

Antarctic sponge spicule mats shape macrobenthic diversity and act as a silicon trap

Julian Gutt^{1,*}, Astrid Böhmer^{1,2}, Werner Dimmler³

¹Alfred Wegener Institute for Polar and Marine Research, 27568 Bremerhaven, Germany

²Carl von Ossietzky University Oldenburg, Institut für Biologie und Umweltwissenschaften, 26129 Oldenburg, Germany

³Fielax Gesellschaft für wissenschaftliche Datenverarbeitung mbH, 27568 Bremerhaven, Germany

ABSTRACT: Sponge spicule sea-bed cover was analysed and related to the mega- and macro-epibenthos along one video-recorded and one still image sea-bed transect in the southeastern Weddell Sea, Antarctica. The origin of the patterns of spicule mats and their associated fauna was conceptually reconstructed and interpreted to be a result of iceberg scouring as the main driver. Spicule beds were not necessarily correlated with a diverse fauna, which was shown by a comparison of sponge spicule cover and macrobenthic and megabenthic abundance and biodiversity. On the one hand, this result might reflect slow recolonisation processes, especially by the megabenthos. On the other hand, local maximum densities of adult sponges were found where spicule cover was highest. A simple numerical model revealed that biogenic silicon converted from living to dead material by iceberg scouring accounts for 0.69% of the global silicon flux to the deep sea, which originates from primary production. However, the sponge-derived silicon sequestration occurs over only 2.4% area of the global ocean. On the Antarctic continental shelf, flux rates of silicon that originated from primary production are similar to or twice as high as silicon sequestration due to iceberg-induced sponge mass mortality.

KEY WORDS: Macro-epibenthos · Mega-epibenthos · Disturbance · Iceberg · Global marine silicon cycle

— Resale or republication not permitted without written consent of the publisher —

INTRODUCTION

Sound knowledge of ecological driving forces is essential to understand the functioning of marine ecosystems and to develop projections for their future in a changing environment (Barnes & Peck 2008, Convey et al. 2010, Brandt & Gutt 2011). Within Antarctic macrobenthic and megabenthic communities, a surprisingly high spatial heterogeneity (Gutt et al. 2010) can cause difficulties for generalisation, especially for bioregionalisation approaches (Grant et al. 2006) or species distribution models (Gutt et al. 2012). Generally, well-known large-scale drivers of benthic systems such as sediment and water mass characteristics only weakly correlate with faunistic patterns on the Antarctic shelf (Gutt 2000, 2007,

Cummings et al. 2010). However, Antarctic-specific environmental factors, such as oligotrophic currents from under the ice shelf and ice scouring, fractionating the shelf habitat, can explain biodiversity hotspots and coldspots (Dayton & Oliver 1977, Barry & Dayton 1988, Gutt & Starmans 1998, Thrush et al. 2006, Gutt & Piepenburg 2003, Barnes & Conlan 2007, Smale 2007). Sponges can contribute to a high temporal variability and complexity of benthic assemblages since different species obviously recruit and grow at extremely different rates (Dayton 1989, 1990). In addition, recent structures might also mirror long-term colonization processes, e.g. incomplete recolonisation since the end of the past glaciation, when shelf areas became exposed due to the retreat of grounded ice shelves. Such developments cannot be

*Email: julian.gutt@awi.de

directly observed and are understood only in a few cases if at all, but some can be reconstructed (see e.g. Post et al. 2007, Thatje et al. 2008, Barnes & Kuklinski 2010, Barnes & Hillenbrand 2010).

Sponges are spread all around the Antarctic continent, especially in water depths between 30 and 300 m and are regionally dominant components of benthic communities (Koltun 1968, Barthel 1992, Jannussen & Tendal 2007, Gutt 2007). They can shape the habitat through various processes, e.g. by providing a microhabitat for a variety of species, which they attract, or by providing food for predators and thus forming the basis for a complex trophic structure (Dayton et al. 1974, Gutt et al. 1996, Gutt & Schickan 1998, Hogg et al. 2010). Abundant species of Demospongiae and Hexactinellida demand at least locally high amounts of silicon for spicule synthesis (Maldonado et al. 2011).

Two sites in the Eastern Weddell Sea were surveyed along one ROV video recorded transect and one still image transect, in which sea-bed images show an obvious spatial heterogeneity of dead and living sponges and their associated fauna. The first aim of this study was a spatially explicit analysis of these assemblages, including faunistic bulk parameters, and of the amount of dead sponge material. The results provided the basis for a reconstruction of ecological processes that cause the fragmentation of the Antarctic benthic system. The dead sponge material was correlated with the megabenthic and macrobenthic diversity to check whether sponge spicules attract or host a high benthic biodiversity as hypothesised or shown by Dayton et al. (1970) and Barthel (1992), for example.

The second aim was related to the cycle and fate of marine silicon (see e.g. Geibert et al. 2005). In this context, sponges had been 'overlooked' in the past, but recent calculations combined with experiments demonstrated that their contribution to the marine silicon cycle is generally not negligible (Maldonado et al. 2005, Krautter et al. 2006, Chu et al. 2011, Maldonado et al. 2011). When siliceous Demospongiae and Hexactinellida grow, they use silicon to synthesize their spicules, and thus act as a sink within the pelagic silicon cycle. When they die, their spicules are exposed to the ambient bottom water; however, spicules dissolve at a much lower rate than diatom frustules (Maldonado et al. 2005, Chu et al. 2011). As soon as they are buried in the sediment and the pore water is saturated, especially due to the fast dissolution of diatom skeletons, further dissolution will stop and most of the sponge-derived biogenic silica will not be recycled for primary production. As a conse-

quence, mass mortality of Antarctic siliceous sponges and successive accumulation of biogenic silicate in the sediment generally contributes to the long-term marine silicon cycle, e.g. centuries, millennia and longer. With this background, sponge-derived silicon converted to spicule mats by iceberg scouring and related processes was quantified in a simple numerical model. This rate was compared with the global and regional sequestration of silicon by diatoms, which deposit at the sea-bed. The results presented here can be used in the future to refine models of the global and regional marine silicon budgets.

MATERIALS, METHODS AND ASSUMPTIONS

During the 2003 ANTXXI/2 (PS65) Eastern Weddell Sea expedition, 2 transects were recorded from the RV 'Polarstern', one using ROV video recording and the other using conventional still photographs. For the cruise report, see Arntz & Brey (2005).

The second part of the ROV video transect at Stn 184, which was 910 m long and situated in 261–228 m water depth between 70.93930° S, 10.509967° W and 70.93328° S, 10.49060° W was analysed. At the beginning of this ROV transect a disturbance experiment was performed a few days prior to the video observations, and the results presented here should be least biased from effects of the disturbance experiment. Transect length was calculated from minute-wise ROV positions obtained by the POSIDONIA tracking system in combination with the ship's GPS (repository reference including metadata of the study site: see Gutt et al. 2011). All recognisable organisms ≥ 2 cm were considered as megae-pibenthos sensu Gage & Tyler (1991), and were identified to the lowest possible systematic level and counted in 5-s intervals. The speed of the ROV resulting from the GPS positions and time elapsed was smoothed using a running mean covering 18 time intervals because the extent of the variations of speed were not plausible. A variable number of such intervals were summed to obtain roughly equal-length (~10 m) transect sections to present the lowest spatial unit for the analysis. Eighty percent of these sections ranged between 9 and 11 m. Exceptions were made if one 10 m section had covered the transition between 2 discrete habitats characterised by different levels of spicule cover. In such cases, sections were shortened to a minimum of 5.9 m or extended to a maximum of 14.4 m to form sections that covered only one relatively homogenous habitat. The width of the analysed strip was estimated to be

80 cm based on 2 parallel laser beams producing a scale in the image. As a consequence, each 10 m transect section represented an area of $\sim 8 \text{ m}^2$.

The photographed (still image) transect was situated at Stn 247-1 of the same expedition at a water depth between 70 and 114 m. The total transect length between 71.12148°S , 011.47274°W and 71.12269°S , 011.47981°W was 322 m, calculated from minute-wise ship's GPS positions (repository reference including still images and metadata: see Gutt et al. 2007). Still images were taken vertically from the drifting ship. The camera (Photosea 70) and flash were triggered by a weight, hanging at constant distance below the camera. Thus the area photographed can be assumed to be relatively constant, representing 1 m^2 . Images were ground-truthed during one cast using a configuration with a trigger weight of known size in the image. A total of 45 still images were selected for analysis of the habitat at a constant level of quality. Based on the high resolution of the images (70 mm film, ISO 64) in combination with the area covered, all recognisable organisms $\geq 2 \text{ mm}$ were identified to the lowest possible systematic level and defined as macro-epibenthos. Sixty-one such taxonomic units were identified from the videos and 75 from the still images. Consequently, the megabenthos and macrobenthos at Stns 184 and 247, respectively, overlap in terms of size considerably, but not completely.

