



## Benthic communities and their drivers: A spatial analysis off the Antarctic Peninsula

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### Abstract

Multiple environmental factors control benthic community patterns, and their relative importance varies with spatial scale. Since this variation is difficult to evaluate quantitatively, extensive sampling across a broad range of spatial scales is required. Here, we present a first case study on Southern Ocean shelf benthos, in which mega-epibenthic communities and biota-environment relationships have been explored at multiple spatial scales. The analyses encompassed 20 seafloor, water-column, and sea-ice parameters, as well as abundances of 18 mega-epibenthic taxa in a total of 2799 high-resolution seabed images taken at 28 stations at 32–786 m depth off the northern Antarctic Peninsula. Based on a priori nesting of sampling stations into ecoregions, sub-regions, and habitats, analyses indicated most pronounced patchiness levels at finest (within transects among adjacent seabed photos) and largest (among ecoregions) spatial scale considered. Using an alternative approach, explicitly involving the spatial distances between the geo-referenced data, Moran's Eigenvector mapping (MEM) classified the continuum of spatial scales into four categories: broad (> 60 km), meso (10–60 km), small (2–10 km), and fine (< 2 km). MEM analyses generally indicated an increase in mega-epibenthic community complexity with increasing spatial scale. Moreover, strong relationships between biota and environmental drivers were found at scales of > 2 km. In contrast, few environmental variables contributed to explaining biotic structures at finer scales. These are likely rather determined by nonmeasured environmental variables, as well as biological traits and interactions that are assumed to be most effective at small spatial scales.

Benthic community composition and distribution are generally determined by the combined effects of a variety of processes acting on a range of scales: (1) the evolutionary history that created a pool of species adapted to present large-scale conditions (Arntz and Gallardo 1994; Clarke and Johnston 2003; De Broyer et al. 2014), (2) intermediate-scale ecological conditions selecting for regionally occurring species from the large-scale species pool, and (3) rather short-term biological and physical processes, such as grazing or disturbances, respectively. Often direct effects are not directly “visible” anymore, but modulate and contribute to the intermediate-termed effects on distribution patterns (*see, e.g.,* Gutt 2000; Gray

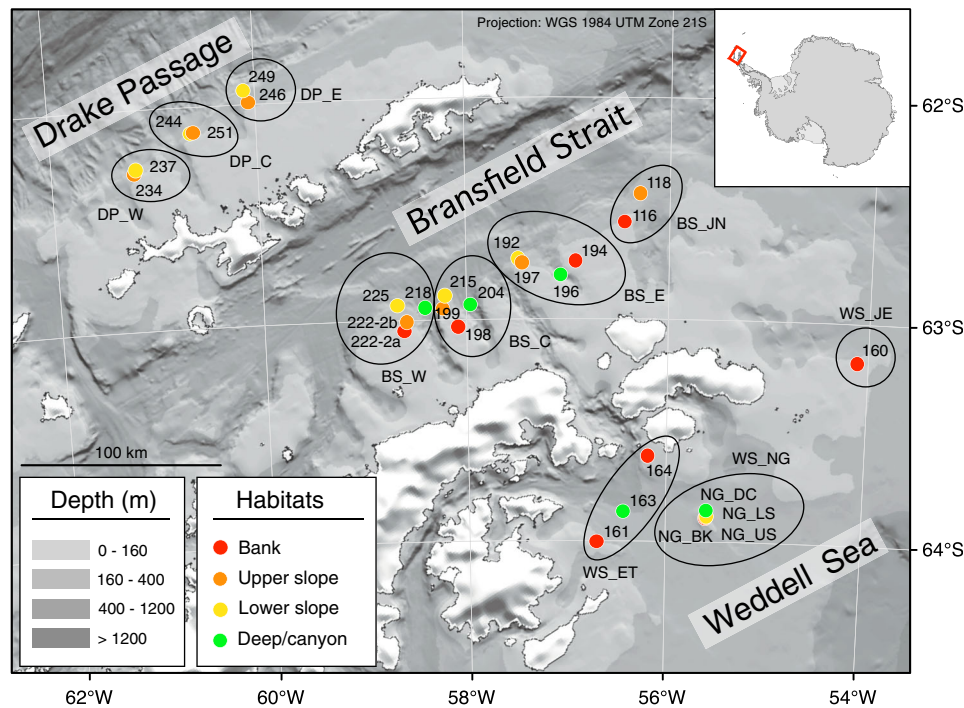
2001; Thrush et al. 2006). Disentangling and understanding the scale-dependency of these drivers and their effects on benthic community structure is important for fundamental and applied science, such as biosphere modeling under climate-change scenarios (Smale and Barnes 2008; Turner et al. 2009) and developing sound evidence-based strategies for nature conservation and sustainable use of living resources. For research perspectives, *see, e.g.,* Kennicutt (2014a).

Our current knowledge on interactions between seafloor biota and their environment, however, is relatively poor in the Southern Ocean. Therefore, the overarching objective of this study was to gauge the role of the three above-mentioned complexes of drivers for mega-epibenthic assemblages off the northern Antarctic Peninsula. Specifically, we focused on the Bransfield Strait, southern Drake Passage, and northwestern Weddell Sea (Fig. 1; for cruise report, *see* Gutt 2013). These ecoregions are suited for such an analysis due to high spatial and temporal gradients in physical and chemical conditions (Dorschel et al. 2016), ensuring sufficient environmental variation to expect pronounced contrasts in

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**Fig. 1.** Map of study area off the northern tip of the Antarctic Peninsula, showing the locations of seabed photo-transects during the PS81 cruise of R/V *Polarstern* in 2013. Habitats are color coded, and subregions encircled. Abbreviations: Ecoregions—WS, Weddell Sea; BS, Bransfield Strait; DP, Drake Passage; Subregions—JE, Joinville Island East; JN, Joinville Island North; ET, Erebus and Terror Gulf; DU, Dundee Island; NG, Nachtigaller Shoal; W, west; C, central; E, east; Habitats—BK, Bank; US, Upper slope; LS, Lower slope; DC, Deep/canyon.

benthic community structure. To cover small- to large-scale variability, a photographic seabed survey was carried out. It provided data on the seafloor coverage of key megafauna organisms, most of which are epibenthic (De Broyer et al. 2014). Mega-epibenthos is defined here to include organisms  $\geq 3$  mm, of which at least part of the body protrudes the sediment surface. Environmental data comprised information on small-scale bottom topography taken at a similar spatial resolution as the biological data, sea-ice cover and chlorophyll concentration (indicating phytoplankton biomass) gained from satellite-based observations, as well as water-mass data collected only at one point for each photo-transect. The sampling design consequently offered information from single photos to entire transects and larger spatial and environmental units.

The waters off the northern tip of the Antarctic Peninsula are generally known for their high benthic species richness (Griffiths 2010) and their relevance for climate-change related biogeography research (Barnes et al. 2009). One reason for the high diversity may be that species occurring in this region are adapted to high-latitude conditions, in terms of hydrography and ice cover, but also to a less polar environment, where the southern boundary of the Antarctic Circumpolar Current hits the Peninsula (Orsi et al. 1995; Sokolov and Rintoul 2009). These conditions cause complex oceanographic patterns (Huneke et al. 2016) and seasonally pulsed primary production (Thomalla et al. 2011; for details, see Supporting Information Table S1). The latter provides food for benthic organisms and is influenced by sea-ice extent and sea-ice dynamics (Norkko et al.

2007; Dorschel et al. 2016). Additionally, the southernmost part of the Drake Passage is almost ice-free the entire year and characterized by the relatively warm Transitional Zonal Water with Bellingshausen Sea and Circumpolar Deep Water influence. The waters of the Bransfield Strait are generally characterized by a broad temperature range, in the southern part by low temperatures, due to the influence of the glaciers of the Antarctic Peninsula, and in the north by even lower temperature, due to the inflow of water from the Weddell Sea surrounding the tip of the Peninsula. Sea ice occurs regularly in winter. The Shelf Water in the Weddell Sea is set apart by the coldest waters, with temperatures close to the freezing-point of seawater, and an almost year-round sea-ice cover. The bottom topography of the shelf in the southeastern Bransfield Strait is characterized by shallow banks, incised by canyons deeper than 800 m. The stations in the Drake Passage had a similar seafloor structure, however, canyons were less distinct. In the Weddell Sea, banks with slopes, of which one was classified as a shoal (Dorschel et al. 2014), and inner-shelf depressions characterize the bottom topography.

