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The influence of the geo-morphological and sedimentological settings on the distribution of epibenthic assemblages on a flat topped hill on the over-deepened shelf of the Western Weddell Sea

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Abstract

Epibenthos communities play an important role in the marine ecosystems of the Weddell Sea. Information on the factors controlling their structure and distribution are, however, still rare. Especially the interactions between environmental factors and biotic assemblages are not fully understood. Nachtigaller Hill, a newly discovered seabed structure on the over-deepened shelf of the Northwest Weddell Sea (Southern Ocean), offers a unique site to study these interactions in a high-latitude Antarctic setting. Based on high-resolution bathymetry, geo-referenced biological data, the effect of the terrain and related environmental parameters on the epibenthos was assessed. At Nachtigaller Hill, both geo-morphological and biological data showed complex distribution patterns, reflecting local processes such as iceberg scouring and locally amplified bottom currents. This variability is also generally reflected in the variable epibenthos distribution patterns although statistical analyses did not show strong correlations between the selected environmental parameters and species abundances. By analysing the interactions between environmental and biological patterns, this study provides crucial information towards a better understanding of the factors and processes that drive epibenthos communities on the shelves of the Weddell Sea and probably also on other Antarctic shelves.

1 Introduction

Epibenthos distribution patterns often correlate with environmental parameters such as e.g. substrate, food supply and temperature. Some of these parameters are influenced by the morphology of the terrain (geo-morphology) including relevant ecological drivers (Dorschel et al., 2007; e.g. Genin et al., 1986; Gutt, 2000; Wienberg et al., 2013; Williams and Leach, 1999). Bottom currents for example are often enhanced at hill flanks and around obstacles (Dorschel et al., 2007; Guo et al., 2000). These enhanced bottom currents can increase the food supply for filter feeders and remove fine sediments causing winnowing. This has already been demonstrated for a range of mounds and seamounts (e.g. Dorschel et al., 2007; Genin, 2004; Genin et al., 1986; Piepenburg and Müller, 2004). Remaining coarse lag sediments or exhumed consolidated sediments can provide substrates suitable for sessile life forms. On the other hand, less dynamic and sheltered environments provide habitats preferred by dominantly deposit-feeding benthic organisms.

In the marine ecosystems of the Weddell Sea shelves, epibenthos communities play an important role (Dayton, 1990; Gutt et al., 2011; Starmans et al., 1999). Biological and environmental data regarding the environmental factors controlling their distribution patterns on the scale of the entire Antarctic shelf are, however, still rare (Post et al., 2011; Raguá-Gil et al., 2004). Furthermore, it cannot be ruled out that biological interactions rather than physical factors are the dominant drivers (Gutt, 2000). Towards a comprehensive understanding of these ecosystems, information on the interaction, responses and feedback mechanisms between seabed communities and environmental conditions are crucial. This is especially true since it is known that some important physical drivers, such as ice cover, current regime and sediment characteristics, potentially shape these high-latitude Antarctic marine communities (Cummings et al., 2010).

During cruise ANT-XXIX/3 of the German R/V *Polarstern*, we coincidentally discovered a so far unknown hill on the shelf of the Northwest Weddell Sea that we named Nachtigaller Hill (Fig. 1). It is located east off the Antarctic Peninsula in the Erebus and Terror Gulf in the extension of the Antarctic Sound (Fig. 1). Climatically, the study site experiences full high-latitude Antarctic conditions typical for the Weddell Sea with low precipitation (Sugden, 1982) and seasonal to perennial ice cover. The general oceanography at the site is characterised by the influence of the western extent of the Weddell Gyre (e.g. Orsi et al., 1993). Detailed information on the oceanic conditions of the continental shelf of the Northwest Weddell Sea are, however, sparse (Camerlenghi et al., 2001).

The unique and obvious shape and pronounced geo-morphology of Nachtigaller Hill makes it a key site for studying habitat and benthic community distribution patterns

across a range of environmental settings in full, high-latitude Antarctic conditions. At sub-marine hills with distinct geo-morphologies, like Nachtigaller Hill, the biological patterns potentially reflect the environmental settings more clearly than in areas with a less pronounced geo-morphologies. Thus, this study provides valuable information towards a better understanding of ecosystem functioning and bio-environmental interactions in the Western Weddell Sea and other areas on the Antarctic shelf.