In both data sets the amount of visible sponge spicules deposited on the sea-bed was estimated by eye and classified into 4 levels of spicule cover: <1, 1–20, 21–50 and 51–100%. For cases with high amounts of epibenthos, the values refer only to the visible sediment surface. For calculations and illustrations, the means of these ranges were used. Applying the Primer v6 software package (Clarke & Warwick 2001), multidimensional scaling (MDS) was performed for ordination of faunistic data, ANOSIM was used to check data for differences in taxonomic composition between levels of spicule cover, and dominance plots were generated to display patterns of diversity (in a broad sense). Binomial and linear regression models were calculated using Microsoft Excel; at Stn 184, only levels of spicule cover $\geq 1\%$ were considered for such calculations because the <1% spicule cover level was obviously a fresh iceberg scour and represents a principally different and non-mature microhabitat (see 'Discussion'). This was not assumed for Stn 247. Tests for significance of correlations were carried out according to Sachs (2002).

For the calculation of sponge-derived silicon sequestration, the following sources of data were used (see also Table 1): (1) primary production rate on the Antarctic continental shelf calculated by Arrigo et al. (2008), (2) silica production rate on the Antarctic continental shelves (Leynaert et al. 1993), (3) silica flux to the sediment in the 'entire South Atlantic' (Geibert et al. 2005), (4) global rate of biogenic silica production (Nelson et al. 1995), (5) sponge mass on the Antarctic shelf and silicon content of sponges (see Table 1), and (6) sponge mortality due to iceberg impact (Gutt & Starmans 2001, present study). All values were converted to rates of silicon mass per year per square metre, and total silicon mass per year for the entire study area. Some of these results, as well as our own and external assumptions, are described here in more detail. In the calculation based on values from Arrigo et al. (2008), a Si:C ratio of 0.4 was used because it refers to particulate organic matter, which is assumed to be a better proxy for total primary production than the ratio of 0.45 determined by Spencer (1983) for only diatoms. The 2% burial of phytoplankton-originated Si in the sediment was averaged from the conclusion of Leynaert et al. (1993) 'that no more than 1% of the silica produced annually by phytoplankton in the upper water column reaches a depth of 800 m', the assumption that this value for the Weddell Sea is exceptionally low (Leynaert et al. 1993), and the value of 3% calculated for the global deposition in the deep sea (Nelson et al. 1995). For the calculation of the sponge-derived Si, an extrapolation of the locally known standing stock to the entire Antarctic shelf was necessary. Sponges occur almost everywhere around the continent, but their abundance can vary considerably. These were the basic conditions used to assume that the total standing stock of silica-rich sponges on the entire shallow shelf is 10% of that of a given sponge assemblage. The calculation of the area for the shallower Antarctic shelf between 0 and 300 m depth is based on the $2.97 \times 10^6 \text{ km}^2$ not covered by ice shelves (Clarke & Johnston 2003) in combination with the proportions of 100 m depth classes published by Griffiths et al. (2011). The 0 to 300 m depth range is considered to be potential habitat for sponges and it comprises the main area exposed to iceberg impact; deeper scours are extremely rare. A small strip of water depth of less than $\sim 30 \text{ m}$ where sponges are quite rare has been neglected because of its small area compared with depths between 30 and 300 m. The sea-bed disturbance rate of each 1 m^2 affected once in 340 yr (Gutt & Starmans 2001) was first converted to $2611 \text{ km}^2 \text{ yr}^{-1}$ using the

Table 1. Rates of silicon deposition on the sea-bed (relative rate: grey shading; absolute rate: bottom line) calculated from primary production, silicon flux to the sediment and sponge mortality due to iceberg scouring for different spatial scales and regions. Conversion factors are *italicised*. WW: wet weight

Nelson et al. (1995) global primary production	Tréguer et al. (1995) global	Pondaven et al. (2000) Polar Front zone – permanently open ocean zone	Gelbert et al. (2005) total silica flux to the sediment, S. Atlantic	Leynaert et al. (1993) Antarctic continental shelves silica productivity	Arrigo et al. (2008) Antarctic continental shelf primary production	Present study
200–280 × 10 ¹² mol Si yr ⁻¹						12.7 kg sponge WW m ⁻² in sponge assemblages ^e
<i>World's oceans: 362 × 10⁶ km²</i>						<i>Sponge: other assemblages = 10%^c</i>
0.663 mol Si m ⁻² yr ⁻¹						1.27 kg sponge WW m ⁻²
<i>Si: 28.1 g mol⁻¹</i>						30% = ash weight = SiO ₂ ^{f,g}
18.63 g Si m ⁻² yr ⁻¹						0.381 kg SiO ₂ m ⁻²
2% on sea-bed ^b	0.017 mol Si m ⁻² yr ⁻¹	0.075–0.210 mol Si m ⁻² yr ⁻¹	0.023 mol Si m ⁻² yr ⁻¹	3.5 mol SiO ₂ m ⁻² yr ⁻¹	109 g C m ⁻² yr ⁻¹	<i>Si: SiO₂ mass ratio = 28.1:60.1</i>
	<i>Si: 28.1 g mol⁻¹</i>		<i>Si: 28.1 g mol⁻¹</i>	<i>Si: SiO₂ mass ratio = 28.1:60.1</i>	<i>C: 12 g mol⁻¹</i>	0.178 kg Si m ⁻²
	0.478 g Si m ⁻² yr ⁻¹	2.1–5.9 g Si m ⁻² yr ⁻¹	0.66 g Si m ⁻² yr ⁻¹	1.636 mol Si m ⁻² yr ⁻¹	9.08 mol C m ⁻² yr ⁻¹	<300 m = 0.87 × 10 ⁶ km ² ^{d,h}
	362 × 10 ¹² m ²		18 × 10 ¹² m ²	45.97 g Si m ⁻² yr ⁻¹	3.63 mol Si m ⁻² yr ⁻¹	0.3% directly disturbed yr ⁻¹ ⁱ
	173 × 10 ⁹ kg Si yr ⁻¹		11.9 × 10 ⁹ kg Si yr ⁻¹	2% on sea-bed ^b	3.63 mol Si m ⁻² yr ⁻¹	plus 0.3% indirectly disturbed yr ⁻¹ ^c
					2.04 g Si m ⁻² yr ⁻¹	
					2.97 × 10 ¹² m ²	
					2.97 × 10 ¹² m ²	
					6.06 × 10 ⁹ kg Si yr ⁻¹	
					0.930 × 10 ⁹ kg Si yr ⁻¹	
					1.068 g Si m ⁻² yr ⁻¹	
					0.87 × 10 ¹² m ²	

^aCopin-Montegut & Copin-Montegut (1978); ^bAveraged from Nelson et al. (1995) and Leynaert et al. (1993); ^cAssumption; ^dClarke & Johnston (2003); ^eGerdes et al. (2003); ^fBarthel (1995); ^gMaldonado et al. (2005); ^hGriffiths et al. (2011); ⁱGutt & Starmsans (2001)

calculation of the area for the shallow shelf, and then to 0.300% area per year. Mortality within a scour is assumed to be 100%, and in areas to the left and right, in total twice as large as the proper ice scour, is assumed to be 50%. Mortality left and right of the ice scour can be caused indirectly, e.g. by extremely high sedimentation during iceberg scouring or bulldozing. These assumptions result in a total mortality rate of 0.600% area per year. Dissolution of sponge-derived silicate until its burial in the sediment is neglected based on observations and conclusions on long-term processes by Krautter et al. (2006), and results from experiments showing high resistance to dissolution after periods up to 8 mo for selected species by Maldonado et al. (2005) and Chu et al. (2011). According to Barthel (1995), sponge ash weight averaged for some of the most abundant species/genera, such as *Rossella*, *Anoxycalix* (= *Scolymastra*), *Cinachyra*, and *Mycale* on the Antarctic shelf, comprises 30% of their wet weight, and according to Dayton et al. (1974) and Maldonado et al. (2005), sponge ash weight consists almost completely of biogenic silica. Barthel (1995) also provided data from Dayton et al. (1974) and McClintock (1987) that show similar dry weight:ash weight ratios for McMurdo Sound. However, the wet weight:dry weight ratios of Dayton et al. (1974) were much higher than those of Barthel (1995).