Gutt et al. (2016) have recently reported the composition of 96 macrobenthic taxa, ranging from species to phyla, that were collected from 25 Agassiz-trawl catches obtained during the same cruise (PS81 of R/V *Polarstern*) in the same study area off the northern Antarctic Peninsula as the seabed photos analyzed in the present study. However, the results of Gutt et al. (2016) only allowed to identify intermediate- to large-scale spatial patterns and their environmental drivers (see also the

“Discussion” section). Between-station variability in benthic composition and biomass were very high. Abundant taxonomic groups were demosponges and hexactinellid sponges in the Weddell Sea and Drake Passage, ascidians in the Weddell Sea and echinoderms in the Bransfield Strait and Drake Passage. Similarly, Segelken-Voigt et al. (2016) studied distribution patterns of ascidian assemblages in seabed photos taken during PS81. The ascidians showed a high spatial heterogeneity, which is not surprising for a group of benthic animals known to respond faster than others to environmental changes, such as physical disturbance or changes in water mass characteristics. The response can be rapid recruitment, high individual growth rates, or population collapse (Gutt et al. 1996, 2013; Gutt and Piepenburg 2003; Sahade et al. 2015). Both Gutt et al. (2016) and Segelken-Voigt et al. (2016) did not assess the significance of scale-dependent drivers. A similar study on the benthos biodiversity and composition in and in front of fjords of the western Antarctic Peninsula, southwestward of our investigation area, also showed a high spatial heterogeneity in these hotspots for benthic abundance and diversity (Grange and Smith 2013).

With this background the detailed objectives of this study were:

1. Describe the faunistic composition of mega-epibenthic communities, based on class-level taxonomic analysis, at multiple, a priori defined ecologically relevant spatial scales:
    - a. Stations, represented by photo transects of 2 km length
    - b. Subregions comprising the different habitats within a limited area, such as a single canyon-system, crossed with the ecoregions (100-km scale)
    - c. Seabed habitats, defined by water depth and bottom topography (Bank, Upper slope, Lower slope, and Deep/canyon), nested within subregions
    - d. Ecoregions, i.e., southern Drake Passage, southeastern Bransfield Strait and northwestern Weddell Sea (400-km scale)
- and check hypotheses on differences within these scales.
2. Analyze for each of the three ecoregions, independently of the other above made a priori assumptions, the scale-dependency of
    - a. Mega-epibenthic community patterns
    - b. Relationships between biotic community composition and potential environmental drivers.

## Materials and methods

### Data collection

Our study was based on a photographic seabed survey that was conducted during expedition ANT-XXIX/3 (PS81) of R/V *Polarstern* to the waters off the northern Antarctic Peninsula in January–March 2013 (Fig. 1; for a cruise report, see Gutt 2013).

This study area encompassed three ecoregions: (1) the southern Drake Passage north of the South Shetland Islands, (2) the

southeastern Bransfield Strait northwest of the northern tip of the Antarctic Peninsula, and (3) the northwestern Weddell Sea. Within these ecoregions, the station plan was designed to cover three, four, and three subregions, respectively, which represented distinct geographic and geomorphologic features on a 100-km scale. In addition, up to four depth-related habitats were differentiated within the subregions: (1) Bank, (2) Upper slope, (3) Lower slope, and (4) Deep/canyon. Due to ship-time limitations and seafloor morphology, however, not all habitats were represented within each subregion. In all but one subregion, water depths hardly varied within the photo-transects. Exceptions were the stations at the Nachtigaller Shoal in the western Weddell Sea, where three transects spanned water depths from 30 to 400 m water. Photos taken along these transects needed to be reassembled to depth-related “pseudo-stations” to meet the requirements of the ecological concept (for details, see Supporting Information Fig. S1).

Seabed photos were taken with the Ocean Floor Observation System (OFOS) at 28 stations (Fig. 1) at water depths ranging from 32 to 786 m. At each station, photo-transects were of  $\geq 2$  km length. On average, single photos depicted a seabed area of 4.5 m<sup>2</sup> (standard deviation = 1.6 m<sup>2</sup>) with an average pixel size of 0.46 mm  $\times$  0.45 mm. For a detailed description of the OFOS and its mode of operation during the PS81 cruise, see Piepenburg et al. (2017). All seabed photos obtained during the PS81 expedition, including metadata, are publicly available from the ICSU World Data System PANGAEA (Piepenburg et al. 2013). In this study, we analyzed for each of the 28 stations, 100 seabed photos that were randomly selected from each 2-km transect. The average distance between the GPS-determined positions of the analyzed photos was 7.4 m (standard deviation = 3.7 m). At “pseudo-station” NG-BK, only 99 photos were selected from the photo-transect (Segelken-Voigt et al. 2016).

### Faunistic data

For faunistic analyses, a total of 18 major mega-epibenthic groups were distinguished in the photos (only taxa, which covered > 0.5% area of seafloor across the entire data set): Demospongia (DEM), Hexactinellida (HEX), Gorgonaria (GOR), Hydrozoa (HYD), Anthozoa (ANT), mobile Polychaeta (mo\_POL), Bryozoa (BRY), filter-feeding Holothuroidea (f\_HOL), deposit-feeding Holothuroidea (d\_HOL), Echinoidea (ECH), Crinoidea (CRI), Asteroidea (AST), Ophiuroidea (OPH), solitary Ascidiacea (so\_ASC), colonial Ascidiacea (sy\_ASC), Hemichordata (HEM), infauna indicators (INF\_ind), and other epifauna (oth\_EPI). These groups constituted the vast majority of the living mega-epibenthic organisms visible in the photos. The abundance of these 18 mega-epibenthic functional and systematic groups was assessed by estimating their percentage seafloor coverage in five classes (except ophiuroids; see below): 0%, 0–1%, 1–5%, 5–30%, and > 30%. The centers of these coverage classes (0.0%, 0.5%, 3.0%, 17.5%, 50.0%) were used for subsequent numerical analyses. Based on a visual check, the center for the highest class was down-weighted from 65% to 50% since the statistical distribution of coverage within this size class was right-skewed for all taxa. Ophiuroids

were first assessed in five numeric abundance classes: 0, 1–10, 11–30, 31–50, 51–100, and > 100 individuals. Based on a visual check and best expert knowledge, the upper and lower limits of these classes were converted to seafloor coverage, using a conversion factor of 0.15 to obtain values comparable with the coverage-based abundance values of the other benthic groups. For these classes, the centers (0%, 1%, 3%, 6%, 11%, and 30%) were used for further analyses.

### Environmental data

To identify environmental drivers of the mega-epibenthic communities, extensive information published by Dorschel et al. (2016) and already partly considered by Gutt et al. (2016) and Segelken-Voigt et al. (2016) were used in this study (Supporting Information Table S1). These data comprised small-scale (single-photo) information on the structure of the seafloor, intermediate-scale (1-km) satellite-derived information on sea-ice cover dynamics, and sea-surface chlorophyll concentrations, as well as oceanographic data from CTD casts (lowest near-bottom measurements) conducted at stations that were located between 0.06 and 5.73 km, in most cases less than 2 km, away from the center of the OFOS transects (Dorschel et al. 2016). Water depths were calculated from bathymetric terrain models (BTM) generated from corrected and post-processed multibeam echosounder measurements. They had a resolution of 33 m and formed the basis for all subsequent geomorphological analyses. From the BTMs, seafloor ruggedness and seabed slope were calculated using ArcGIS (Burrough et al. 2015). Resulting values were extracted for each photo. Seafloor topography was classified by calculating bathymetric position index (BPI) grids (<http://resources.arcgis.com/en/comunites/oceans/02pp00000007000000.htm>, last accessed 24 April 2019). For the BPIs, annulus shaped reference areas were applied with an inner radius of 30 m and an outer radius of 60 m for fine-scaled classifications. In addition, BPIs with a reference area with 900 m inner radius and 1500 m outer radius were used for coarse-scaled classifications. The Benthic Terrain Modeler (BTM) classification into 13 categories was carried out based on BPIs using the BTM extension version 3.0 (beta) for ArcGIS 10.1. Specific values for each cell were extracted from these grids. Ruggedness and seabed slope were log-transformed because original values had a skewed distribution. Oceanographic measurements provided data on near-bottom water temperature, salinity, and oxygen (% saturation). Satellite-derived remote sensing data for each photo included 5-yr (2008–2012) and 10-yr averages (2003–2012) of chlorophyll *a* (Chl *a*) concentration in  $\text{mg m}^{-3}$  previous to the year of sampling with resulting standard deviations based on monthly averaged satellite data. In addition, the average Chl *a* concentration for the period of 31 d before sampling to the sampling day (based on daily satellite observations) was calculated. Analyses were done for a  $3 \times 3$  grid cell area with the photo in the central cell, each quadratic cell had a length of 4.63 km. This relatively large area was chosen because it was assumed that the benthos is potentially shaped by phytoplankton-conditions in a larger area around the exact position of the photo. Similarly, for sea-ice

concentration, also year-round averages for 5- and 10-yr periods as well as for a period of 31 d before sampling with standard deviations were calculated. For description of chlorophyll measurement errors, see Dorschel et al. (2016); for sea-ice concentration, a summary on its error is given at [https://seaice.uni-bremen.de/fileadmin/user\\_upload/ASluserguide.pdf](https://seaice.uni-bremen.de/fileadmin/user_upload/ASluserguide.pdf) (last accessed 06 March 2019). Sea-ice cover was measured similarly to Chl *a* for  $3 \times 3$  arrays of  $6.25 \times 6.25$  km large grid-cells with the position of the individual photos in the central cell. Hard substrates were visually checked and classified in % seafloor coverage; centers of classes in parentheses: 0% (0%), 0–5% (2.5%), 5–30% (17.5%), and 30–100% (65%). For more technical details about environmental data collection and processing, please refer to Dorschel et al. (2016), Gutt et al. (2016), Huneke et al. (2016), and Segelken-Voigt et al. (2016).

