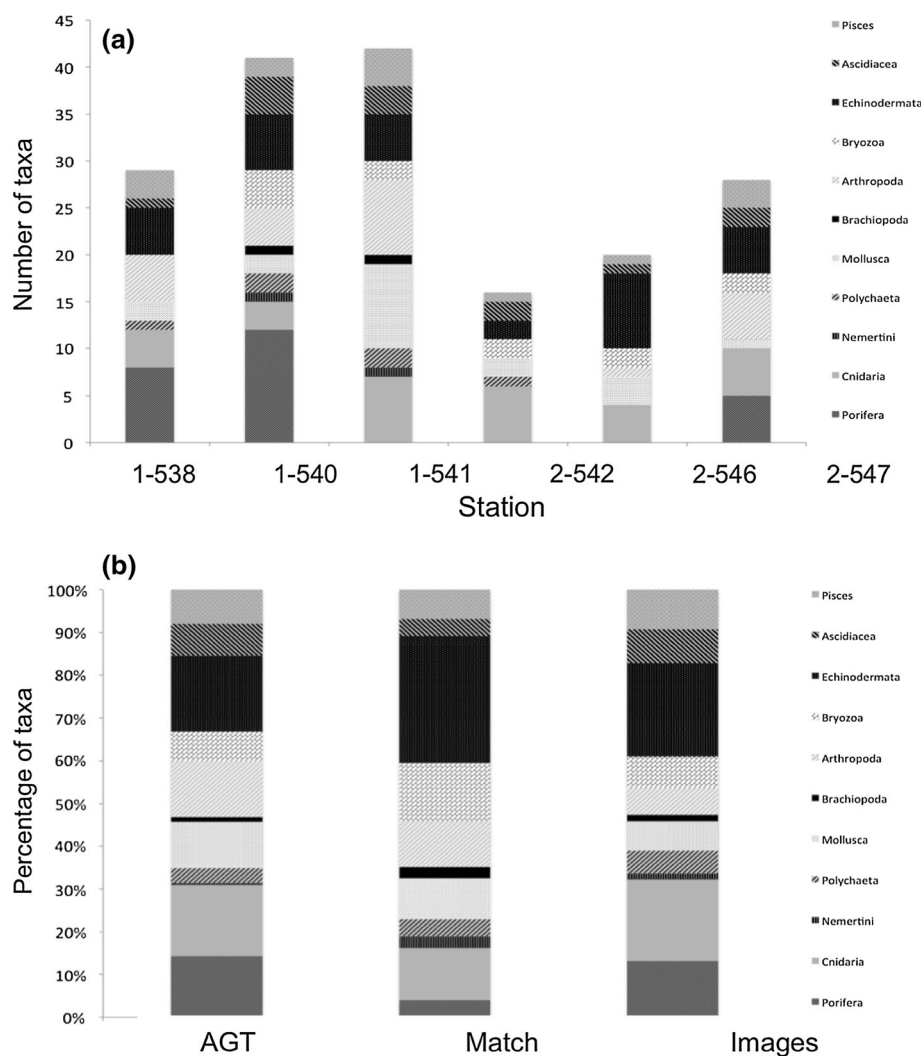
individual of the Atlantic king crab *Lithodes maja*, which is also not listed in the report of Gulliksen et al. (1999), was recorded at 80°32′N.

As very often reported from marine field studies (e.g., Starmans et al. 1999), we found a pronounced depth zonation to be the most evident spatial pattern in our data, indicating that environmental factors that strongly vary with water depth are most important for determining the distribution of benthic species. There are a number of such factors that are well known as drivers of benthic community patterns, such as seabed composition (Graf 1992; Grebmeier et al. 2006) and food availability (Josefson 1987; Grebmeier et al. 1988; Graf 1992; Rosenberg 1995). According to Piepenburg (2005), seabed attributes are usually most significant at small (local) scales, while food supply to the benthos is the prime driver at larger (regional) scales. Differences in food availability are strongly related to water depth, hydrodynamics and various processes of particle transport (Graf 1992), resulting in an inverse

relationship between sedimentation rates (and hence food supply to the benthos) and water depths (Suess 1980; Martin et al. 1987). This can also explain the exponential decline of the benthic standing stock from Arctic shelves to deep-sea basins (Curtis 1975).