RESULTS

The distribution of the megabenthos along the video-transect (Stn 184) shows sections with a sponge-spicule cover between 1 and 100% interrupted by 3 areas without any visible spicules (Fig. 1a). Abundances of benthic bulk groups or key taxa varied considerably within and between sections with different levels of spicule cover and among animal groups. The 500–800 m segment of the transect lacked spicules while the 480–500 m segment had 51–100% cover. There was one large area without spicules. In front of it the amount of spicules was highest not only in terms of sea-bed cover ($\leq 100\%$) but also in terms of dead sponge material, which was piled up to a height of >1 m. The proportion of mobile species was generally low, especially in areas devoid of spicules. Large hexactinellid sponges were rare in these sections and small specimens of this taxon were underrepresented. The demosponge *Cinachyra barbata* s.l. was very abundant only in the last 100 m of the transect (Fig. 1a). Recently it was discovered that this species deviates in some important morphological details from the original description (M. J. Uriz, pers. comm.). As a consequence, it is called *C. barbata* (s.l.) here.

The still images at Stn 247 depict a similar distribution (Figs. 1b & 2). In contrast to the video transects, all sponges from the still image transects were ana-

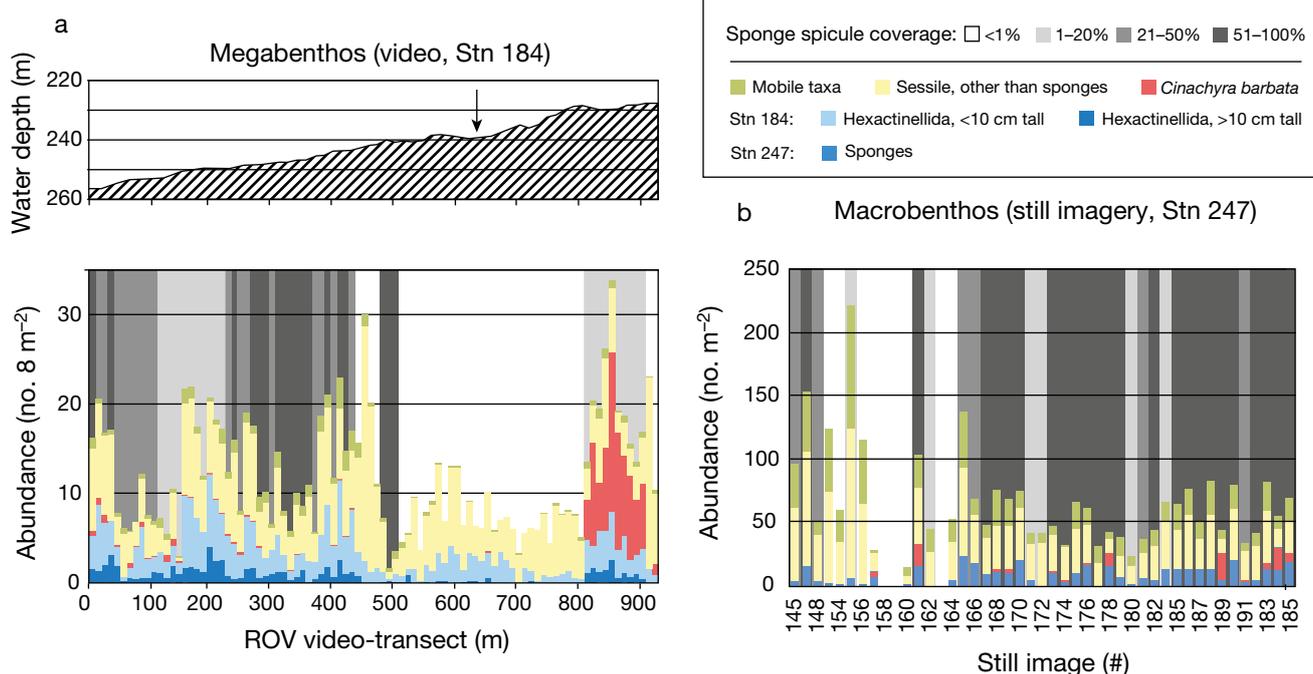


Fig. 1. Sponge spicule sea-bed cover and abundances of systematic/functional bulk groups analysed along transects using imaging methods. (a) Megabenthos analysed by sea-bed video (arrow: assumed scour mark), (b) macrobenthos analysed along a still image transect



Fig. 2. Selected sea-bed still images along the transect at Stn 247, showing different levels of sponge spicule sea-bed cover and different macrobenthic assemblages. The abundant spherical greenish-grey sponge had previously been described from catches and images in the same area of investigation as *Cinachyra barbata* s.l. For uncertainties in identification, see 'Results'. All images represent 1 m²

lysed as a bulk group because of a lack of a clear dominance of one key species. In gaps with a low spicule cover of <1%, living sponges were comparably rare; abundances of mobile and other large sessile taxa varied more within these gaps than outside these gaps.

Among the videotaped mega-epibenthic taxa (Stn 184), weak but significant binomial regressions between decreasing abundances of small and large hexactinellids and increasing levels of spicule cover

were found (Fig. 3a). The demosponge *Cinachyra barbata* s.l. reached high abundances of up to 18 ind. 8 m⁻² only at the 1–20% level of spicule cover at the end of the transect. Abundance of photographed sponges was positively correlated with spicule cover (Fig. 3b). Sessile organisms other than sponges (video, Stn 184; Fig. 3a) had an optimum at 21–50% spicule cover, but no correlation was found for the photographed sessile animals other than sponges (Stn 274). Mobile taxa were evenly abundant among

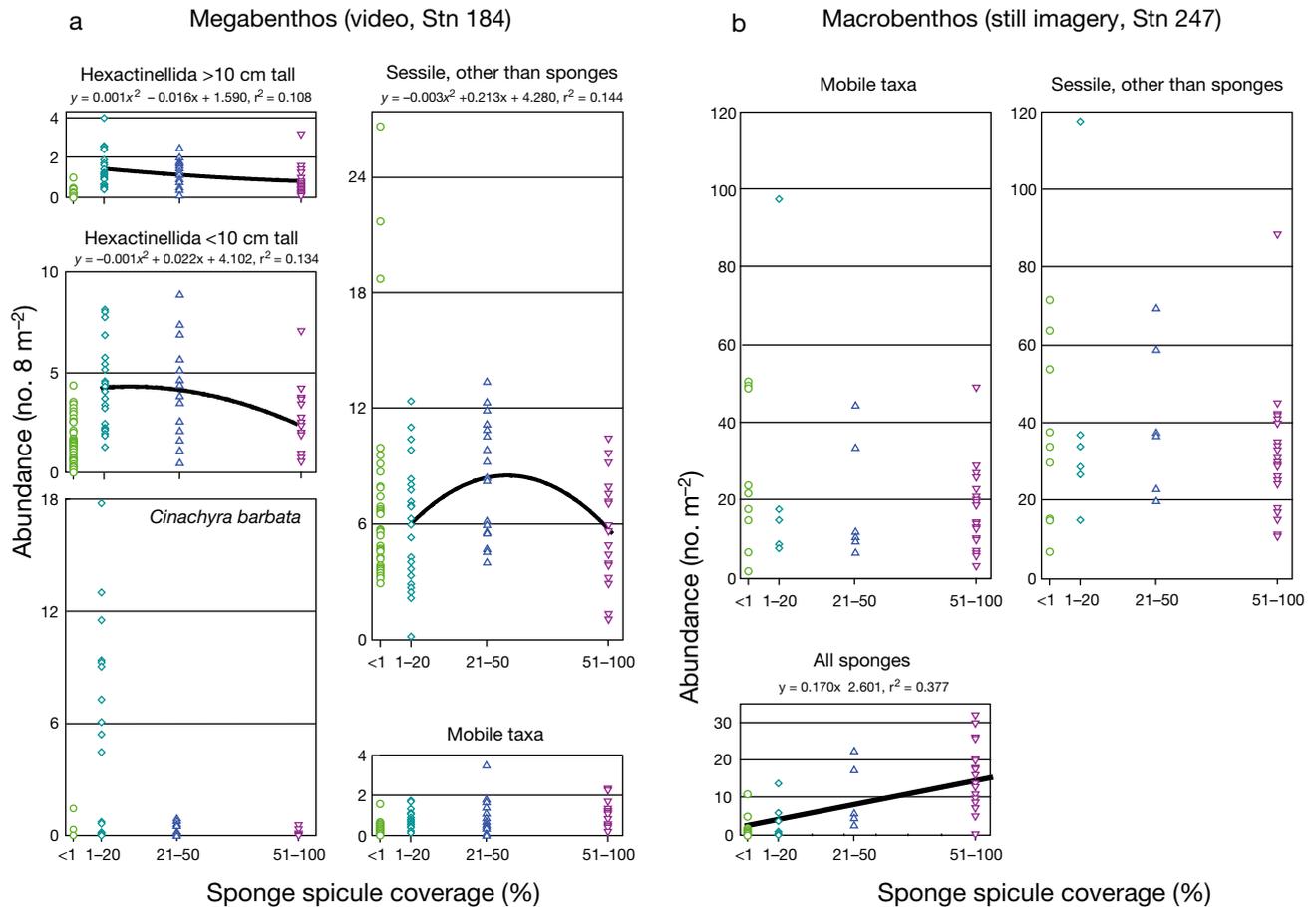


Fig. 3. Relationships between systematic/functional bulk groups and sponge spicule sea-bed cover. (a) Megabenthos, (b) macrobenthos

the spicule-cover levels at both stations, with much higher abundances and variance found on the still images than from the videos. Correlation between organism abundance and spicule cover at both stations was not significant ($\alpha = 0.05$).