### Community and diversity analyses

Multidimensional scaling (MDS) was performed to visualize the pattern of pairwise between-photo resemblances (Bray-Curtis similarities) in mega-epibenthic composition. An Analysis of Similarity test (ANOSIM) was used to check the significance of differences in community composition among ecoregions, subregions, and habitats. Prior to the analyses, 19 photos without any organisms and one photo with only one 0.5% cover value were excluded as outliers. Seabed-coverage values were square root-transformed before computation of Bray-Curtis similarities. The statistical software package PRIMER v7 was used for all analyses, if not mentioned otherwise.

$\beta$ -diversity was analyzed to study the faunistic heterogeneity or turnover by calculating between-photo Bray-Curtis similarities (Magurran 1988). The higher the similarities are the more similar the faunistic composition of the pair of photos is and the more homogeneous the community is. Kruskal-Wallis ANOVA was used to test the significance of differences among medians of  $\beta$ -diversity for each ecoregion, habitat, and subregion (global test), and pairwise multiple comparison procedures (Dunn's method) were applied to test the significance of differences between each pair of medians (SigmaStat 3.5).

Seriation analysis was used to describe spatial discontinuities in small-scale (i.e., within-station) distribution patterns. For each station (= photo transect), the index of multivariate seriation (IMS) was determined by computing the Spearman rank correlation ( $\rho$ ) between the spatial distances of all pairs of photos (assuming a constant distance between adjacent photos) and the between-photo faunal Bray-Curtis similarities in mega-epibenthic composition. A high  $\rho$  value indicates a strong serial trend along a photo transect, because of generally decreasing faunistic similarity with increasing distance between photos, while a low  $\rho$  value suggests that there are pronounced faunistic differences between adjacent photos along the transect.

### Multiscale spatial analysis

The community analyses described above do not account for geographic distances between seabed photos. As a result, they do not allow for an explicit treatment of multiple spatial

scales in the data. Therefore, we used a further approach, Moran's Eigenvector mapping (MEM), to analyze the multiscale associations between environmental factors and mega-epibenthic structure (see, e.g., Borcard et al. 2011; Dray et al. 2012; Legendre and Legendre 2012; Kraan et al. 2015). We did this separately for each ecoregion, on scales ranging from broad (among subregions) to fine (along-photo-transect). MEM uses a connectivity matrix, describing the spatial (Euclidean) distances between photos to determine linear independent eigenvectors. These eigenvectors represent distinct spatial scales in the data and can be related to faunistic composition and environmental conditions. MEMs eigenvectors are extracted in the order of decreasing positive eigenvalues, which consequently are related to successively smaller scales. The MEM approach has seldom been applied in marine community studies, although it is more suitable for presenting complex spatial structures than traditional spatial descriptors based on geographic coordinates (Griffith and Peres-Neto 2006).

Prior to employing the MEM framework, community coverage-data were Z-standardized and subsequently linearly detrended, using geographical photo coordinates, to remove large-scale spatial gradients and focus on capturing small- and meso-scale patterns (Kraan et al. 2015). The residuals of this model were used in the further analyses. Then, we quantified the spatial connectivity between photos, to gauge whether sampling locations were considered spatial neighbors (Dray et al. 2006). Due to the lack of prior knowledge about the spatial structuring of Antarctic benthic diversity, we applied a data-driven approach based on the corrected Akaike Information Criterion and adjusted explained variance (Supporting Information Table S2). We chose weighted Gabriel neighborhood to define spatial distance between the photo locations of all ecoregions, after comparatively exploring the performance of six different neighbor matrices: Delaunay triangulation, minimum spanning tree, relative neighborhood, nearest neighbors, distance thresholds, and Gabriel neighborhood. Subsequently, weighted Gabriel neighborhoods were used for the Eigen decomposition of community data, providing spatial Eigen functions (MEM variables) that can be used as spatial predictors for ordination approaches (see, e.g., Borcard et al. 2011; Dray et al. 2012; Kraan et al. 2015).

To a posteriori identify which spatial scales the MEM eigenvectors relate to, we constructed histograms of the geographic between-photo distances (Supporting Information Fig. S2). These suggested the presence of three to four distance clusters, which matched relatively well our delineation of four MEM subsets identified through visual comparison of similarities in the spatial range of significant positive MEM variables (i.e., those variables that represented positive spatial autocorrelation [ $p < 0.05$ , 9999 permutations; see Borcard et al. 2011]). These MEM subsets thus represented four spatial scales within each ecoregion: broad (> 60 km; i.e., between distant subregions and distant stations belonging to the same habitat), meso (10–60 km; i.e., between adjacent subregions and between adjacent stations belonging to the same habitat), small (2–10 km; i.e., within subregions), and fine (< 2 km; i.e., within station = along one photographic transect).

Furthermore, each MEM-subset was used in a redundancy analysis with environmental variables to identify the set of abiotic variables that were most linked to the scale represented by the particular MEM subset. Forward selection with a significance level of 0.05 and 9999 random permutations was then used to obtain the model with the most parsimonious set of abiotic variables. In addition, this approach was also applied in a similar fashion to identify which mega-epibenthic species were most associated with which scale. Finally, to determine how much of the community variation was related to abiotic variables or spatial structure, we performed variance partitioning in each ecoregion for each spatial submodel. All analyses were done with R (R Development Core Team 2017) using the package *adespatial* (Dray 2018).