In a cross-disciplinary approach, we:

1. describe, classify and interpret the geo-morphology of Nachtigaller Hill based on bathymetric data
2. analyse (a) the sedimentary settings and (b) epibenthos communities based on seabed imagery and, using a Geographical Information System (GIS),
3. assess and explain epibenthos distribution patterns in relation to environmental factors by correlating environmental with biological observations.

The descriptive part of this study contributes to the general knowledge about an, in some respects, “white spot” on geo-morphological and biogeographical maps.

Southwest of our research area, Gutt et al. (2011) have surveyed the Larsen A and B areas (Fig. 1) in 1995 and 2002, to study the response of the benthos to the collapse of the Larsen ice shelves. As reference sites, they chose locations in the vicinity of Nachtigaller Hill (east of Ross Island and south of Joinville Island), where the seabed is massively disturbed by grounding icebergs. Both phenomena, disintegration of ice shelves and iceberg scouring, represent very specific environmental processes, which can a priori not be applied to our study area. Results from Bertolin and Schloss (2009) and Peck et al. (2010), however, showed that in the Larsen bights and in the former ice shelf areas, which are relatively close to the Nachtigaller Hill, primary production can be high. Furthermore, Gutt et al. (2012) demonstrated that sponge communities, as they are known from the Southeast Weddell Sea (see also Sañe et al., 2013), and other “normal” shelf areas in the Southern Ocean (Gutt et al., 2013) can also occur in this part of the Weddell Sea. Because of the extremely slow growth of large glass sponges and also some demosponges (Dayton, 1989; Dayton et al., 2013), such communities, if mainly composed of large specimens, are indicators of long-term environmental stability. However, it has been shown that populations of ascidians and ophiuroids (Gutt et al., 2013), young hexactinellid sponges (Fillinger et al., 2013; Gutt et al., 2012) as well as generally fast growing demosponges known for their highly dynamic performance (Gutt et al., 2012), including reproduction, recruitment, growth, and mortality, can also occur in the same area. Since we know that almost everywhere on the "normal" Antarctic shelf, albeit with different proportions, two community supra-types (those dominated by epifaunal suspension feeders and those dominated by infaunal or vagrant deposit feeders) coexist, we can assume that this can also be applied to the area of this study. The typical high-Antarctic suspension-feeder communities that are rich in biomass and diversity occur in regions, such as the Southeast Weddell Sea, where a relatively strong coastal current flows along a less structured coastline over a relatively narrow shelf or where certain geo-morphological features (Gutt, 2007; Lavaleye et al., 2005) enhance the advective transport of food for benthic filter feeders, mainly in the form of phytodetritus. Since the North-Western Weddell Sea shelf is relatively broad, we hypothesize that suspension-feeder communities are not particularly abundant and rich in the surroundings of the Nachtigaller Hill. On the other hand, the presence of some typical elements of high-Antarctic epibenthic communities in the wider study area provides evidence that the benthos of the Western Weddell Sea generally resemble that of the Eastern Weddell Sea with a certain proportion of suspension feeders. In this regard, both Weddell Sea regions are clearly different from the area west of the Antarctic Peninsula, where the environmental setting is characterised by a much more complex coastline, different water masses, and less sea ice (Smith et al., 2006). There, the benthos is generally a food-bank system, where deposited phytodetritus serves as a the major energy source, mainly for deposit feeders such as polychaetes and vagrant holothurians (Sumida et al., 2008). A rare if not unique char-

acteristic of our study site is, however, the shape of the Nachtigaller Hill with a complex intermediate- to small-scale geomorphological terrain heterogeneity.

2 Material and methods

All data sets used in this study were collected during cruise ANT-XXIX/3 of the German R/V *Polarstern* in February 2013 (Gutt, 2013). The data sets include high-resolution multibeam bathymetry data, seabed imagery and hydrographic water-column data. The new data sets span across a depth range from 17 m to 460 m water depth (wd).

2.1 Hydro-acoustic data

On Nachtigaller Hill, an area of 120 km^2 was mapped during the survey. Due to the shallow water depth above the plateau and the prevailing ice conditions, a full coverage was not achieved. Nevertheless, several survey tracks crossed the hill lengthwise and across (Fig. 2), thus providing sufficient data coverage for characterising also its shallowest parts. While the west, northeast and southeast slopes of the hill were fully mapped, its southwest sector was blocked by icebergs and could not be surveyed (Fig. 2).