Diversity (in a broad sense) showed contrasting results for the mega- and macro-epibenthos (Fig. 4). Richness of mega-epibenthic taxa was weakly but significantly correlated with spicule cover (Stn 184; Fig. 4a). The negative slope, however, and thus a decreasing trend with increasing spicule cover, was not significant, whilst it was significantly positive for the macro-epibenthos (Stn 247; Fig. 4b). The dominance patterns for the mega-epibenthos (Stn 184) were quite even at all levels of spicule cover, starting with a relatively low dominance of approximately 20% for small hexactinellid sponges, the most abundant taxon (Fig. 4a). Among the macro-epibenthos on the still images, the lower spicule-cover levels had a more uneven dominance pattern, starting with approximately 45 and >55% dominance for the most abundant taxon, indicating a low diversity (Fig. 4b).

The curves for the higher spicule-cover levels resembled those of the mega-epibenthos, with a more even relative numeric composition of the taxa.

The MDS plot for the mega-epibenthos showed a clear separation between the micro-habitat defined by the <1% spicule-cover level and all others, which were comparably homogenous (Fig. 5a). The ANOSIM test revealed significant differences in species composition within the entire data set across all assemblages with a global R-value of 0.474 ($p = 0.001$). A pairwise test showed the least difference between the 21–50% and 51–100% spicule cover levels (ANOSIM, $p = 0.024$, $R = 0.07$) and the greatest difference between the <1% spicule cover level and all others ($p < 0.0001$, $R > 0.69$). The macro-epibenthic composition (Fig. 5b) was more homogenous than that of the mega-epibenthos, with a global R of 0.266 ($p = 0.002$). In the pairwise test, a significant difference was found only between the most extreme <1 and 51–100% spicule-cover levels ($R = 0.474$, $p = 0.001$) and between the 1–20 and 51–100% levels ($R = 0.239$, $p = 0.044$).

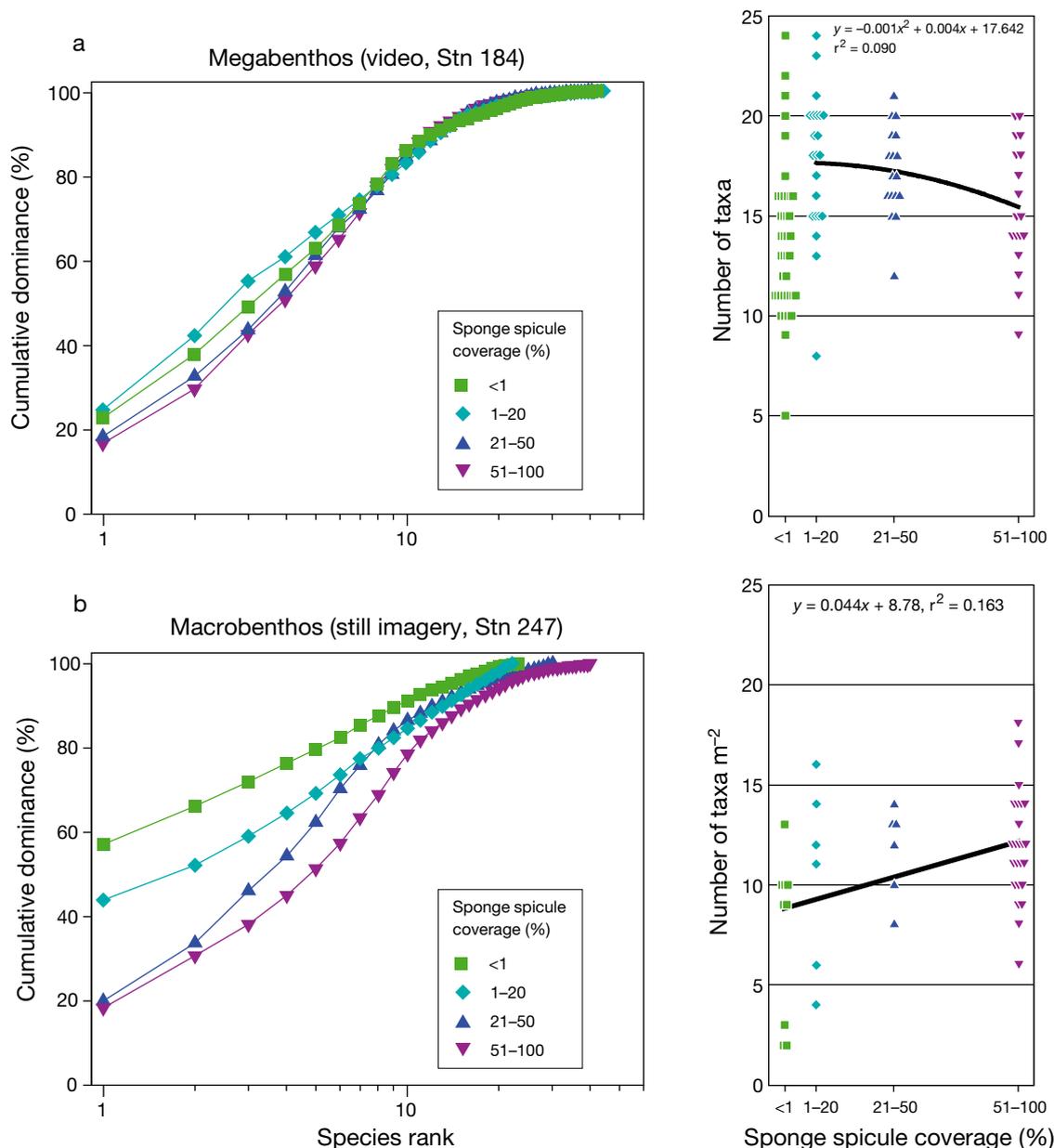


Fig. 4. Dominance patterns and richness of taxa related to sponge spicule sea-bed cover. (a) Megabenthos, (b) macrobenthos

A simple numerical model might be able to demonstrate the relevance of sponge devastation by icebergs for the marine Si cycle at different spatial scales (Table 1). The main objective of this approach is a comparison between turnover rates from living to dead biogenic Si deposited at the sea floor, derived from diatom productivity and sponge mortality. The total amount of sponge-derived Si deposited on the shallower shelf is 15 to 34% of that originating from diatom production reaching the sea-bed of the entire Antarctic shelf. The

absolute amount of dissolved Si, transferred to sponge biomass and fixed in Antarctic shelf sediments after iceberg-induced sponge mortality, amounts for only 0.69% of the total Si derived from primary production and arriving at the total global sea-bed. Standardised values per unit area (m^{-2}) for the Antarctic shelf amount to 50 to 100% of the diatom-derived Si in the same area. Comparable flux rates for larger areas, such as the South Atlantic and the global ocean, are lower but within the same order of magnitude.

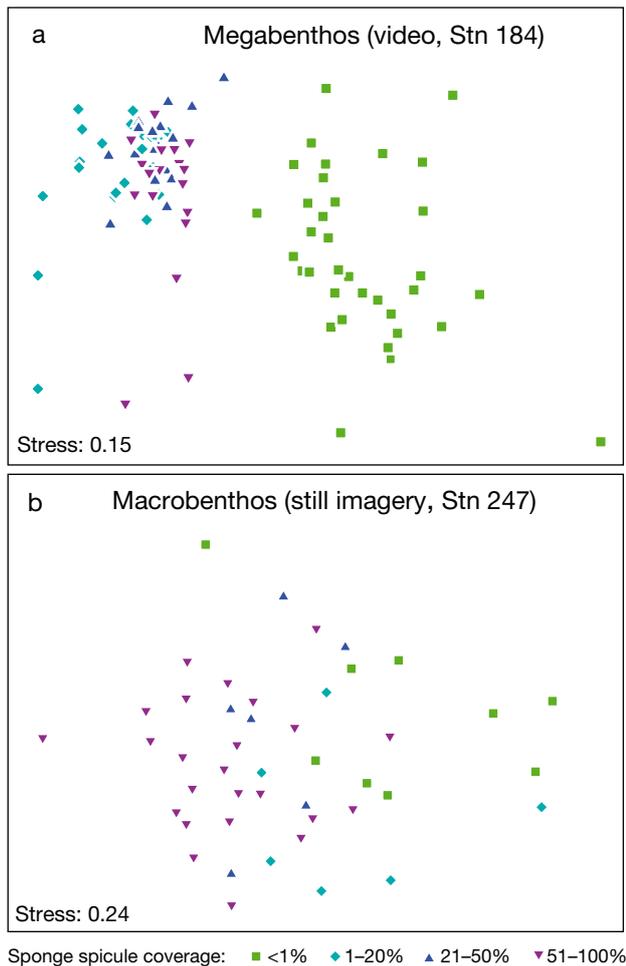


Fig. 5. Multidimensional scaling (MDS) plot, showing spatial heterogeneity or beta-diversity (species turnover) at different levels of sponge spicule sea-bed cover. (a) Megabenthos, (b) macrobenthos