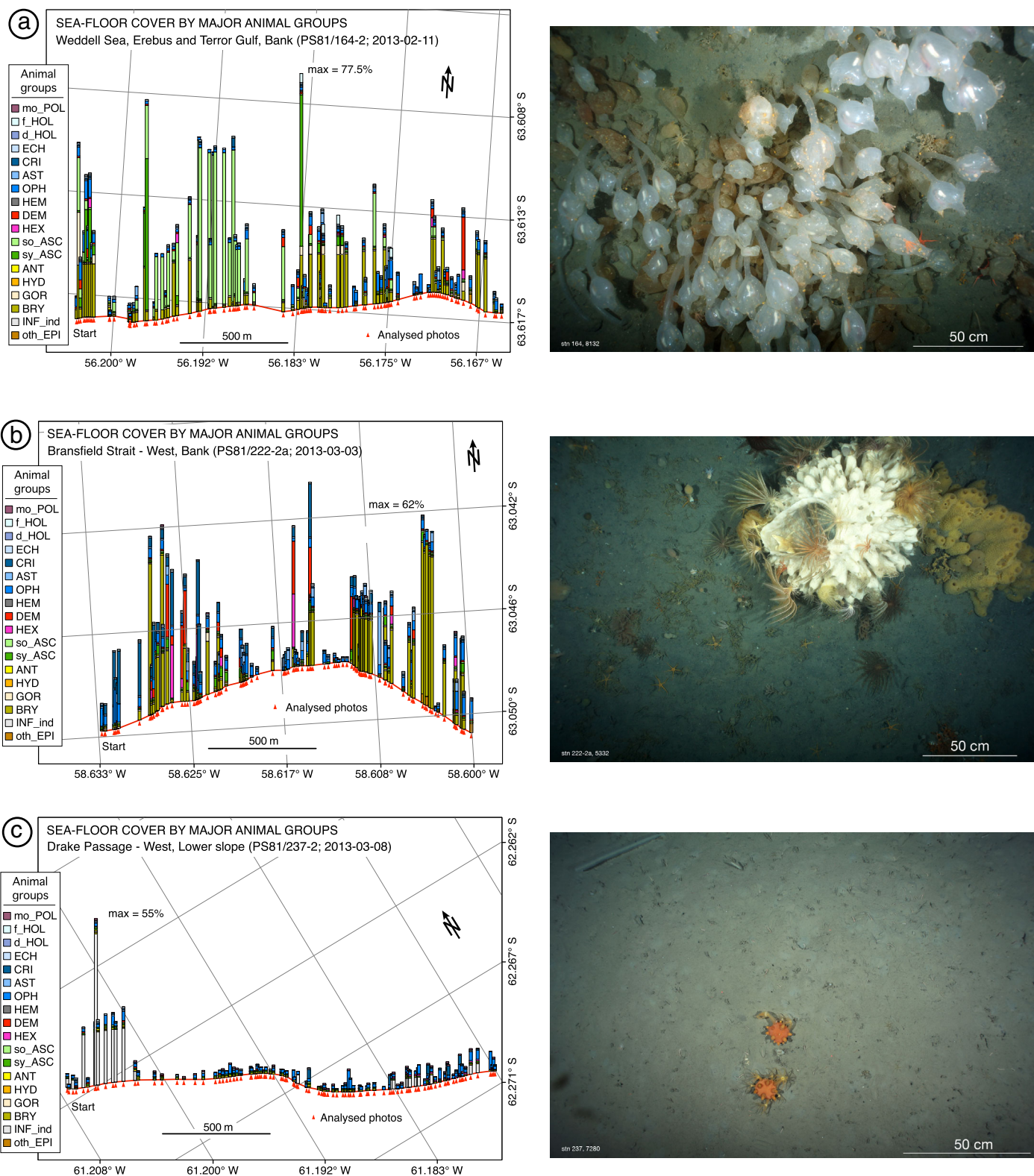
## Results

### Local faunistic composition

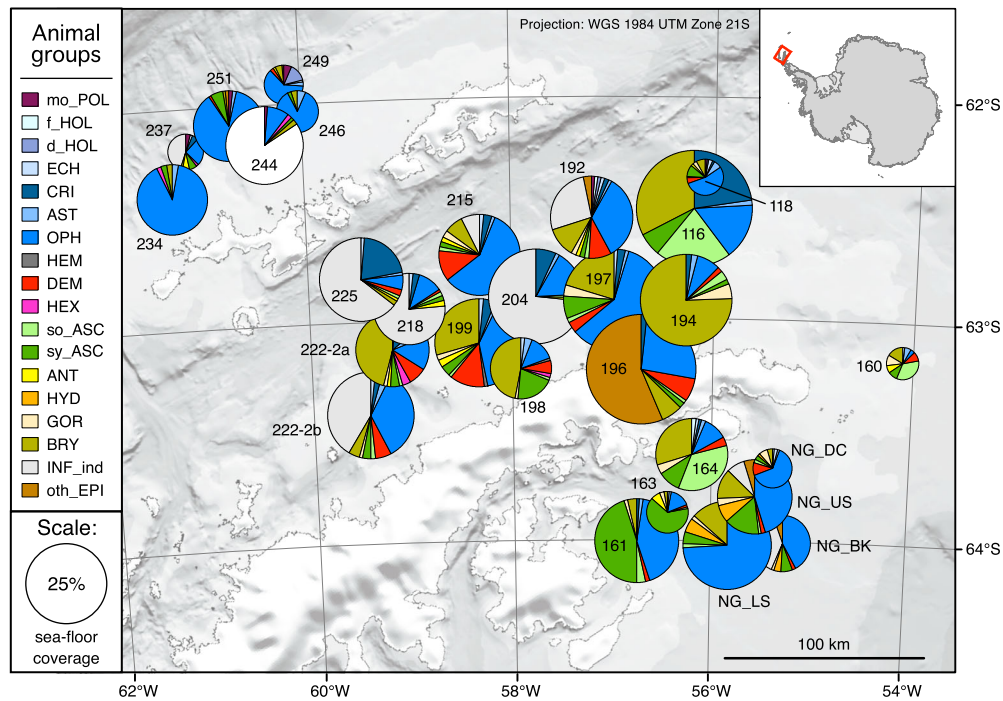
In general, within-station abundance (i.e., seafloor cover) and composition of mega-epibenthic fauna varied pronouncedly (Fig. 2 and Supporting Information Fig. S1).

At the next coarser spatial scale, i.e., among stations (= photo transects), similarities in faunistic composition were also generally low, even between adjacent transects (Fig. 3). This pattern was especially evident for dominant animal groups, with some exceptions, e.g., in the Drake Passage. Among-station variability was most pronounced in the Weddell Sea.

The IMS, determined for each station, was plotted vs. the average between-photo Bray-Curtis similarities ( $\beta$ -diversity, Supporting Information Fig. S3). The plot was split into four quadrants, separated by the 50% percentiles at both axes. Most stations (18) fell into the quadrant with low Bray-Curtis similarities and low IMS (upper left) and with high IMS in combination with high Bray-Curtis similarities (lower right). With the exception of the upper right quadrant, all habitats and ecoregions were represented in the different combinations of high/low seriation and high/low  $\beta$ -diversities (quadrants). At some stations with a relatively homogeneous community composition, e.g., at station 294, seriation was not significant ( $p < 0.05$ ). It was intermediate in cases of a very heterogeneous faunistic composition with, consequently, also a high  $\beta$ -diversity (low Bray-Curtis similarity) as at Sta. 160 and 161. High seriation in combination with low Bray-Curtis similarity was rare, e.g., at Sta. 185, 186, and 189 (Nachtigaller Shoal), which were characterized by a particularly heterogeneous seafloor topography. Seriation was also high at Sta. 116 and 237, due to clearly defined patches of bryozoans, solitary ascidians, and infauna indicators. Such distinct patches, especially of solitary ascidians and bryozoans, were also visible at Sta. 164 (see also Fig. 2a). However, the IMS was only intermediate, since for bryozoans such a patch occurred twice within the transect. IMS values were low, when relatively often adjacent photos were different and patches were small, e.g., at Sta. 222-2a (Fig. 2b), and when no clear structure was recognizable, e.g., at Sta. 234 (Supporting Information Fig. S1).



**Fig. 2.** Three examples of the within-station (= along-transect) variation (10-m scale) in faunistic composition (stacked-bar color coding) and abundance (seafloor cover = bar height) among seabed photos taken along transects, as well as one example seabed photo for each station. Abbreviations of animal groups: DEM, Demospongia; HEX, Hexactinellida; GOR, Gorgonaria; HYD, Hydrozoa; ANT, Anthozoa; mo\_POL, mobile Polychaeta; BRY, Bryozoa; f\_HOL, filter-feeding Holothuroidea; d\_HOL, deposit-feeding Holothuroidea; ECH, Echinoidea; CRI, Crinoidea; AST, Asteroidea; OPH, Ophiuroidea; so\_ASC, solitary Ascidiacea; sy\_ASC, colonial Ascidiacea; HEM, Hemichordata; INF\_ind, infauna indicators; oth\_EPI, other epifauna. Note the different scaling of the bars among stations. For similar information about all transects, see Supporting Information Fig. S1. **(a)** Numerous solitary ascidians, *Cnemidocarpa verrucosa* (light brownish) and *Molgula pedunculata* (whitish), most likely colonizing a boulder; **(b)** A hexactinellid sponge *Rossella* sp. providing the substratum for crinoids and a yellow demosponge (upper right); **(c)** Two orange alcyonarians on soft sediment with hits of a rich infauna comprising mostly buried ophiuroids.



**Fig. 3.** Mega-epibenthic composition and seafloor coverage, integrated for stations (i.e., photo-transects). For better recognizability of results, some pie charts have been dislocated, thus, centers of circles do not exactly represent the position of the station. For correct positions of stations, see Fig. 1 and Segelken-Voigt et al. (2016). Abbreviations: Animal groups—DEM, Demospongia; HEX, Hexactinellida; GOR, Gorgonaria; HYD, Hydrozoa; ANT, Anthozoa; mo\_POL, mobile Polychaeta; BRY, Bryozoa; f\_HOL, filter-feeding Holothuroidea; d\_HOL, deposit-feeding Holothuroidea; ECH, Echinoidea; CRI, Crinoidea; AST, Asteroidea; OPH, Ophiuroidea; so\_ASC, solitary Ascidiacea; sy\_ASC, colonial Ascidiacea; HEM, Hemichordata; INF\_ind, infauna indicators; oth\_EPI, other epifauna. Ecoregions—WS, Weddell Sea; BS, Bransfield Strait; DP, Drake Passage. Subregions—JE, Joinville Island East; JN, Joinville Island North; ET, Erebus and Terror Gulf; DU, Dundee Island; NG, Nachtigaller Shoal; W, west; C, central; E, east. Habitats—BK, Bank; US, Upper slope; LS, Lower slope; DC, Deep/canyon.