2.1.1 Data acquisition

The bathymetric data acquisition was done with an Atlas Hydrosweep DS 3 deep-water multibeam echosounder permanently installed on R/V *Polarstern*. The Hydrosweep DS3 was operated in "equal footprint" mode with 313 hard beams and a maximum of 920 soft beams on the receiver side. Most of the time a total coverage of 400 % water depth was achieved. Motion information, provided by the ship's Ratheon-Anschütz® Marine Inertial Navigation System (MINS), was used to compensate the multibeam data for pitch, roll and heave. Positioning information was recorded by 2 Trimble® Marine SPS 852 GPS receiver and provided through the MINS to the multibeam system.

This resulted in a horizontal position accuracy of 2–5 m. The vertical accuracy of the Atlas DS3 hydrosweep multibeam system was better than 0.2 % of the water depth according to the manufacturer's specification.

During post-processing with the hydrographic software package Caris Hips & Sips® 8.0, the multibeam data were cleaned for artefacts related to erroneous calibration values, spurious soundings, vessel motion, navigational jumps, and sound velocity refractions. Sound velocity corrections were applied to the data based on sound velocity profiles calculated from CTD data using the approach by Chen and Millero (1977). In addition, the pre-processed data were imported in the editing and visualization software package QPS Fledermaus® for area-based editing.

2.1.2 DTM generation

From the cleaned swath bathymetry data sets, a digital terrain model (DTM) was created (Fig. 1). Gaps in the multibeam coverage of Nachtigaller Hill were filled and interpolated on the basis of the IBCSO grid (Arndt et al., 2013). By applying a "remove-and-restore techniques" (Arndt et al., 2013; Jakobsson et al., 2000, 2008, 2012). Horizontal resolutions were 10 m for areas with multibeam coverage recorded during our cruise, 500 m for areas previously mapped and 2000 m for areas where the bathymetry was derived from the General Bathymetric Chart of the Ocean (GEBCO) and satellite altimetry. For a better consistency of the DTM and to minimise artefacts arising from the use of various data source, an integration (bending) algorithm (Arndt et al., 2013) was applied. The final DTM was projected to UTM Zone 21S with a datum of WGS1984. For all subsequent analyses raster data sets were derived from this DTM.

2.2 Geo-statistical analyses

Geo-statistical analyses were performed with the ESRI® in ArcGIS® software package including the toolbox extensions Benthic Terrain Modeller (BTM) (Wright et al., 2005) and the LandSerf software (Wood, 2009a). In both software packages, raster

analyses were performed at a number of scales following a trial-and-error approach to find the best representation of the different geo-morphological features encountered at the Nachtigaller Hill. For consistency, these analyses were limited to the areas with high-resolution (10 m) multibeam coverage and the shallow parts of the hill (Fig. 1). To further reduce the influence of potential artefacts from outer beams of the multibeam sonar swath, the outer 50 m of the multibeam coverage and hill area were ignored in all geo-statistical analyses

For visual inspections, and for a more natural representation of the bathymetric data, hillshade images were calculated in ArcGIS®. Hillshade images provide an illuminated, pseudo-3-D impression that allows for the identification of small morphological structures that were otherwise unrecognisable in the bathymetry data. In addition, slope (the first derivative of the topography) and ruggedness (a second derivative of the topography) were calculated as topographic terrain descriptors. Slope calculation were performed in ArcGIS® applying the equation described in Burrough and McDonnell (1998). Ruggedness was calculated with the LandSerf software (Wood, 2009a) from a bivariate quadratic approximated terrain surface (Wood, 2009b) and is measure for the roughness or "bumpiness" of the seabed (Wilson et al., 2007). For more advanced geo-statistical analyses, a focal statistic approach was applied. Both, broad-scale and fine-scale Bathymetric Position Index (BPI) grids were calculated using the BTM extension version 3.0 (beta) for ArcGIS 10.1 (Wright et al., 2005). The BPI represents a marine equivalent of the topographic position index commonly used in terrestrial landscape studies (Lundblad et al., 2006; Weiss, 2001) and is a second-order derivative of the bathymetry (Guinan et al., 2009). It calculates the depth differences between each bathymetric raster cell and the average depth of a surrounding reference area (in this study an annulus-shaped area). Consequently, cells with positive BPI values represent parts of elevated features or convex seabed, while cells with negative BPI values belong to depressions or concave seabed. BPI raster were used for geo-morphological analyses and for a seabed classification with the BTM (Wright et al., 2005). The BTM comprises a set of algorithms designed for seabed classifications solely on the basis