DISCUSSION

Reconstruction of Antarctic benthic habitat fragmentation by iceberg impact

The spatial distribution of the mega-epibenthos along the video transect showed generally high total abundances with a varying composition of a few bulk groups of taxa and the key species *Cinachyra barbata* s.l., interrupted by 3 sections with different fauna. The largest such gap, in the second part of the transect, extended to ~300 m in length. Not far from this, a much smaller gap was visible in the middle of the transect and the third gap started almost at the end of the transect. Gutt & Starman (2001) introduced criteria to identify iceberg scours, with an abrupt change in species composition at their mar-

gins and the occurrence of assumed pioneer species as the main characteristics. These criteria are fulfilled by the 3 gaps. The almost complete absence of any visible spicule cover, the virtual absence of intermediate-sized to large sponges (>10 cm tall), and the absence of a plausible alternative hypothesis are additional reasons to interpret these 3 sections as relatively recent iceberg scours.

In some parts of the video, where it was apparent that *Cinachyra barbata* s.l. was present on the seabed in locally high abundances, it was difficult to distinguish between dead spicule mats and spicule strands. The strands can belong to living sponges and may be up to 1 m long and 10 cm wide. An extremely large number of spicules estimated from the videos was piled up to >1 m in height in direct proximity to the largest iceberg scour. It was this structure that initiated the development of a conceptual scenario on how this fragmentation could have originated.

Before one or more icebergs impacted the sea-bed, mega-epibenthic organisms colonized the area at Stn 184 in a relatively homogenous manner, but the presence of a gradient from a hexactinellid- to a demosponge-dominated mega-epibenthos cannot be excluded. Gutt & Koltun (1995) and Gutt & Starman (2003) described such disturbance-independent patchiness for sponges and other sessile and mobile benthic animals on Antarctic shelves at all spatial scales between a few and several hundreds of metres. However, spatial species turnover between such patches was never as abrupt and discrete as that observed at the margin of assumed iceberg scours analysed in the present and other studies (see e.g. Barthel & Gutt 1992). Before the physical disturbance happened, hexactinellid sponges exhibited a normal demographic structure in the entire area, with smaller individuals being more common than larger individuals. These biogenic structures attracted a variety of associated sessile and mobile epibenthic and epibiotic fauna (see also Gutt & Schickan 1998). When one or more icebergs grounded, they acted like a bulldozer. A large amount of sponge material was pushed downslope, where it was piled up to a height of >1 m. At this moment the iceberg must have moved predominantly parallel to the slope. When it grounded, it scoured a plateau into the otherwise gentle slope (see Fig. 1a) towards the glaciated coast at approximately 7 km distance. Most of the dislocated sponges died immediately after the impact. In addition, a 'cloud' of suspended sediment drifted with the predominant NE–SW direction of the coastal current towards the first half of the analysed

transect and caused an indirect disturbance; most *Cinachyra barbata* s.l. died, but most hexactinellids survived. This most likely development is based on the following assumptions and ideas.

(1) No other ecological drivers or environmental gradients are likely to have caused the difference between the high abundance of *C. barbata* s.l. in one place and its rarity 300–800 m away. Only mass mortality due to discrete iceberg disturbance or other reasons can have shaped this pattern of *C. barbata* s.l. distribution in the Antarctic. Such mortality due to unknown reasons is known from the NE Atlantic (Barthel et al. 1996) and the Mediterranean (Hogg et al. 2010).

(2) The hypothesis of an indirect disturbance by a 'cloud' of suspended sediment is supported by the lowest abundances or absence of *C. barbata* s.l. close to the iceberg scour and higher values at the beginning of the transect approximately 400 m from the impact area. If an *a priori* low abundance of *C. barbata* s.l. and other sessile organisms reflects a generally unfavourable habitat with a high coverage of sponge spicules independent of the iceberg impact, one would expect higher abundances in the sections with lower spicule cover (1–20% and especially <1%), but the opposite was found.

(3) An additional indication that *C. barbata* s.l. is an especially susceptible species and was more abundant in the first part of the transect during the pre-impact phase is the co-occurrence of living hexactinellid sponges and dead remnants of the above-described strands acting as 'roots' or raised platforms for *C. barbata* s.l. to live on.

(4) The best evidence that the benthic pattern is shaped by iceberg impact is the presence of all size classes of hexactinellid sponges outside and only small specimens of the same species, mainly *Rossella racovitzae* and *Anoxycalix joubini*, inside the assumed iceberg scour.

All of these arguments support the hypothesis of a combination of direct mortality of most species due to a typical iceberg disturbance and subsequent indirect species-specific lethal effects. Our data give no indication of why hexactinellid sponges and other sessile species already recruited and grew in the obvious iceberg scour whilst *C. barbata* s.l. was unsuccessful. Similarly, Dayton et al. (2013) recently documented unexpected dynamics of the glass sponge *A. joubini*, which is generally abundant in McMurdo Sound in the Ross Sea, including successful recruitment, fast growth and mass mortality, probably due to significant shifts in important ecosystem characteristics. A less likely alternative sce-

nario, ignoring the varying abundance of spicules, is that the impact caused mortality of all sponges along most of the transect, and hexactinellids recovered faster than *C. barbata* s.l. However, this hypothesis requires the rejection of the assumption that *C. barbata* s.l. grows much faster than hexactinellids (Gatti 2002), even though their absolute growth rates and differences in growth performance are not sufficiently documented. Further, a possible faster recruitment of hexactinellids alone cannot explain the very low abundance of *C. barbata* s.l. close to the scour, since this species co-exists with larger specimens of hexactinellids at the beginning of the transect.

A reconstruction of the photographically documented macrobenthos at Stn 247 differs from that at Stn 184. Sections with high spicule cover looked different from comparable areas in the videos. In the still images taken at Stn 247, the sediment surface consisted of compressed spicule mats rather than piles of sponge spicule material or dead bodies of single sponges already partly disintegrated, as observed in the video (at Stn 184). These findings lead to the hypothesis that the spicule mats were formed by a physical impact acting as a vertical press rather than a horizontally moving bulldozer. Also, 3 gaps without visible spicules were found. In these, the abundances of mobile and other sessile animals were extremely variable, whilst sponges were rare. If this hypothesis is true, recent iceberg impacts that cannot be associated with the event that shaped the spicule mats created these gaps. The small-scale patchiness and different faunistic composition within these gaps can be interpreted to represent independent early stages of recolonisation. Seiler & Gutt (2007) developed a simple concept for a similar process, which described sponge mortality after dislocation by icebergs with a few survivors, interestingly of the same species, *C. barbata* s.l.

Suitability of spicule mats as habitat for mega- and macro-epibenthos?

Sessile mega-epibenthic animals had only slightly higher abundances but not higher taxon richness in areas with 21–50% spicule cover compared with the highest and lower spicule levels. For hexactinellid sponges the correlation between abundance and spicule cover was negative but weak. For mobile fauna no significance was found. Consequently, our data do not provide clear evidence that sponge spicules shape the substratum so that it attracts or repels additional megabenthic species. It could be

hypothesized that the observed 'piles' of sponges are still too young for a rich assemblage to develop on them. However, assuming that one single event shaped the scour, the spicule 'piles' had a relatively long period of time for colonisation. This follows from a considerable abundance of several species in the iceberg scours, e.g. the cnidarian *Ainigmaption antarctica*, the bryozoan *Camptoplites tricornis*, the sponges *Stylocordyla chupachups* (in earlier papers on the benthos of the Weddell Sea identified as *S. borealis*, spherical form) and small hexactinellids of the genera *Rossella* and *Anoxycalix*, which have been classified as later colonisers rather than first pioneers (Gutt & Piepenburg 2003). Independent of whether a high spicule level attracts a variety of megabenthic species during a late stage of succession, as postulated and described by Dearborn (1965, 1967), Dayton et al. (1970), Arnaud (1974, p. 534–535) and Barthel (1992), and analysed for the meio-benthos by Lee et al. (2001), the formation of spicules might have slowed down the development of a rich benthos after disturbance. Both the direct and indirect destructive effects described above can probably last not only for decades but also for centuries. This will be the case even when the impact is not directly recognisable anymore because the negative effects are superimposed by a successful but incomplete succession of recolonisation resulting in a high biodiversity, according to the intermediate disturbance hypothesis (Huston 1994).