### Regional faunistic composition

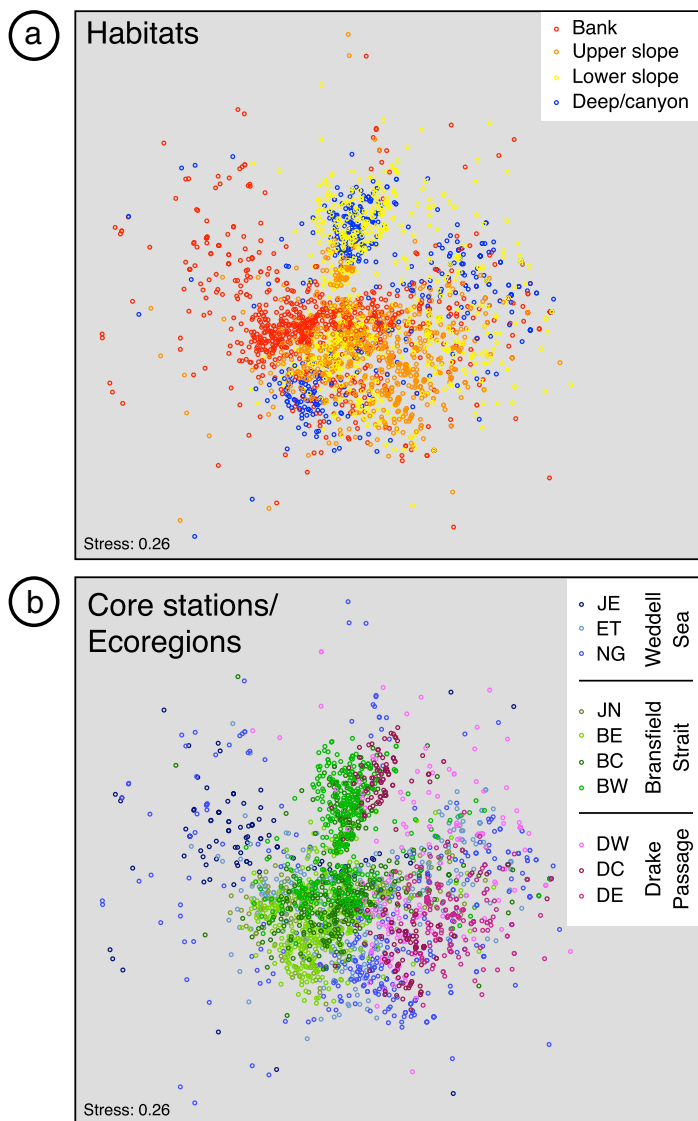
On a spatial scale of the a priori defined subregions and ecoregions (Supporting Information Figs. S4, S5), mega-epibenthic abundance and diversity were generally highest in the Bransfield Strait. Stations in the Drake Passage were most homogeneous and least diverse. Homogeneity between groups of stations was most obvious within subregions, which comprised, with exceptions, all habitats. With regard to the also a priori defined habitats, “Bank” was least dominated by only one animal group, followed by “Deep/canyon.” At the “Upper slope,” ophiuroids were most dominant.

The MDS plot (Fig. 4) indicated a high faunistic heterogeneity of the mega-epibenthic fauna depicted in single photos. All faunistic compositions varied significantly but to a different degree among both ecoregions and nested subregions (two-way nested ANOSIM: Global  $R = 0.239$  among subregions and  $R = 0.611$  among ecoregions). Pairwise differences between ecoregions were highest between Bransfield Strait and Drake Passage ( $R = 0.963$ ) and lowest between Weddell Sea and Drake Passage ( $R = 0.481$ ). At subregion level, differences were highest ( $R > 0.7$ ) at two pairs of subregions between Weddell Sea and Bransfield Strait, two between Weddell Sea and Drake Passage, and one between Bransfield Strait and Drake Passage. Lowest differences were

found in two cases within the Bransfield Strait and between two subregions in the Bransfield Strait and the Weddell Sea ( $R < 0.13$ ). Differences among habitats were significant but did not vary considerably (two-way crossed ANOSIM, global  $R = 0.554$ ). Pairwise  $R$  values ranged between 0.465 (Upper slope vs. Lower slope) and 0.621 (Upper slope vs. Deep/canyon), i.e., spatial proximity of habitats was reflected by the results of the ANOSIM analysis only for the two slope habitats. All differences between data sets were significant ( $p < 0.05$ ), even in case of  $R$  values being close to 0.

### Faunistic heterogeneity ( $\beta$ -diversity)

Within the categories habitats, ecoregions, and subregions, the total of the medians of  $\beta$ -diversities (spatial turnover of animal groups, Fig. 5) did not belong to one statistical population ( $p < 0.05$ ). The differences for most single pairs of medians within these categories were significant ( $p < 0.05$ ). At habitat level, heterogeneity was lowest at Upper slope and highest at Deep/canyon. At ecoregion level, highest heterogeneity was recorded in the Weddell Sea, especially as the Nachtigaller Shoal was included, and lowest in the Bransfield Strait. At subregion level, heterogeneity was highest at the Nachtigaller Shoal and in the Erebus and Terror Gulf in the Weddell Sea as well as in two subregions of the Drake Passage, while it was lowest in two subregions of the



**Fig. 4.** Two-dimensional ordination plot of the MDS. Each dot represents the community composition in a single seabed photo. Both plots visualize the same faunistic similarities between single photos but differ in the color coding according to habitats **(a)**, ecoregions and subregions **(b)**. Abbreviations of subregions: In the Weddell Sea—JE, Joinville Island East; ET, Erebus and Terror Gulf; NG, Nachtigaller Shoal; In the Bransfield Strait—JN, Joinville Island North; BE, Bransfield East; BC, Bransfield Central; BW, Bransfield West; In the Drake Passage—DW, Drake West; DC, Drake Central; DE, Drake East.

Bransfield Strait. Only four pairs of medians did not show a significant difference, between the subregions JE and JN, DW and ET, JE and DC, and DC and JN.

#### Scale-dependent faunistic composition and environment-biota relationships

MEM modeling indicated high spatial heterogeneity in the distribution of most taxa, especially at broad and intermediate scales (Table 1). Overall, pronounced spatial patchiness across

a wide scale range was evident in the Bransfield Strait, while in the Drake Passage most taxa did not exhibit significant patchiness at fine spatial scales and in the Weddell Sea most taxa showed significant spatial heterogeneity at a broad spatial scale. The ecoregions also differed considerably in the composition of taxa with high spatial heterogeneity across a wide range of spatial scales. For example, crinoids, asteroids, ascidians, and bryozoans displayed a particularly pronounced and largely scale-independent patchiness in the Bransfield Strait, while in the Drake Passage such a distribution pattern was evident for anthozoans, ophiuroids, and bryozoans, and in the Weddell Sea for ophiuroids, anthozoans, and hydrozoans.

Moreover, MEM analysis showed that most of the environmental water-column and seabed variables were significantly associated with the composition of mega-epibenthic communities at broad and intermediate spatial scales, especially in the Drake Passage and Bransfield Strait. The proportion of the explained variance in community composition decreased from larger to smaller spatial scales (Table 2). At small and fine spatial scales, the number of significant correlations varied among ecoregions. Several seafloor descriptors with local variations, e.g., ruggedness, seabed slope, and BTM, correlated at least in some ecoregions with the faunistic composition. Pertaining to water-column variables, a significant environment-fauna relationship was observed in only two cases, for “Chl *a*, 31 d, *std*” in the Drake Passage and “Sea-ice, 31 d, mean” in the Weddell Sea.

Partitioning of the variance revealed that with increasingly finer spatial scales, more variation was explained by the environmental variables; while at larger spatial scales, the spatial components become more important (Supporting Information Table S3). Residuals, representing unknown nonenvironmental and non-spatial components that were not included in our data and, thus, in the MEM models, increased with decreasing spatial scale. The explanation of the faunistic composition by the environmental and the spatial components was weakest in the Weddell Sea, at all spatial scales, and similar in the two other ecoregions.