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of bathymetric data and bathymetry derivatives (Erdey-Heydorn, 2008; Lundblad et al., 2006; Weiss, 2001; Wright et al., 2005). The BPI raster formed the backbone of the classification. For the BTM, broad-scale and fine-scale BPI raster were computed. For these BPIs, the sizes of the reference areas were selected on the basis of trial-and-error decisions. Eventually, for the broad (fine) BPI an inner radius of 1000 m (30 m) and an outer radius of 1500 m (50 m) were chosen. With these parameters, the overall shape of the hill, its plateau, slopes, terraces and the background seabed, were well captured. The fine BPI raster highlighted local feature such as iceberg scours and escarpments. To avoid the influence of spatial auto-correlation in the broad and fine scale BPIs, the BPIs were standardised relative to 1 standard deviation each (Wright et al., 2005). The BTM furthermore requires a classification table to define a classification scheme. In this study, a modified version of the classification table of Erdey-Heydorn (2008) and Wienberg et al. (2013) provided the best results (Table 1).

2.3 Seabed imagery

Seabed imaging surveys were carried out with the Ocean Floor Observation System (OFOS) of the AWI deep-sea group. OFOS is a surface-powered, deep-towed gear equipped with a high-resolution (21 MPix), wide-angle CANON EOS 1Ds Mark III camera system. Towed behind the ship at a speed of 0.5 kn, OFOS was operated at a preferred height of 1.5 m above the seabed. The recorded high-resolution vertical seabed images show on average an area of 4.76 m^2 (σ = 2.49 m^2). Three 50 cm spaced laser markers provided a scale in each photo. OFOS had two modes of operation. In automatic mode, a seabed photograph was taken every 30 s along the transects. With a ship speed of 0.5 kn, the average distance between the seabed images was approximately 8 m. In addition to the automatic mode, the camera was triggered manually, when the vertical ship's movement caused high variation of the height of the camera above the bottom (and consequently high variation in the area covered per image) and to record additional images from sites or organisms of specific interest.

In total, 1875 seabed photographs were taken along four transects on the north-eastern side of Nachtigaller Hill. Together, the photographs depicted more than 8900 m^2 of seafloor. All transects were run downslope in south–north-direction. The westernmost transect (185-1, Fig. 1) ranged from 36 m wd to 397 m wd and covered parts of the plateau and almost the entire slope along a distance of 4287 m. Transect 189 (Fig. 1) was 1095 m long and covered only the upper slope between 29 and 186 m wd. The two easternmost transects (186-1 and 188-1, Fig. 1) partly overlapped and were combined 8224 m long. They ranged from 31 m wd on top of the hill, across the slope and the hill foot onto the background shelf at 413 m wd (Fig. 1). Images that were taken too close to or too far away from the seabed were discarded from the analyses. To identify these pictures, the seabed footprint of each image was calculated, using the opening angle of the camera and its altitude above the seabed. After discarding the lower and upper 5-percentile of images closest and furthest from the seabed, a total of 1730 stills remained for the seabed image analyses.

2.4 Seabed image analyses

From each photograph, environmental and biological parameters were analysed. Due to the relevance of hard substrate for benthic species distribution, the abundances of ice rafted detritus (IRD) (i.e. boulders and pebbles), were semi-quantitatively assessed using the following categories: single boulders or gravel, boulder or gravel coverage of less than 10 %, 10–30 %, 30–50 %, 50–70 %, 70–90 % and more than 90 %. IRD is the main source of hard substrate in the study area. It is furthermore a potential proxy for the strength of bottom currents and, hence, advective food supply. In addition, broken-up outcropping rocks were mapped as hard substrate, but also as proxy for erosion processes that are, in turn, also indicators of enhanced bottom currents. Soft substrate was categorised into sand and consolidated and soft fine sediment. The occurrence of sand (often with ripple structures) was regarded as evidence of winnowing and enhanced energetic regimes. Exposed consolidated sediments represented intermediate substrate (neither hard nor soft substrate) capable of forming steep cliffs and escarpments. Information on bioturbation and erosion processes was qualitatively extracted from the images (Fig. 3). Bioturbation represented intense burrowing in soft sediments. Ripples, only identified in sandy substrate, were indicative of lateral sediment transport and, thus, enhanced bottom currents. Erosion features and escarpments were proxies for enhanced bottom currents undercutting successions and forming cliffs. Trails of coarse sediments behind obstacles provided an additional proxy for moderately enhanced bottom currents. Striations on the seabed marked the impacts and scouring of icebergs (Figs. 3 and 4). Heavily bioturbated soft sediments on the foot of the hill and in the adjacent areas represented the background sedimentation.