In terms of a specific substrate preference, the macrobenthos at Stn 247 provided different insights from the megabenthos at Stn 184. At Stn 247, the hypothesis of sponges growing successfully on the specific spicule substratum formed by an earlier generation of these organisms can be accepted (Figs. 1b & 3b). The diversity of the macrobenthos growing on the sponge spicule mats and the co-occurrence of taxa apparent from single still images is also clearly higher than in the spicule gaps (Fig. 4b), whilst abundance of motile and sessile taxa other than sponges was not obviously supported by the dense spicules (Fig. 3b). It remains unclear whether the sponge spicules just provide a substratum as favourable as the normal sediment or whether they provide an even more suitable habitat for a variety of species. However, a locally extremely high abundance of up to 20 *C. barbata* s.l. per square metre alone represents the maximum utilisation of sea-bed space.

The difference in the compositional heterogeneity (beta-diversity or turnover of taxa) between macrobenthos and megabenthos shown by the 2 MDS plots is quite obvious. This can be explained by an

assumed younger stage of recolonisation of the megabenthos at the lowest sponge spicule cover level (= fresh iceberg scour), by the different mechanisms that generated the spicule mats, and by the coarser identification level of the megabenthos, which provides less detail regarding biodiversity than the photographic surveys. As the results show a higher heterogeneity at the deeper site, depth-dependent ecological factors seem unlikely to have caused these differences.

Combining the interpretations of both data sets, one can conclude that spicule mats serve as a suitable substratum for the macro- and mega-epibenthos only in a late stage of recolonisation. A delay rather than acceleration in benthic succession can be assumed for the phase after iceberg impact when spicule mats were formed and allowed growth of only a benthos poor in abundance, biomass and diversity, until intermediate stages are reached. A recolonisation after simple devastation of the benthic habitat without formation of spicule mats (Gutt & Piepenburg 2003) might proceed faster. In the final stage of recolonisation, abundances of animals on spicule mats can reach maximum values, but there is still no evidence for especially elevated diversities compared with the 'normal' rich Antarctic benthic assemblages, which are obviously not growing on conspicuous spicule mats (Gutt & Starmans 1998).

Contribution of sponge spicule mat formation to the global and regional silicon cycle

The global comparison reveals that the total standing stock of Si sequestered due to sponge mortality after iceberg scouring is only 0.69% of that of the diatom-derived accumulation of Si in marine sediments worldwide. This value might appear low; however, it has to be considered that the deposition of Si due to sponge mortality occurs potentially on only 2.5% of the global sea floor. This value coincides with the 'very tentative estimate of the global Si consumption by sponges' as 'about 2 to 4 orders of magnitude smaller' than the Si demands of diatoms (Maldonado et al. 2011, p. 6).

A major problem in comparing Si sequestration from sponges with that from primary production is the poor knowledge on the fate of biogenic Si after its deposition on the sea-bed. When sponges die, a certain but unknown proportion of silicon will be fixed for ecologically relevant if not geological time scales because dissolution rates are low, especially when the spicules are buried in the sediment. This assump-

tion is based on experiments of Maldonado et al. (2005), in which they found no detectable dissolution of demosponge spicules and 5% dissolution of hexactinellid spicules after 8 mo, in contrast to 'severe dissolution' of diatom frustules. Similar experiments were performed by Chu et al. (2011), showing 4% dissolution rates of fixation of Si by growth, and by Krautter et al. (2006). However, the described iceberg scouring can also contribute to a release of Si when the icebergs displace the surface sediment.

If a complete marine silicon cycle is considered, 2 principal biological processes, growth and mortality, play an important role. If, however, sequestration from the water column is the main focus, only one of these processes can be considered. When sequestration happens, at the moment of biosilification or when, due to sponge mortality, living biogenic is converted to dead material is a matter of perspective, be it biological or geochemical. In such a macroecological context, the question of how sponges grow and die can be of relevance. Some non-Antarctic species grow rapidly in the first period of their life but very slowly as they get larger (Ayling 1981). If, correspondingly, in the Antarctic sponge mass mortality increases their population growth due to immediate recruitment and fast growth of pioneers, we have to expect an overall increased rate of benthic biosilification and deposition of Si in the sediment. In that case, sponge mortality and not sponge productivity can be the primary process that drives this part of the marine Si budget. An experimentally simulated predation had a similar effect of enhanced biosilification since it was observed to accelerate growth among encrusting sponges in temperate waters (Ayling 1981, Maldonado et al. 2005).

Despite the low global proportion of Si sequestered by Antarctic sponges, a high regional relevance of this process is reflected by the similarity of diatom- and sponge-derived Si deposition in the highly productive waters above the Antarctic continental shelf (Arrigo et al. 2008). One weakness of this calculation is due to the spatial local heterogeneity of planktonic and benthic processes, which are known from only few comprehensive spatially explicit studies, which allow rough conclusions for various spatial scales. At a local scale, which is relevant for the direct and indirect mortality of sponges by icebergs, a deposition rate of $356 \text{ g m}^{-2} \text{ event}^{-1}$ can be calculated from the values provided in Table 1. A similar calculation for diatom-derived Si in areas of high accumulation, where 10–25% of the primary production is assumed to reach the sea-floor, leads to a deposition rate of $10.2\text{--}25.5 \text{ g Si m}^{-2} \text{ yr}^{-1}$. However, due to poor infor-

mation about their spatial and temporal performance, we cannot compare these 2 phenomena based on absolute values. Scale-dependent differences can be caused by the extreme concentration of sponge biomass (average of $1.27 \text{ kg wet weight m}^{-2}$), its local and sudden devastation, and the fact that a high proportion (30%) of the sponge wet weight (Barthel 1995) is assumed to consist mainly of biogenic silica (according to Maldonado et al. 2005). This value is comparable to values for sponges off British Columbia (Chu et al. 2011, see also Barthel 1995), but is high compared with the 6.7% provided by Dayton et al. (1974) for the Antarctic sponge *Homaxinella balfourensis*. The biosilification by this fast-growing species lasted over one decade, with a rate of $234 \text{ g Si m}^{-2} \text{ yr}^{-1}$ (Maldonado et al. 2005). It is even higher than the $119 \text{ g Si m}^{-2} \text{ yr}^{-1}$ converted from living to dead material by iceberg scouring (present study), which was accumulated in decades to maybe millennia within assemblages dominated by other slower-growing demosponges and hexactinellid species. The latter 2 classes are common on the shallower Antarctic shelf but they do not occur everywhere, whilst the explosive growth of the species *H. balfourensis* is rarely described and only at a local scale. *Homaxinella* species grow in high abundances almost exclusively in areas formerly disturbed by anchor ice, glaciers or icebergs (Gutt 2007). It can be concluded that, due to iceberg impact devastating all siliceous sponges, half the Si of the extremely fast-growing of *Homaxinella* population is fixed only if the local spatial scale is considered.

The values for sponge standing stocks in high-latitude Antarctic benthic communities, and thus for their Si, are high compared with those for other regions of the world, e.g. a Caribbean reef-mangrove habitat with 1.9 to $304 \text{ g biogenic Si m}^{-2}$ (average of $>70 \text{ g m}^{-2}$; Maldonado et al. 2005, 2010). Other high values reported so far for sponge assemblages outside the Antarctic are 12.6 g Si m^{-2} for a living population of *Sericolophus hawaiiicus* off Hawaii, and 43 g Si m^{-2} for *Crambe crambe* in the Western Mediterranean. This could be compared with the Antarctic sponge assemblage cited above, with an average wet weight of 12.7 kg m^{-2} , which can be converted to approximately 2 kg Si m^{-2} . Extreme values of $<100 \text{ kg wet weight m}^{-2}$ for single cores which hit a large specimen translate to 15 kg Si m^{-2} . Extremely high silica standing stock values were calculated by Chu et al. (2011) for 3 sponge reefs with mean depths between 80 and 164 m off British Columbia, Canada, and the Eastern Pacific, based on earlier discoveries (Conway et al. 1991, 2001, 2005, Krautter et al. 2001,

Leys et al. 2004). Some details are missing that would allow a direct comparison with the results presented here. Nevertheless, the standing stock per unit area is estimated to be roughly 10 times higher than that within an average Antarctic sponge community. It could only be comparable to a spot with a very high density of Antarctic sponges as mentioned above. The growth of the sponges in British Columbia results in approximately $100 \text{ g Si m}^{-2} \text{ yr}^{-1}$, which is generally locked in living sponge material, whilst rates due to mortality by iceberg scouring in the Antarctic were calculated to be $10 \text{ g Si m}^{-2} \text{ yr}^{-1}$ for sponge communities and $1 \text{ g Si m}^{-2} \text{ yr}^{-1}$ for the entire shallower Antarctic shelf. Due to the differences in the sizes of the areas considered, the Antarctic shelf sequesters roughly $1 \times 10^9 \text{ kg Si yr}^{-1}$ (only due to iceberg scouring) whilst the rate on the much smaller reefs off British Columbia is only $1 \times 10^3 \text{ kg Si yr}^{-1}$. However, the latter sponge reefs are larger than the area for which this value was calculated (Conway et al. 1991, Krautter et al. 2006). Additional areas with locally high concentrations of sponges, which experience similar natural physical disturbances, are Arctic waters shallower than 60 m (Starmans et al. 1999), but information is too sparse to perform a similar coarse comparison.