Our findings are in general agreement with the long-standing notion that benthic species distribution is strongly affected by seafloor habitat structure (Snelgrove and Butman 1994). Moreover, substrate type can be used as a proxy of the bottom-current regime, with coarser sediments being indicative of higher velocities (Snelgrove and Butman 1994). A strong correlation between depth-related seabed composition and benthic distribution patterns was reported from several places, for instance, the shelves of the southeastern Chukchi Sea and northeastern Bering Sea (Feder et al. 1994). The most obvious difference is between hard-bottom and soft-bottom habitats. In hard-bottom communities of the Beaufort Sea, the limiting resource has been shown to be space, as sessile organisms cover most of

Table 4 Abundances (ind m^{-2}) of coarse-level megabenthic taxa present in seabed images and Agassiz trawl catches taken north of Svalbard in 2010 and 2011

| Depth zone	Shallow											Intermediate								Deep					Transition	
Station #	1-1	1-8b	1-9	2-1	2-2	2-3	2-4	2-7	2-8	2-9	2-10	1-2	1-3a	1-4	1-10	2-0a	2-0b	2-6a	2-545	1-5	2-6b	1-537	1-539	2-543	1-6	1-7
Porifera	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.1	0.2	0.1	0.2	0.7	2.6	2.1	0.0	0.0	0.2	6.2	1.8	0.1	0.0	0.0	0.0	0.0	0.0	0.1
Actiniaria	0.1	3.4	0.3	0.2	0.6	0.3	2.1	0.1	0.1	0.6	0.2	0.3	0.0	0.0	0.6	0.3	1.9	0.1	5.2	0.1	0.0	0.0	0.0	0.0	0.7	0.3
Alcyonaria	0.0	1.4	0.8	0.1	0.0	0.2	0.1	0.0	0.0	0.5	0.0	0.1	0.1	0.0	0.0	0.5	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.1
Decapoda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.4	0.8	0.5	0.2	1.8	1.6	0.1	0.2
Crinoidea	0.4	0.6	0.1	0.0	0.1	0.3	0.1	0.8	0.0	0.7	0.0	0.0	0.9	0.0	0.3	0.3	0.2	0.0	8.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1
Ophiuridea	16.2	0.4	0.8	4.3	1.5	1.9	0.1	6.0	13.6	10.8	11.3	2.8	0.0	0.0	8.7	0.7	0.0	0.0	25.6	0.0	0.0	37.1	3.4	28.4	9.6	6.6
Asteroidea	0.0	0.0	0.0	0.1	0.1	0.0	0.1	0.0	0.0	0.0	0.1	0.1	0.2	0.0	0.0	0.2	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Echinoidea	0.4	0.0	0.2	0.5	0.5	0.1	0.0	0.0	4.8	0.6	0.5	0.4	0.0	0.0	0.8	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.3	0.3
Ascidiacea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.6	0.0	39.6	30.4	4.4	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	11.1	0.0
Pisces	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.1	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Totals	17.1	5.9	2.2	5.1	3.0	2.8	2.6	7.2	18.7	13.3	12.9	4.5	43.4	32.6	14.6	2.0	3.2	6.3	42.6	1.0	0.5	37.3	5.2	30.1	22.2	7.7
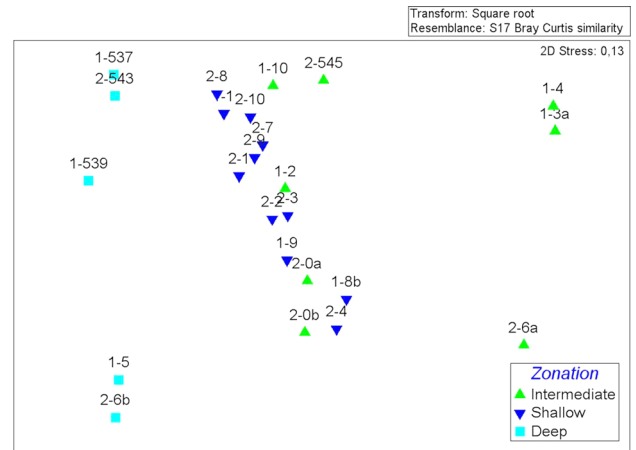
Fig. 8 MDS plot visualizing the pattern of Bray–Curtis resemblances among stations, computed using abundance data of epibenthic taxa recorded in seabed images taken off northern Svalbard in 2010 and 2011

Table 5 List of stations featuring pronounced seabed marks (putative trawl scours) or maerl recorded in seabed images taken off northern Svalbard in 2010 and 2011