For the biological analyses, the occurrences of the most abundant higher taxa (encrusting red algae, erected red algae, brown algae, sponges, hydrozoans, solitary ascidians, compound ascidians, gorgonarians, bryozoans and ophiuroids) were semi-quantitatively assessed. For each seabed image, the seafloor cover of these taxa was estimated, serving as a gross proxy for biomass. Abundance categories were "absent", 1–5 %, 6–30 % and >30 % cover. Ophiuroids were categorised into "absent", 10, 11–100 and >100 individuals per image, assuming that this abundance measure corresponds best with the seafloor-cover of the sessile taxa. In addition, the number of animal phyla in each image was categorised into three classes (1–3 phyla, 4–8 phyla and >8 phyla per image) representing a gross indicator for overall biodiversity. In addition, also the presence of brownish benthic diatoms films on the sediment surface and the occurrence of very high abundances of suprabenthic krill (>200 individuals per image) were recorded. All results from the seabed image analyses were geo-referenced and included in the GIS to generate maps of the relevant proxies and parameters (Fig. 5).

2.5 Biostatistical analyses

Correlations between biological and environmental data were calculated using the BIOENV routine of the statistical package PRIMER (Clarke and Gorley, 2006). Similarities between images were calculated for both the biological data (using the Bray–Curtis index) and the environmental variables (after normalisation; using the Euclidean

distance). The strength of the relationship between the biotic and environmental patters was quantified with a Spearman rank correlation coefficient between all (chosen) biological parameters (taxa) and any number and combination of environmental parameters. The BIOENV computations were performed for any of the following combination of approaches:

1. for similarities based on (1) single photographs (representative of a 10 m scale) and (2) averages of groups of 10 adjacent photographs (representative of a 100 m scale).

2. for similarities based on (1) all photographs of single stations, (2) all photographs of the stations 186 and 188 combined (because they represent a continuous transect) and (3) all photographs of all four stations combined in one data set.

3. for similarities based on the (1) biomass proxies for all high taxa, (2) number-of-phyla classes.

Prior to the similarity calculations, data were transformed in cases of skewed distribution of values for environmental parameters. A square-root transformation was applied in case of IRD and log transformations in case of slope and seabed ruggedness. Environmental parameters without a standard deviation (only photographs with exclusively zero values within one data set) were eliminated from BIOENV computations.

The influence of the seabed terrain, expressed through the qualitative BTM classification scheme (Table 1), on the composition of the epibenthos, determined through the semi-quantitative (0–3 scale) abundances of the most common higher taxa (see 2.6), was investigated by plotting the relative proportions of the selected taxa averaged within each BTM class. Moreover, within-BTM averages of the abundance of each selected taxon were computed and plotted to analyse potential distribution preferences of the taxa for certain BTM types.

2.6 Hydrographic data

The hydrographic water column profiles were recorded with a Seabird® SBE911 plus conductivity, temperature and depth probe (CTD). To determine the distance to the seabed, a Benthos® altimeter was mounted on the CTD. All CTD casts were performed for the full water column less a safety distance to the seabed of 1–2 m.

3 Results

Nachtigaller Hill is a flat topped, truncated NW-SE striking, elongated elliptical geomorphological feature seated in ca. 350 m wd on the over-deepened shelf of the Northwest Weddell Sea (Fig. 1). It measures ca. 15 km along its main axis and ca. 9.5 km across according to the 350 m depth contour. Morphologically, the hill can be divided in 3 main units: the flat summit area (further referred to as plateau), the slopes down to approximately 250 m wd and the hill foot 250–350 m wd). Beyond the hill foot follows the background shelf setting (Fig. 1).

3.1 Plateau

3.1.1 Morphology

The plateau measures ca. 6.9 km along its main axis and ca. 2.7 km across covering an area of ca. 15.4 km^2. Water depths on the plateau are on average 43 m and range from 20 m to 50 m (Fig. 1). Seabed inclination hardly exceeds 5° (Fig. 2). Consequently, the broad scale BPI represents the plateau as smooth homogeneous area. Only the fine scale BPI and the terrain ruggedness highlight local variations (Fig. 2). These local variations are low, metres-scale ridges and shallow trough that can also be identified on the seabed images (Fig. 4). Due to better multibeam coverage, these ridges and troughs are more obvious in the northeast than in the southwest sector of the plateau.