A secondary effect of elevated benthic Si sequestration could be a limitation of Si availability for primary production in the water column (Tréguer & Pondaven 2000). This would control the growth of primary food for the benthos in the form of diatoms, as at least partly assumed by Rützler & Macintyre (1978) for a coral reef in Belize. This feedback is potentially one of the most important processes within the marine silicon cycle since it can have a momentous effect on the pelagic ecosystem. The question how efficient this mechanism is depends on the proportion of silicon that is accumulated in the sediment for long-lasting ecological or even geological time scales compared with the proportion that is dissolved and, thus, 'recycled' at the sediment surface. Similarly, one can raise the question of whether high biosilification rates due to growth of sponges reduce local silicic acid in their habitat and limit its availability for the growth of the sponges themselves (Maldonado et al. 1999). This might be relevant especially in habitats where the sponges grow rapidly and have a high standing stock, e.g. in stages of early recolonisation after iceberg impact. However, in the Antarctic, most sponges do not live in the euphotic layer and Antarctic waters are unusually rich in dissolved Si, which makes the negative feedback effect relatively unlikely.

In summary, our results on iceberg disturbance to the Antarctic benthos and thus to the regional marine Si cycle strengthen earlier results indicating a considerable contribution of sponges and their population dynamics to such biogeochemical processes.

Acknowledgements. Thanks to M. Rutgers van der Loeff and Marum University of Bremen for providing the Cherokee ROV, and to P. Dayton for critical review.

LITERATURE CITED

- Arnaud P (1974) Contribution à la bionomie marine benthique des régions antarctiques et subantarctiques. *Tethys* 6:1–464
- Arntz WE, Brey T (2005) The Expedition ANTARKTIS XXI/2 (BENDEX) of RV 'Polarstern' in 2003/2004. *Ber Polar Meeresforsch* 503:1–149
- Arrigo KR, van Dijken G, Long M (2008) Coastal Southern Ocean: a strong anthropogenic CO₂ sink. *Geophys Res Lett* 35:L21602, doi:10.1029/2008GL035624
- Ayling AV (1981) The role of biological disturbance in temperate subtidal encrusting communities. *Ecology* 62: 830–847
- Barnes DKA, Conlan C (2007) Disturbance, colonization and development of Antarctic benthic community. *Philos Trans R Soc Lond B Biol Sci* 362:11–38
- Barnes DKA, Hillenbrand CD (2010) Faunal evidence for a late quaternary trans-Antarctic seaway. *Glob Change Biol* 16:3297–3303
- Barnes DKA, Kuklinski P (2010) Bryozoans of the Weddell Sea continental shelf, slope and abyss: Did marine life colonize the Antarctic shelf from deep water, outlying islands or *in situ* refugia following glaciations? *J Biogeogr* 37:1648–1656
- Barnes DKA, Peck LS (2008) Vulnerability of Antarctic shelf biodiversity to predicted regional warming. *Clim Res* 37: 149–163
- Barry JP, Dayton PK (1988) Current patterns in McMurdo Sound, Antarctica, and their relationship to local biotic communities. *Polar Biol* 8:367–376
- Barthel D (1992) Do hexactinellid sponges structure Antarctic sponge associations? *Ophelia* 36:111–118
- Barthel D (1995) Tissue composition of sponges from the Weddell Sea, Antarctica: not much meat on the bones. *Mar Ecol Prog Ser* 123:149–153
- Barthel D, Gutt J (1992) Sponge associations in the eastern Weddell Sea. *Antarct Sci* 4:137–150
- Barthel D, Tendal OS, Thiel H (1996) A wandering population of the hexactinellid sponge *Pheronema carpenteri* on the continental slope off Morocco, northwest Africa. *PSZNI: Mar Ecol* 17:603–616
- Brandt A, Gutt J (2011) Biodiversity of a unique environment: the Southern Ocean benthos shaped and threatened by climate change. In: Zachos FE, Habel JC (eds) *Biodiversity hotspots*. Springer, Berlin, p 503–526
- Chu JWF, Maldonado M, Yahel G, Leys SP (2011) Glass sponge reefs as a silicon sink. *Mar Ecol Prog Ser* 441: 1–14
- Clarke A, Johnston NM (2003) Antarctic marine benthic diversity. *Oceanogr Mar Biol Annu Rev* 41:47–114
- Clarke KR, Warwick RM (2001) Change in marine commu-