Station #	Water depth (m)	Remarks
2-1	51–87	Maerl
2-9	90	Maerl
2-10	55–60	Shells/maerl
1-5	366–446	Dents
1-537	286	Dents
1-539	350	Dents
1-7	90–330	Dents
2-543	361	Dents
2-6b	368–405	Dents

the surfaces of hard substrates like boulders and stones (Konar and Iken 2005), whereas in Arctic soft-bottom communities, sediment grain size and homogeneity seem to be main drivers of faunal composition (Grebmeier and Barry 1991; Hop et al. 2002). As in our study, Arctic seabeds most often consist of a mixture of soft-bottom habitats (sediment) and hard-bottom substrates (e.g., boulders), the latter usually derived from ice-transport processes (Whittington et al. 1997; Lippert et al. 2001). The presence of hard-bottom habitats is particularly important for sessile and semi-sessile suspension feeders, which need special settling substrates (Levinton 1992). In general, more gravel, stones and boulders were found at the shallower stations in our field survey, providing suitable habitats for the attachment of sessile organisms and hence their associated fauna. Soft bottoms clearly prevailed at depths >250 m. There, the absence of boulders or
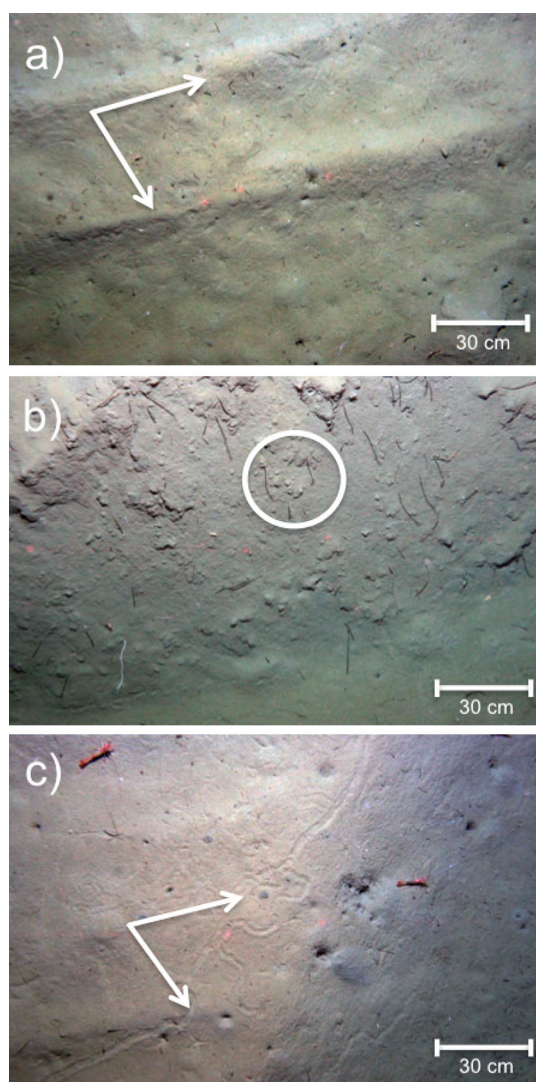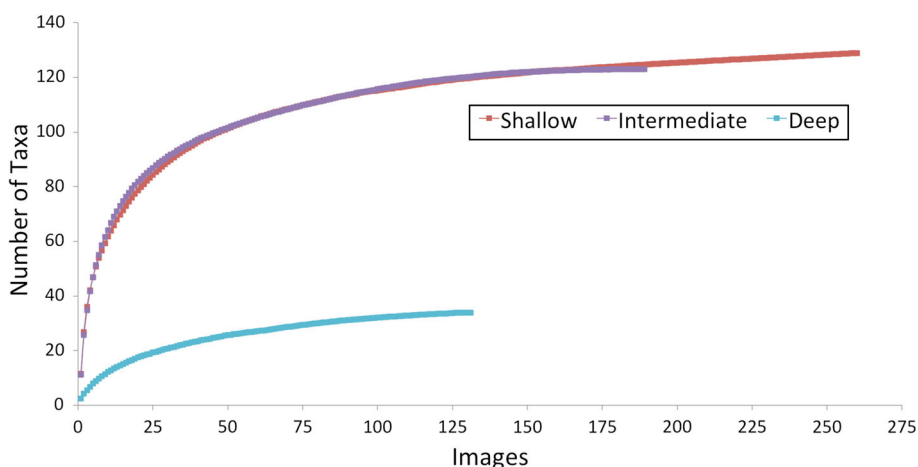
Fig. 9 Sample images of the seabed, taken off northern Svalbard in 2010 and 2011 at station 1-539 (350 m), showing **a** dents (putative trawl scours; *arrows*), **b** excavated fauna (*circle*) and **c** *lebensspuren/* live tracks (*arrows*)

rocks to attach to is certainly the main reason for the lack of sessile organisms.