In the BTM, “plateau” is an individual seabed category that represents the central part of the hill (Fig. 2). The rim of the plateau is classified as “flat ridge tops” (Fig. 2). This is due to the abrupt change in morphology from the plateau to the slope and the resulting convexity of the seabed. In addition to the rim of the plateau, the northwest slope and the upper southeast slope are also classified as “flat ridge tops” (Fig. 2). Unfortunately, for these areas no seabed images are available for groundtruthing.

3.1.2 Substrate

At water depths shallower than 50 m, iceberg scouring and winnowing are the dominant process affecting sedimentological and biological process. Consequently, all surveyed areas on the plateau show strong influences of erosion indicated by, coarse lag deposits and exposed consolidated and lithified sediments. Gravel and boulder pavements are common in the shallow depressions and troughs. Sand patches with subtle but recognisable ripples are less common but also present on the plateau indicating sediment transport due to enhanced bottom currents. Abrasions by icebergs at the crest of low ridges expose consolidated fine sediments (Figs. 3 and 4).

3.1.3 Biology

Encrusting and erect red as well as brown algae occur with low to moderate seabed abundances on the plateau (Fig. 5a–c). At transect 186, brown algae are abundant on several seabed images covering >30 % of the seafloor. The biodiversity on the plateau is generally low, with less than 8 animal phyla encountered (Fig. 5d). Occasionally, low abundances of porifera and compound ascidiacea have been recorded from sheltered areas (Fig. 5e, h). Ophiuroidea occur in varying numbers. Along transect 185 their numbers increase towards the rim of the plateau. At comparable sites along transects 186 and 189 their numbers are however low (Fig. 5k). Hydrozoa, solitary Ascidiacea, Gorgonaria and Bryozoa are almost absent from the plateau area (Fig. 5f, g, i, j).

3.2 Slope

3.2.1 Morphology

Beyond the clearly defined edge of the plateau, the seabed drops in 4 to 6 terraces to approximately 300 m wd (Fig. 1). In general, the slopes can be characterised as geomorphologically variable and rugged terrain (indicated by the ruggedness data and the fine scale BPI, Fig. 2d, f). Also consecutive seabed photographs often showed characteristics of different terrains (Fig. 5) thus highlighting the high variability in geomorphology. From the bathymetric data, the slope can be sub-divided into a steep upper slope (down to ca. 150 m) where seabed inclinations often exceed 20° and a lower slope with 3–5 flat terraces (0–5°) separated by escarpments with approximately 10–20° inclination (Figs. 2b and 4). This terraced slope morphology is also pronounced in the broad scale BPI raster and consequently in the seabed classification (Fig. 2c, e).

3.2.2 Substrate

On the hill slopes, the effect of iceberg scouring is mainly restricted to the areas shallower than 100 m wd and generally decreases away from the plateau (Fig. 3c). In the same way, the abundance of hard substrate in the form of IRD decreases and exceeds hardly 50 % coverage on the slopes (Fig. 3a). In addition to IRD, consolidated sediments exhumed by erosion occur in many places on the slope (Figs. 3e and 4) often forming steeply inclined seabed (Fig. 2b).

3.2.3 Biology

The hill slope show the highest diversity of phyla (often >8 animal phyla per image, Fig. 5d). Hydrozoans and ophiuroids are generally more abundant at the slope than at the shallower and deeper parts of the transects (Fig. 5j, k). Most of the other animal groups (compound ascidians, bryozoans, and sponges) show higher abundances only on a few photographs. Solitary ascidians are mostly moderately abundant (Fig. 5g).

Only along transects 186/188, in a few places, high abundances occur where also gorgonarians are more abundant (Fig. 5i). Generally these taxa show the least distinct depth zonation. In many cases, faunal abundances vary greatly, even between consecutive images. Ophiuroids at the upper to intermediate slope seem to be most equally distributed at a high abundance level (Fig. 5k).

3.3 Hill foot and background shelf setting

3.3.1 Morphology

The hill foot below 300 m wd in the NW and 250 m wd in the SE of the study area was generally less than 5° inclined. In this area, several small, irregular escarpments with 5–10° inclination were found (Fig. 2b). The background shelf setting was characterised by smooth even seabed (slope angles <5°). As opposed to the foot of the hill, small escarpments were absent. Only in the northeast corner of a the multibeam coverage the sides of a trench-like feature displayed slope angles of 5–10°. This feature was likely to be the scour mark of a large iceberg (Fig. 2b). The unrealistically smooth areas on the southwest slope, south of 63°55′S are grid integration artefacts outside the multibeam coverage not representing the true geo-morphology (Figs. 1 and 2).