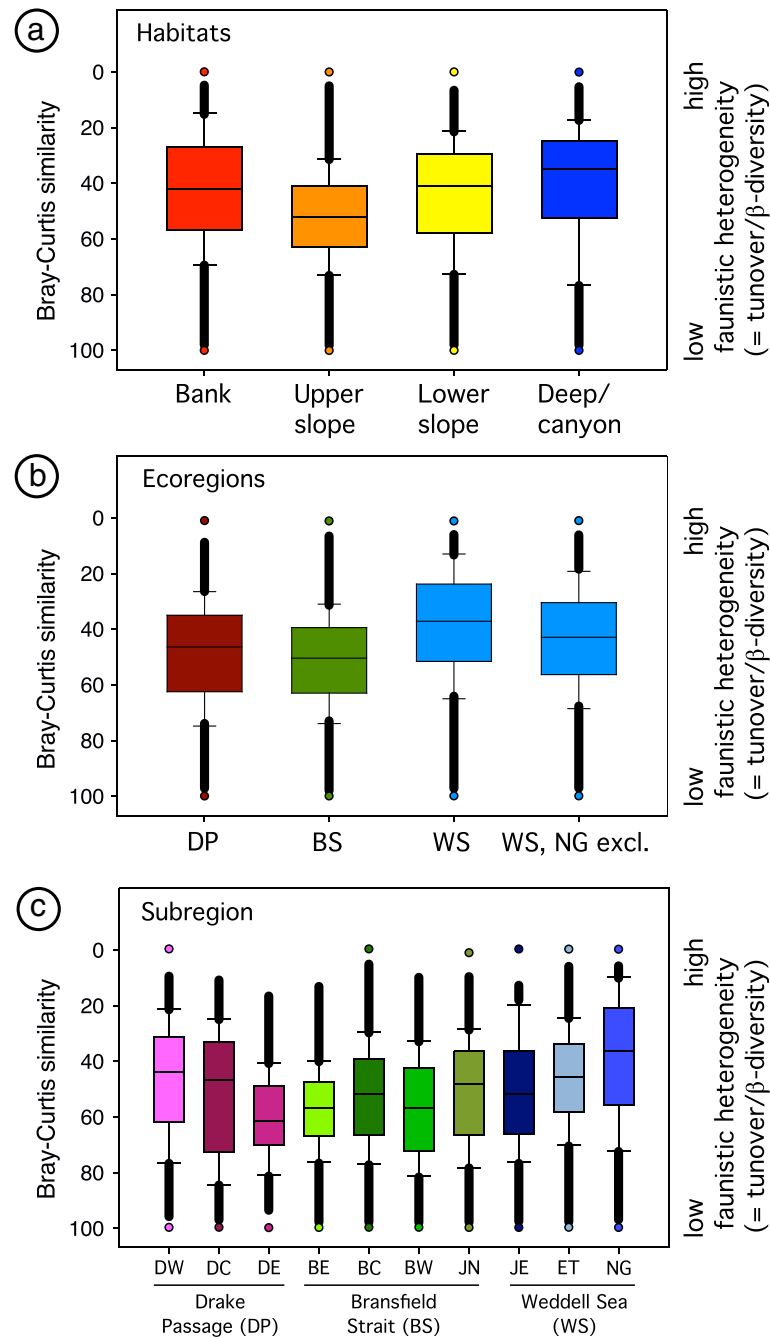
#### Discussion

Benthic patterns, especially when analyzed over a broad range of spatial scales, are determined by the combined effects of multiple physical, chemical, and biological drivers. These include measured and observed factors, but also so-called nonpredictable (= unknown) environmental variables that are generally thought to cause “random” patterns (Connell 1978). The combination of traditional community and diversity analyses with the scale-explicit MEM approach highlighted that the mega-epibenthic shelf communities around the tip of the Antarctic Peninsula are distinctly structured at a range of spatial scales, which are often linked to a different set of environmental drivers.

#### Small-scale patterns and drivers

At the smallest spatial scale, which was a priori defined as the within-station variation along the OFOS transects, we often





**Fig. 5.** Distribution of  $\beta$ -diversities (between-photo Bray–Curtis similarities) for habitats (**a**), ecoregions (**b**), and subregions (**c**). Abbreviations of ecoregions: DP, Drake Passage; BS, Bransfield Strait; WS, Weddell Sea. Abbreviations of subregions: In the Weddell Sea—JE, Joinville Island East; ET, Erebus and Terror Gulf; NG, Nachtigaller Shoal; In the Bransfield Strait—JN, Joinville Island North; BE, Bransfield East; BC, Bransfield Central; BW, Bransfield West; In the Drake Passage—DW, Drake West; DC, Drake Central; DE, Drake East.

recorded a pronounced patchiness of mega-epibenthic biota. Abrupt changes in faunistic composition were evident even between adjacent seabed images, as for example with regard to compound ascidians at Sta. 164 (Fig. 2a), demosponges at Sta. 196 and 215, and hexactinellid sponges at Sta. 234 (see Supporting Information Fig. S1). Pronounced small-scale patchiness became also evident by the generally low along-transect seriation (IMS)

values, indicating a poor spatial autocorrelation. At an even smaller spatial scale (i.e., within seabed photos, each showing approximately 4 m<sup>2</sup> of the seafloor), which we did not statistically analyze, a notable patchiness was also visible for assemblages, and not only for single taxa (Fig. 2; for additional examples, see Supporting Information Fig. S6a–c). Within the 2-km OFOS transects, long sections of faunistically rather

**Table 1.** Spatial variability (structured patchy distribution) of mega-epibenthic taxa or groups at broad (B), meso (M), small (S), and fine (F) scales resulting from MEM models for the three ecoregions.

	Drake Passage				Bransfield Strait				Weddell Sea			
	B	M	S	F	B	M	S	F	B	M	S	F
Mobile Polychaeta									x	x	x	x
Filter-feeding Holothuroidea												
Deposit-feeding Holothuroidea												
Echinoidea												
Crinoidea												
Asteroidea												
Ophiuroidea												
Hemichordata	x	x	x	x								
Demospongia												
Hexactinellida												
Solitary Ascidiacea												
Colonial Ascidiacea												
Anthozoa												
Hydrozoa	x	x	x	x								
Gorgonaria												
Bryozoa												
Infauna indicators												
Other epifauna												
# of significantly structured taxa	12	10	9	6	18	17	9	6	13	9	9	7

White = not significant; light gray =  $p < 0.05$ ; dark gray =  $p < 0.01$ ; black =  $p < 0.001$ ; x = not present.

homogeneous seabed photos were rare. Within-station Bray–Curtis similarity values were calculated across all pairs of seabed photos (used as measures of  $\beta$ -diversity). Therefore, in comparison to IMS, they quantify the faunistic heterogeneity at a slightly larger spatial scale. Notable exceptions from an intermediate heterogeneity were the transects at the Nachtigaller Shoal where steep environmental gradients (Dorschel et al. 2014) caused distinct small-scale benthic patches (Supporting Information Fig. S1) and high  $\beta$ -diversities, as it is known for seamounts in general (Samadi et al. 2008).

MEM models also indicated significantly structured patterns at the fine (i.e., within-transect) spatial scale. Since patchily distributed mega-epibenthic taxa were visible on consecutive photos along a transect, most specimens within such patches might have belonged to one species, characterized by a specific sensitivity to their small- to intermediate-scale drivers. In the MEM models, particularly the abundant taxa were significantly structured, such as echinoids, crinoids, ophiuroids, anthozoans and bryozoans in the Drake Passage,

solitary and colonial ascidians, asterooids, gorgonians and bryozoans in the Bransfield Strait, and infauna indicators, ophiuroids, gorgonians and demosponges in the Weddell Sea. As an exception, ophiuroids were abundant, e.g., in the Bransfield Strait but were not significantly structured.

Generally, high within-station heterogeneity (=  $\beta$ -diversity) was primarily found in the Weddell Sea. The special conditions at the Nachtigaller Shoal obviously contributed to this pattern. In the Bransfield Strait, the station-specific numeric compositions showed the broadest range between low and high  $\beta$ -diversities. The stations in the Drake Passage had similar taxa compositions and intermediate similarities. MEM models also indicated weak along-transect homogeneities, at both fine and small spatial scale, the latter referring to the distances between the farthest photos from one station (= within one transect) or between the photos from adjacent stations. There were, however, pronounced differences among taxa. For instance, while in the Weddell Sea demosponges, hemichordates and ophiuroids were highly significantly structured, as they had also been reported from the

**Table 2.** Environmental variables linked to community composition in the MEM models of the three ecoregions at each distinct scale: B(road), M(eso), S(mall), and F(ine).

	Drake Passage				Bransfield Strait				Weddell Sea			
	B	M	S	F	B	M	S	F	B	M	S	F
$R^2$	0.15	0.04	0.04	0.02	0.22	0.09	0.02	0.01	0.16	0.05	0.05	0.03
Water depth (m)	■	■	■	■	■	■	■	■	■	■	■	■
Seabed ruggedness	■	■	■	■	X				■	■	■	■
Seabed slope	■	■	■	■	■	■	■	■	■	■	■	■
Benthic Terrain Modeller	■	■	■	■	■	■	■	■	■	■	■	■
Potential temperature (°C)	■	■	■	■	■	■	■	■	■	■	■	■
Salinity (psu)	■	■	■	■	■	■	■	■	■	■	■	■
Oxygen (%)	■	■	■	■	■	■	■	■	X			
Hard substrate	X				■	■	■	■	■	■	■	■
Sea-ice, 31d, mean (%)	X				X				■	■	■	X
Sea-ice, 31d, <i>std</i> (%)	X				X				■	■	■	X
Sea-ice, 10yr, mean (%)	X				■	■	■	■	■	■	■	X
Sea-ice, 10yr, <i>std</i> (%)	X				■	■	■	■	■	■	■	X
Chl <i>a</i> , 31d, <i>std</i> (mg m <sup>-3</sup> )	■	■	■	X	■	■	■	■	X			
Chl <i>a</i> , 10yr, mean (mg m <sup>-3</sup> )	■	■	■	X	■	■	■	■	X			
Chl <i>a</i> , 10yr, <i>std</i> (mg m <sup>-3</sup> )	■	■	■	X	■	■	■	■	■	■	■	X

White denotes not significant; light gray denotes  $p < 0.05$ ; dark gray denotes  $p < 0.01$ ; black denotes  $p < 0.001$ ; *std* = standard deviation. X indicates that environmental variables were not available for analyses in that region due to too little variation in their values, e.g., many zero values, resulting in model failure. For the Drake Passage, none of the environmental variables were significant for the fine-scale model.  $R^2$  is the amount of variation captured by the model.

eastern Weddell Sea (Gerdes et al. 1992), in the Drake Passage only the common ophiuroids showed a similarly patchy distribution pattern, as Piepenburg et al. (2002) recorded off King George Island and in the Bransfield Strait.