- nities: an approach to statistical analysis and interpretation, 2nd edn. PRIMER-E, Plymouth
- Convey P, Bindschadler R, di Prisco G, Fahrbach E and others (2010) Antarctic climate change and the environment. *Antarct Sci* 21:541–563
- Conway KW, Barrie JV, Austin WC, Luternauer JL (1991) Holocene sponge bioherms on the western Canadian continental shelf. *Cont Shelf Res* 11:771–790
- Conway KW, Krautter M, Barrie JV, Neuweiler M (2001) Hexactinellid sponge reefs on the Canadian continental shelf: a unique 'living fossil'. *Geosci Can* 28:71–78
- Conway KW, Barrie JV, Krautter M (2005) Geomorphology of unique reefs on the western Canadian shelf: sponge reefs mapped by multibeam bathymetry. *Geo-Mar Lett* 25:205–213
- Copin-Montegut C, Copin-Montegut G (1978) The chemistry of particulate matter from the south Indian and Antarctic Oceans. *Deep-Sea Res* 25:911–931
- Cummings VJ, Thrush SF, Chiantore M, Hewitt JE, Cattaneo-Vietti R (2010) Macrobenthic communities of the north-western Ross Sea shelf: links to depth, sediment characteristics and latitude. *Antarct Sci* 22:793–804
- Dayton PK (1989) Interdecadal recruitment and destruction of an Antarctic sponge population and its effect on local populations of Asteroids. *Science* 245:1484–1486
- Dayton PK (1990) Polar benthos. In: Smith WO (ed) *Polar oceanography, Part B: Chemistry, biology, and geology*. Academic Press, San Diego, CA, p 631–685
- Dayton PK, Oliver JS (1977) Antarctic soft-bottom benthos in oligotrophic and eutrophic environments. *Science* 197: 55–58
- Dayton PK, Robillard GA, Paine RT (1970) Benthic faunal zonation as a result of anchor ice in the benthic community at McMurdo Sound Antarctica. In: Holdgate MW (ed) *Antarctic ecology*. Academic Press, New York, NY, p 244–258
- Dayton PK, Robilliard GA, Paine RT, Dayton LB (1974) Biological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecol Monogr* 44:105–128
- Dayton PK, Kim S, Jarrell SC, Oliver JS and others (2013) Recruitment, growth and mortality of an Antarctic hexactinellid sponge, *Anoxycalyx joubini*. *PLoS ONE* 8: e56939
- Dearborn JH (1965) Ecological and faunistic investigations on the marine benthos at McMurdo Sound, Antarctica. PhD thesis, Stanford University, CA
- Dearborn JH (1967) The fauna of the Ross Sea. Stanford University invertebrate studies in the Ross Sea, 1958–61: general account and station list. *Bull NZ Dept Sci Ind Res* 176:31–47
- Gage JD, Tyler PA (1991) *Deep-sea biology: a natural history of organisms at the deep-sea floor*. Cambridge University Press, Cambridge
- Gatti S (2002) The role of sponges in high Antarctic carbon and silicon cycling: a modelling approach. PhD dissertation, University of Bremen
- Geibert W, Rutgers van der Loeff MM, Usbeck R, Gersonde R, Kuhn G, Seeberg-Elverfeldt J (2005) Quantifying the opal belt in the Atlantic and southeast Pacific sector of the Southern Ocean by means of ^{230}Th normalization. *Global Biochem Cycles* 19:GB4001, doi:10.1029/2005GB002465
- Gerdes D, Hilbig B, Montiel A (2003) Impact of iceberg scouring on macrobenthic communities in the high-Antarctic Weddell Sea. *Polar Biol* 26:295–301
- Grant S, Constable A, Raymond B, Doust S (2006) Bioregionalisation of the Southern Ocean: Report of Experts Workshop, Hobart, September 2006. WWF Australia and Antarctic Climate and Ecosystem Cooperative Research Centre, Sydney
- Griffiths HJ, Danis B, Clarke A (2011) Quantifying Antarctic marine biodiversity: The SCAR-MarBIN data portal. *Deep-Sea Res II* 58:18–29
- Gutt J (2000) Some 'driving forces' structuring communities of the sublittoral antarctic macrobenthos. *Antarct Sci* 12: 297–313
- Gutt J (2007) Antarctic macro-zoobenthic communities: a review and an ecological classification. *Antarct Sci* 19: 165–182
- Gutt J, Koltun VM (1995) Sponges of the Lazarev and Weddell Sea (Antarctica): explanations for their patchy occurrence. *Antarct Sci* 7:227–234
- Gutt J, Piepenburg D (2003) Scale-dependent impact on diversity of Antarctic benthos caused by grounding of icebergs. *Mar Ecol Prog Ser* 253:77–83
- Gutt J, Potthoff M (2007) Sea-bed photographs (benthos) from the Weddell Sea (Antarctica) along profile PS65/247-1. doi:10.1594/PANGAEA.666994
- Gutt J, Schickan T (1998) Epibiotic relationships in the Antarctic benthos. *Antarct Sci* 10:398–405
- Gutt J, Starmans A (1998) Structure and biodiversity of megabenthos in the Weddell and Lazarev Seas (Antarctica): ecological role of physical parameters and biological interactions. *Polar Biol* 20:229–247
- Gutt J, Starmans A (2001) Quantification of iceberg impact and benthic recolonisation patterns in the Weddell Sea (Antarctica). *Polar Biol* 24:615–619
- Gutt J, Starmans A (2003) Megabenthic patchiness at small scales: ecological conclusions by examples from polar shelves. *Polar Biol* 26:276–278
- Gutt J, Starmans A, Dieckmann G (1996) Impact of iceberg scouring on polar benthic habitats. *Mar Ecol Prog Ser* 137:311–316
- Gutt J, Hosie G, Stoddart M (2010) Marine life in the Antarctic. In: McIntyre AD (ed) *Life in the world's oceans: diversity, distribution and abundance*. Wiley-Blackwell, Oxford, p 203–220
- Gutt J, Arntz WE, Dimmler W, Schulz H and others (2011) Sea-bottom videos and photographs (benthos) along six shelf profiles from the eastern Weddell Sea, Antarctica taken with remote operated vehicle CHEROKEE during 'Polarstern' cruise ANT-XXI/2. AWI/MARUM, University of Bremen, doi:10.1594/PANGAEA.770359
- Gutt J, Zurell D, Bracegirdle TJ, Cheung W and others (2012) The use of correlative and dynamic species distribution modelling for ecological predictions in the Antarctic: a cross-disciplinary concept. *Polar Res* 31: 11091
- Hogg MM, Tendal OS, Conway KW, Pomponi SA and others (2010) Deep-sea sponge grounds: reservoirs of biodiversity. UNEP-WCMC Biodiversity Series No. 32. UNEP-WCMC, Cambridge
- Huston MA (1994) *Biological diversity*. Cambridge University Press, Cambridge
- Janussen D, Tendal OS (2007) Diversity and distribution of Porifera in the bathyal and abyssal Weddell Sea and adjacent areas. *Deep-Sea Res II* 54:1864–1875
- Koltun VM (1968) Spicules of sponges as an element of the bottom sediments of the Antarctic. In: SCAR, SCOR, IAPO, IUBS (eds) *Symposium on Antarctic Oceanogra-*

- phy, Santiago, Chile, 13–16 September 1966. W. Hefer & Sons, Cambridge, p 121–123
- Krautter M, Conway KW, Barrie JV, Neuweiler M (2001) Discovery of a 'living dinosaur': globally unique modern hexactinellid sponge reefs off British Columbia. *Facies* 44:265–282
- Krautter M, Conway KW, Barrie JV (2006) Recent hexactinoidan sponge reefs (silicate mounds) off British Columbia, Canada: frame-building processes. *J Paleontol* 80: 38–48
- Lee HJ, Gerdes D, Vanhoef S, Vincx M (2001) Meiofauna response to iceberg disturbance on the Antarctic continental shelf at Kapp Norvegia (Weddell Sea). *Polar Biol* 24:926–933
- Leynaert A, Nelson DM, Quéguiner B, Tréguer P (1993) The silica cycle in the Antarctic Ocean: Is the Weddell Sea atypical? *Mar Ecol Prog Ser* 96:1–15
- Leys SP, Wilson K, Holeton C, Reiswig HM, Austin WC, Tunnicliffe V (2004) Patterns of glass sponge (Porifera, Hexactinellida) distribution in coastal waters of British Columbia, Canada. *Mar Ecol Prog Ser* 283:133–149
- Maldonado M, Carmona MC, Uriz MJ, Cruzado A (1999) Decline in Mesozoic reef-building sponges explained by silicon limitation. *Nature* 401:785–788
- Maldonado M, Carmona MC, Velásquez Z, Puig A, Cruzado A, López A, Young CM (2005) Siliceous sponges as a silicon sink: an overlooked aspect of benthopelagic coupling in the marine silicon cycle. *Limnol Oceanogr* 50:799–809
- Maldonado M, Riesgo A, Bucci A, Rützler K (2010) Revisiting silicon budgets at a tropical continental shelf: silica standing stocks in sponges surpass those in diatoms. *Limnol Oceanogr* 55:2001–2010
- Maldonado M, Navarro L, Grasa A, Gonzalez A, Vaquerizo I (2011) Silicon uptake by sponges: a twist to understanding nutrient cycling on continental margins. *Sci Rep* 1:30
- McClintock JB (1987) Investigation on the relationship between invertebrate predation and biochemical composition, energy content, spicule armament and toxicity of benthic sponges at McMurdo Sound, Antarctica. *Mar Biol* 94:479–487
- Nelson DM, Tréguer P, Brzezinski MA, Leynaert A, Quéguiner B (1995) Production and dissolution of biogenic silica in the ocean: revised global estimates, comparison with regional data and relationship to biogenic sedimentation. *Global Biogeochem Cycles* 9:359–371
- Pondaven P, Ragueneau O, Tréguer P, Hauvespre A, Dezileau L, Reyss JL (2000) Resolving the 'opal paradox' in the Southern Ocean. *Nature* 405:168–172
- Post AL, Hemer MA, O'Brien PE, Roberts D, Craven M (2007) History of benthic colonisation beneath the Amery Ice Shelf, East Antarctica. *Mar Ecol Prog Ser* 344:29–37
- Rützler K, Macintyre IG (1978) Siliceous sponge spicules in coral reef sediments. *Mar Biol* 49:147–159
- Sachs L (2002) *Angewandte Statistik: Anwendung statistischer Methoden*, 10th edn. Springer, Berlin
- Seiler J, Gutt J (2007) Can dead sponges talk? *Antarct Sci* 19:337–338
- Smale DA (2007) Ice disturbance intensity structures benthic communities in nearshore Antarctic waters. *Mar Ecol Prog Ser* 349:89–102
- Spencer CP (1983) Marine biogeochemistry of silicon. In: Aston SR (ed) *Silicon geochemistry and biogeochemistry*. Academic Press, San Diego, CA, p 101–142
- Starmans A, Gutt J, Arntz WE (1999) Mega-epibenthic communities in Arctic and Antarctic shelf areas. *Mar Biol* 135:269–280
- Thatje S, Hillenbrand CD, Mackensen A, Larter R (2008) Life hung by a thread: endurance of Antarctic fauna in glacial periods. *Ecology* 89:682–692
- Thrush S, Dayton P, Cattaneo-Vietti R, Chiantore M and others (2006) Broad-scale factors influencing the biodiversity of coastal benthic communities of the Ross Sea. *Deep-Sea Res II* 53:959–971
- Tréguer P, Pondaven P (2000) Global change: silica control of carbon dioxide. *Nature* 406:358–359
- Tréguer P, Nelson DM, Van Bennekom AJ, DeMaster DJ, Leynaert A, Quéguiner B (1995) The silica balance in the world ocean: a reestimate. *Science* 268:375–379

Editorial responsibility: James McClintock, Birmingham, Alabama, USA

*Submitted: October 2, 2012; Accepted: December 14, 2012
Proofs received from author(s): April 3, 2013*