3.3.2 Substrate

The foot of the hill was characterised by strongly bioturbated sediments similar to the general background sedimentation (Fig. 3f). In this area, hard substrate only occurred in the form of IRD. Trails of coarse sediment behind some boulders (Fig. 3d) indicated that bottom currents were at least temporarily sufficient to remove fine material and to form scours around obstacles.

3.3.3 Biology

With the exception of the shallowest quarter, transect 188 covered the hill foot and background shelf surroundings with a moderate number of phyla (Fig. 5d). Abundances of all animal taxa are generally lower than at the slope. Only ophiuroids show moderate abundances at the deepest part of transect 185 and occasionally at transect 188 (Fig. 5k). Sponges are generally characterized by moderate seabed coverages on single photos taken at the deepest section of the transects (Fig. 5e). Like solitary ascidians and gorgonians they are also absent from several images at the hill foot and shelf setting. In contrast, ophiuroids hydrozoans and compound ascidians are present in almost all images. A few photographs show high abundance of krill swimming close to the seabed at depths between 373 m wd and 385 m wd (Fig. 5l).

3.4 Biostatistics

The best and second best correlation results for all 24 parameter combinations (see materials and methods) for each run are listed in Table 2. Some of these correlations were moderate ($\rho = 0.5$–0.722), some were only poor ($\rho < 0.5$). For most of the individual computations, the ranking of correlations show no discrete step between “moderate” and “poor” correlations. Instead, the values for the correlation coefficient decrease continuously. Furthermore, the results differ considerably among the different approaches used (single photographs, averages of bins of 10 successive photographs, diversity and community approach). Since no clear result was obtained, an overarching analysis for the transects (186 and 188 considered as one transect) was conducted for the community approach. Only runs yielding correlation coefficients >0.5 were considered. All environmental factors were counted that contributed to these results within the single approaches.

Biotic distribution patterns are best explained by the abundance of IRD, followed by water depth. The parameters “escarpment”, “current”, “ruggedness” and “seabed classification” are never among any of the two best correlations. All remaining envi-

ronmental parameters show only poor relationships to the distribution pattern in the biological data.

In case of the computations based on the number-of-phyla (diversity approach), the correlation coefficients of all individual results are too small to be used as a basis for a further comprehensive analysis. Alternatively, data were pooled for all images, independently of the transect. Results with a correlation coefficient >0.5 were only obtained for 10-binned photograph runs. These calculations returned better correlations for biological seafloor cover (or proxy) than for the number of phyla. The relevant environmental factors of both approaches are, however, similar. IRD, consolidated sediment, striated seabed (iceberg scouring) and ripples are relevant in all of the four computations. Sand and slope are relevant in 3 computations, and soft sediment, depth, slope, and ruggedness in only ≤2 runs.

The influence of the seabed terrain on the abundance and composition of the epibenthos was investigated for the six most frequent BTM classes (1, 2, 3, 8, 10, and 12; see Table 1 for explanation). Between 87 and 800 seabed photographs were designated to the individual BTM classes. BTM classes with lower frequencies were assumed to provide spurious results and, hence, excluded. The bar chart of the relative abundance proportions of the most abundant higher taxa averaged within each selected BTM class (Fig. 6a) shows that epibenthic composition did not differ much between the terrain types, except for BTM class 8 (Flat Top Ridges) where algae were abundant while they were rare or absent in the other BTM classes. The compound bar chart of the within-BTM averages abundances of the epibenthic taxa (Fig. 6b) also indicates the pronounced preference of algae for BTM class 8, since this terrain type was confined to the shallow plateau where enough sunlight can penetrate to the seabed to allow for the occurrence of primary producers. In contrast, the other epibenthic taxa were recorded with higher abundances in the other five selected BTM classes, a pattern that is evident for the most abundant taxa, hydrozoans and ophiuroids. These taxa reached highest densities in photos depicting “steep slopes” (BTM class 3) and at “local ridges, boulders, pinnacles on slopes” (BTM class 12).