In the MEM models, a positive correlation between the mega-epibenthic patterns and environmental water-column variables measured near the bottom was detected for the two smallest spatial scales (fine and small) in only 11 of 42 possible cases. It is no surprise that parameters, which do not vary much at small spatial scales (e.g., bottom-water salinity and temperature), showed no relationship to small-scale benthic patchiness. However, strong relationships between bottom-specific parameters and benthic community structures were also relatively rare in our data. At the “small” scale, seabed slope and BTM were influential in the Bransfield Strait and Weddell Sea, and seabed slope also in the Drake Passage. The availability of hard substrates, which is generally important for epibenthic, especially sessile biota (Gray and Elliott 2009), could have been expected to be relevant at small scales because stones and boulders should determine whether recruitment of sessile epibenthos is successful or not. However, in our data, such a correlation was detected in the

Weddell Sea only. In the other ecoregions, a relationship of this kind, if present at all, was likely masked by the effects of other unknown factors.

Only few significant interactions between environmental factors and mega-epibenthic biota were found at the two smallest scales considered in our MEM models. A possible explanation for the general weakness in the environment-biota relationship in our study may be the influence of nonmeasured and, therefore, unknown environmental factors, but also the effects of early-life history traits of benthic animals, which have not been included in our analyses. In the seabed images, we recorded mostly advanced juvenile to adult benthic organisms of a body size of at least 0.3 cm. We virtually do not know anything about the environmental requirements of recently hatched recruits of viviparous species or of recently settled larvae of benthic species. Their small-scale distribution patterns may have been primarily driven by local circumstances, such as the presence of specific biofilms or an “unusual source of food” (Pearse et al. 1991), while such environmental factors in combination with biological traits, do not have a selective impact on adults. A third explanation for the rather weak environment-biota correlation in our analysis could be the classification of the benthos into

rather coarse taxa. However, if species within a higher taxon behave or respond in different ways, we would have had to expect even more diffuse MEM results and less obvious variations between high and very low seafloor cover along the photo transects. Interestingly, evidence for the impact of iceberg scouring, as found frequently in the eastern Weddell Sea and in shallower waters west of the Antarctic Peninsula (Peck et al. 1999; Gutt and Piepenburg 2003; Smale et al. 2008), was rare in our image data (e.g., at the top of the Nachtigaller Shoal in the Weddell Sea, Supporting Information Fig. S6d and at Sta. 222-2a Fig. 2b). Teixidó et al. (2007) demonstrated that patterns within single Southern Ocean seabed images provide important information to explain structures and their driving processes (e.g., recolonization) beyond the scale actually considered in this study. Furthermore, we cannot exclude that regime shifts in the overlying water column affected entire benthic assemblages, as described in the Ross Sea (Dayton et al. 2016). Such effects were, however, not covered in our analyses.

#### Intermediate to large-scale patterns and drivers

The faunistic differences among subregions and ecoregions were weak but statistically significant. Accordingly, the a priori classifications of stations into these spatial scales have been confirmed. Similar results were recorded by Gutt et al. (2016) for the macrobenthos, based on Agassiz-trawl catches in the same study area, and by Segelken-Voigt et al. (2016), for ascidians using the same set of seabed photos. Due to the steep environmental gradients in our study area, especially in sea-ice cover, pelagic production regime, sedimentation dynamics and, ultimately, benthic food availability, it could be expected that the three ecoregions differed pronouncedly in their mega-epibenthic biota and habitats. This expectation was confirmed by the MEM modeling. All environmental parameters, except oxygen, contributed significantly to the benthic structure at this largest spatial scale. Convey et al. (2014) assumed that single overriding mechanisms, largely determining large-scale patterns of Southern Ocean biodiversity, are rare, while Gutt et al. (2016) found that only sea-ice dynamics and water depth were relevant drivers of macrobenthic distribution.

The unexpected result of a higher faunistic similarity between the Drake Passage and the Weddell Sea was probably caused by the high faunistic within-ecoregion heterogeneity of the Bransfield Strait, which is geographically situated between the two other ecoregions.

The average  $\beta$ -diversities differed significantly among all three ecoregions (Fig. 5b). Particularly noticeable were the high values for the Weddell Sea. These were mainly found at the Nachtigaller Shoal (Fig. 5b,c), a submarine hill with an unusual variety of habitats (Dorschel et al. 2014). The faunistic heterogeneity was here even more pronounced than in the canyons of the other two ecoregions. Previous large-scale benthos surveys in the Southern Ocean that are comparable in scope and scale to our study were conducted in the Ross Sea (Bullivant 1967) and the eastern Weddell Sea (Voß 1988).

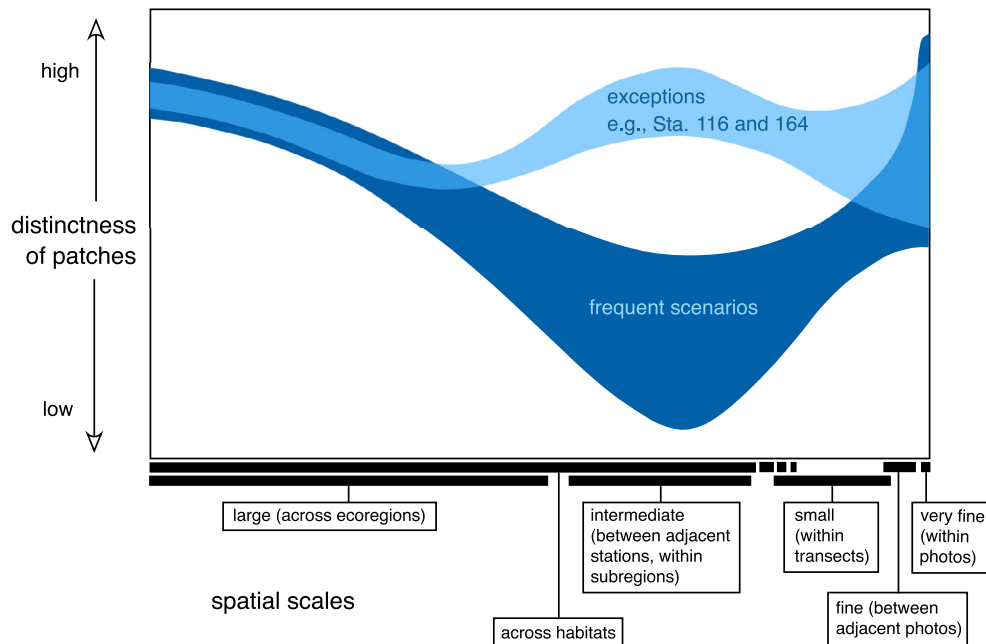
Both surveys reported the occurrence of distinct benthic assemblages, associated with sediment type, pelagic regimes, or both. In our study, the mega-epibenthic biota mostly featured a mixture of the above-mentioned distinct assemblages.

The hypothesis that within-subregion similarities (i.e., between groups of adjacent stations) are higher than among-subregion similarities (i.e., between further apart station groups, presumably representing different environments) was not confirmed due to the high faunistic heterogeneity at this spatial level. Two of four nonsignificant differences in  $\beta$ -diversity were found for subregions located in the most remote ecoregions, Drake Passage and Weddell Sea.

In the MEM models, the meso spatial scale of several tens of kilometers did not include adjacent stations but was related to distance between subregions within the same ecoregion. These findings allow similar conclusions that are largely similar to those drawn for the largest spatial scale considered in the MEM analyses (broad). In general, the entire mega-epibenthic community in the Bransfield Strait displayed the highest degree of complexity, while in the Drake Passage and the Weddell Sea the structuring varied considerably among taxa and between these two ecoregions. For example, deposit-feeding holothurians and hexactinellid sponges were well structured in the Drake Passage but less in the Weddell Sea, while an opposite pattern was found for filter-feeding holothurians.

The environmental drivers of such spatial patterns were most complex in the Weddell Sea. From the water-mass characteristics above the seabed considered in the MEM analyses, two parameters characterizing temperature and salinity were significant, from the five seabed characteristics ruggedness contributed significantly. Since no substantial mixing of different faunas could be expected in this region, which is located at the outflow of high-Antarctic water masses coming from the southern Weddell Sea, we assumed that seabed characteristics had important effects on the distribution of the mega-epibenthic biota. This hypothesis was not confirmed in our analyses. Similarly, sediment properties had not been reported as important drivers from other parts of the Weddell Sea (Gutt and Starmans 1998). Instead, as in our study, ocean dynamics were found to mainly control benthic distribution patterns at a regional scale. Such a high relevance of the water-mass characteristics can only be explained by—currently unknown—regional patterns in ocean dynamics, since all our Weddell Sea stations were influenced by the same water mass, the northward flowing High Salinity Shelf or Surface Water and the Ice Shelf Water (Dorschel et al. 2016; Huneke et al. 2016).