A strong correlation with depth and seabed substrate was also detected for the abundances of the higher taxonomic groups in our study. We found high numbers of brittle stars, which are in general opportunistic species, at deep stations, where erect taxa like sponges, hydrozoans and bryozoans were virtually absent. High abundances of brittle stars have commonly been observed at Arctic shelves and slopes (Piepenburg 2005). In the Barents Sea, *Ophiocten sericeum* was most abundant, while *Ophiura robusta* dominated off Northeast Greenland (Piepenburg and Schmid 1996), and *O. sarsii*, which was also most common in our study, prevailed in the Chukchi Sea (Ambrose et al. 2001). Starmans et al. (1999) also reported brittle stars as being "the most important elements" of the megabenthos off Northeast Greenland (Starmans et al. 1999). Similar to our study, their analyses showed a clear separation between shallow shelves and deep troughs, with a transition zone in between. In contrast to our study, however, they reported low numbers of taxa with high abundances on the shelf and the opposite in the troughs. In our study, we found the opposite pattern with regard to taxonomic diversity (i.e., more taxa at shallow than at deep stations), while we could not identify a distinct pattern with regard to abundances because of the high among-station variability.

We hypothesize that the pronounced marks in the seabed detected at deeper stations (Fig. 9) are very likely scours caused by bottom-trawl doors hauled over the seabed. Differences in conspicuousness are probably a result of their "age": Less pronounced dents, such as those found at station 537, can surely be regarded to be older than very distinct ones, such as those recorded at station 539. Such evidence of trawling was found at all deep stations, which were characterized by soft bottoms and the occurrence of

Fig. 10 Species accumulation curves (based on two approaches: Sobs and Jackknife 1; see Clarke and Gorley 2006) for three depth zones, computed using species presence–absence data recorded in seabed images taken off northern Svalbard in 2010 and 2011

Table 6 List of megabenthic/demersal genera and species that have not been reported in Gulliksen et al. ([1999]) from the region north of Nordaustlandet (Svalbard) and east of Hinlopenrenna (to 35°E)

Porifera	Polychaeta	Vertebrata
Axinella cf. *rugosa*	*Hydroides norvegica*	*Anarhichas lupus*
Axinella infundibuliformis	*Filograna implexa*	*Anarhichas minor*
Mycale lingua	*Dentalium* cf. *dentalis*	*Chirolophis ascanii*
Polymastia thielei		*Gadus morhua*
Weberella bursa	Arthropoda	*Lumpenus lampraeformis*
	Eualus sp.	*Melanogrammus aeglefinus*
Cnidaria		*Pholis gunnelus*
Alcyonium sp.	Echinodermata	*Sebastes* sp.
Bolocera tuediae	*Hipasterias phrygiana*	
Cerianthus lloydi	*Psolus phantapus*	
Drifa glomerata	*Thyonidium* cf. *drummondi*	
Bryozoa	Tunicata	
Exidmonea sp.	*Eudistoma vitreum*	
Retepora sp.	*Molgula griffithsii*	

P. borealis, which is the commercially most important marine invertebrate resource in Svalbard waters (Stiansen et al. [2009]). Our finding of a strong linkage between water depth, seabed characteristics and the distribution of prawns and fishing effort suggests that there are ongoing trawling activities in our entire study area to exploit the stocks of *P. borealis* off northern Svalbard. This development is not surprising. Since the natural and mineral resources in Arctic region are becoming more interesting for human utilization due to the continuing decline of the sea-ice cover (ACIA [2004]), recently and currently pristine areas may be fished in the future. With increasing water temperatures, boreal species extend their distribution ranges northward and may in the long run build up exploitable populations north of Svalbard (Renaud et al. [2008]), e.g., fish species like Atlantic cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*, which we found at more northern locations than recorded before (Gulliksen et al. [1999]).

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