The analysis of the cryo-pelagic-benthic coupling was hampered by the general scarcity of sympagic and pelagic data at appropriate spatial scales. For instance, in the Drake Passage, sea-ice cover was generally low and in the Weddell Sea chlorophyll data from remote-sensing observations were scarce because of long-lasting sea-ice cover. Surprisingly, however, all such variables had a significant effect on the mega-epibenthos in the Drake Passage and the Bransfield Strait. Even in the



**Fig. 6.** Conceptual scheme of the distinctness of patchiness of mega-epibenthic assemblages or key species (on the y-axis) changing with the different spatial scales of decreasing size from left to right analyzed in this study (black bars indicated below the x-axis). Such patchiness is most distinct at the smallest and largest spatial scales. Exceptions are patches of, e.g., ascidians and bryozoans, which have an obvious intermediate size within subregions and within transects.

Weddell Sea, chlorophyll and sea-ice dynamics were important. These results indicate that the typical polar environmental conditions of the atmosphere and upper water column had an important effect on the seabed biota, even at depths of down to 600 m. A similar conclusion was drawn in the study based on Agassiz-trawl catches from the same study area (Gutt et al. 2016) and confirmed by a biogeochemical flux study (Isla 2016). In two shallow-water studies in East Antarctica (Clark et al. 2017) and the Ross Sea (Cummings et al. 2006), referring to spatial scales similar to the intermediate ones of our analyses, sea ice parameters turned out to be important drivers. On the one hand, this is not a surprise, because at shallow sites, a strong cryo-pelagic-benthic coupling can generally be expected. On the other hand, shallow-water benthic habitats are generally characterized by a pronounced variability of seabed properties (partly due to by sea-ice effects), ranging from bedrock to fine sediments with dropstones. These factors, however, seemed not to be the most important drivers of mega-epibenthic community structures. The Ross Sea study also highlighted the importance of multiple stressors (Lenihan et al. 2003), as was also evident in our investigation at the Antarctic Peninsula.

#### Faunistic heterogeneity within and between habitats

We also looked at the faunistic and environmental variation among a priori defined habitats, i.e., Bank, Upper slope, Lower slope, and Deep/canyon, irrespectively of spatial scale and region (Fig. 6). Such habitat-related approaches have been applied more frequently to Arctic than Southern Ocean

benthic systems; for examples, see Piepenburg et al. (1997) and Kędra et al. (2013).

As the Banks are relatively shallow, the benthos is situated close to the sea surface and experiences a pronounced variability of biological and physical processes. This spatial proximity likely explains the high mega-epibenthic heterogeneity of Bank stations (e.g., Fig. 2a). The faunistic composition on the Banks also displayed the common pattern typical for shallow habitats, in which filter feeders, such as bryozoans, ascidians, and crinoids, are especially abundant in oceanographically dynamic systems (see, e.g., Riisgård and Larsen 2017).

Upper slope stations were mainly situated at the shelf break, which is thought to be characterized by high oceanographic heterogeneity (Van Caspel et al. 2015), local upwelling, rapid horizontal transportation, or high deposition of organic material, depending on the current pattern. These conditions enable the co-occurrence of filter-feeding and deposit-feeding benthic organisms (Blake and Grassle 1994). Sta. 199 is a good example of a mixed fauna (Supporting Information Fig. S1). Upper slope stations had the highest proportion of ophiuroids and the highest faunistic homogeneity, suggesting unexpectedly uniform and stable environmental conditions in the overlying water column. Another explanation for the dominance of ophiuroids at the slope is their generally opportunistic life style, even at varying environmental conditions, since ophiuroids comprise sedentary filter- and mobile deposit-feeders. In contrast to the Upper slope, the Lower slope was faunistically as heterogeneous as the Bank

habitat. We explain this finding by the co-occurrence of taxa that prefer the deepest parts of canyons, e.g., infauna indicators, and a typical slope fauna, e.g., ascidians, bryozoans, and sponges (e.g., Sta. 237).

Another unexpected finding was the high heterogeneity ( $\beta$ -diversity) of the Deep/canyon stations. Usually such habitats are characterized by relatively stable and homogeneous environmental conditions, shaped by low current velocities and high deposition rates of phytodetritus, from which the soft-bottom infauna benefits (Vetter and Dayton 1998; Tyler et al. 2009; De Leo et al. 2017). In our study, two Deep/canyon stations in the Bransfield Strait fitted into this picture (e.g., Sta. 204). However, a third station (# 196) was partly dominated by filter-feeding epifauna, which are expected to be more typical for banks and slopes, and partly by ophiuroids, which are assumed to be typical for the bottom of canyons. Ophiuroids were also abundant at the two deepest habitats of the Nachtigaller Shoal in the Weddell Sea. Generally, canyons have been shown to be also a suitable habitat for filter feeders, e.g., in the Bering Sea in the Arctic (Miller et al. 2015), depending on the magnitude of primary productivity and the strength of the pelagic-benthic coupling. This line of arguments may explain why the deepest station in the Erebus and Terror Gulf in the Weddell Sea was dominated by compound ascidians. The station is located in the extension of the Antarctic Sound, a deep strait connecting the Weddell Sea and the Bransfield Strait. Therefore, a strong flow of water through the Antarctic Sound (Huneke et al. 2016) may support filter-feeding ascidians at its eastern entrance independently of the water depth and bottom topography. Li et al. (2016) also reported an onshore-to-offshore gradient for the coupled sea-ice primary production system in a southerly adjacent area west of the Antarctic Peninsula. Such a pattern could also have caused the differences between our Bank and Deep/canyon habitats, since many Bank stations were located closer to the shore than the deeper habitats. Piepenburg et al. (2002) also reported a faunistic depth gradient on the shelf and slope off King George Island (South Shetland Islands) in the southern Drake Passage and the northern Bransfield Strait, without specific reference to a complex bottom topography but over a depth range, which was twice as large as in this study. However, for the deeper Antarctic shelf, Smith et al. (2006) assumed only a poor coupling between summerly phytoplankton blooms and benthic processes.

### Overarching conclusion

Our quantitative multiscale analyses of the patterns and drivers of mega-epibenthic communities off the northern Antarctic Peninsula showed that the spatial structure of most organism groups was associated with more than a single scale. This finding suggests that the organisms considered in our study are generalists in terms of their habitat requirements. However, in part, it may also be caused by the low taxonomic resolution of our study. Moreover, the rather weak correlation between environmental factors and small-scale faunistic patterns may be

caused by nonmeasured environmental parameters or the relatively low number of stations per area. Also, it is very likely that inter- and intra-specific biological interactions, which we did not consider, as well as unknown migration and dispersal processes of different life stages, influenced the spatial patterns of mega-epibenthic biota, especially at small to intermediate scales (Cornell and Harrison 2013). Lastly, it can also be expected that aggregations of hyperbenthic krill and fish have small-scale effects on benthic life (Supporting Information Fig. S6e–g).

Our large-scale results, including the relevance of steep environmental gradients, confirm earlier findings from the same study area that were based on Agassiz-trawl catches (Gutt et al. 2016) or photographically recorded ascidians (Segelken-Voigt et al. 2016). We found only weak hints for a cryo-pelagic-benthic coupling, which may indicate the complexity of ecological conditions, including, e.g., sediment grain size, (re-) suspension events (Supporting Information Fig. S6h), or biofilms on the sediment. A similar study in the Ross Sea on shallow-water benthos also showed that the explanatory power increased with increasing spatial scale and identified ice-related parameters as main environmental drivers (Cummings et al. 2018).

The recurrent finding of high mega-epibenthic diversity and hardly predictable patterns, including high  $\beta$ -diversity, may further motivate ongoing initiatives for introducing area-based environmental protection measures, including high resolution monitoring plans, for this region of the Southern Ocean. Moreover, our specific results also highlight the need for developing novel conservation strategies that explicitly consider multiscale variability and patchiness (Kennicutt 2014b).

Finally, knowledge on benthic diversity dynamics and their drivers is important to assess key marine ecosystem services, such as benthic remineralization of nutrients and the long-term deposition of carbon in Southern Ocean seabed habitats (Barnes and Tarling 2017), which contribute to global marine biogeochemical cycles. There is not yet hard evidence that the benthos off the northern Antarctic Peninsula has already been affected by the pronounced climate-induced changes that have been reported for the hydrography of this Southern Ocean region and for the pelagic communities in a southerly adjacent area (Montes-Hugo et al. 2009; Schofield et al. 2018; for review, see Kerr et al. 2018). Therefore, our results can either serve for assessing the base-line knowledge about the mega-epibenthos prior to future changes or for documenting the first stages of an incipient climate-driven regime shift.

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None declared.

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