3.5 Local hydrography

All water column profiles (Fig. 7a) show strong local effects due to the influence of Nachtigaller Hill acting as obstacle to the general southwest to northeast flow patterns in the area (Absy et al., 2008; Schröder et al., 2002). This influence decrease with increasing distance to the hill.

The profile from station 189-2 represented the local hydrography above the plateau. Despite some highly variable surface effects, all measured parameters show a well-mixed water column above the plateau at the time of the cruise (Fig. 7b–d). The stations 165-1 and 185-5 represent the hydrographic regime above the downstream slopes of the hill. Theses profiles display the perturbation of the hydrographic regime above the hill flanks. Station 190-1 already shows strong influences of the regional oceanography (Fig. 7c, d). At this station, between 100 and 200 m wd, the excursions in the potential temperature clearly display the interleaving of local and background hydrography (Fig. 7c). Also the mixed layer, deepening from station 165-1 to 185-5 and to 190-1, indicate the decreasing effect of the local hydrography away from Nachtigaller Hill (Fig. 7c, d).

4 Discussion

The newly discovered Nachtigaller Hill offers special habitats for benthos communities on the over-deepened shelf of the Weddell Sea. Largely isolated from costal influences, this offshore site is a representation of benthic community structures and habitat zones in a seasonally to perennially ice covered, stable high-latitude Antarctic setting.

4.1 Epibenthos communities

In total, the benthos of the Nachtigaller Hill can be considered as a mixture of a variety of assemblages known from all around the Antarctic continent (Gutt, 2006). A variety of community types classified by Gutt et al. (2013) occur in the relatively small

area. They included "sessile suspension feeders with associated fauna" dominated by sponges or other sessile epibenthic organisms or "mobile deposit feeders and in-fauna". "Mobile deposit feeders and in-fauna" are represented by "bioturbated sediment" and "monospecific" and "physically controlled" assemblages as well as those with very low biomass or absence of trophic guilds. Typical shallow-water elements, the micro- and macroalgae, occur locally in high abundances on the plateau. However, two cnidarians, the hydrozoan *Tubularia* and the octocoral *Clavularia* (Anthozoa) that are most abundant in Antarctic shallow waters, have not been found at the Nachtigaller Hill. These species occur at the Antarctic Peninsula and also far distant in the Eastern Weddell Sea but are absent from the central Weddell Sea (Raguá-Gil et al., 2004 and references therein). On the shallowest part of Nachtigaller Hill they are also missing. There are two possible explanations for this inconsistency. Firstly, their dispersal is so limited that they cannot overcome a distance of approximately 70 km from the costal zones of the Antarctic Peninsula to the Nachtigaller Hill. In this case, the rare occurrence in the Eastern Weddell Sea must be supported by a closer shallow-water population from East Antarctica following the eastward coastal current. With a long-range dispersal from the area west of the Antarctic Peninsula or clockwise with the Weddell Gyre from the Four Season Hill (Fig. 1) is potentially possible, the alternative explanation is that despite the similarity in the environmental conditions at the Four Season Hill and at the Norsel Bank in the Eastern Weddell Sea (Fig. 1), specific ecological conditions do not allow for a successful settlement of these animals at the Nachtigaller Hill. The Four Season Hill is, however, much closer to the coast.

Furthermore, some typical faunistic elements of the high-latitude Antarctic benthos are rare at the Nachtigaller Hill. Glass sponges e.g. occur in several places around the Antarctic continent at very high abundances (e.g. Eastern Weddell Sea). In the Western Weddell Sea, they also occur but are rare. West of the Antarctic Peninsula, they are less abundant than in the Eastern Weddell Sea. Glass sponges have also been reported from an area that is assumed to be frequently disturbed by icebergs off Snow Hill and Dundee Island. Studies form the Larsen A shelf ice area have also shown that these sponges can recruit fast (Gutt et al., 2011 and references therein).

Typical high-latitude gorgonians (e.g. the genera *Thouarella* and *Dasystenella*) are distributed similarly. As a consequence, the epibenthos communities on the Nachtigaller Hill resemble those living along both sides of the Antarctic Peninsula rather than those found in the Eastern Weddell Sea. In this case, (short-distance) dispersal between Nachtigaller Hill and the Antarctic Peninsula must have happened perpendicular to the prevalent current from the south. Nachtigaller Hill is however located in the extension of the Antarctic Sound. This could facilitate recruitment with larvae from the western side of the Antarctic Peninsula. Larval drift, from the South-Eastern and Southern Weddell Sea must have happened over a longer distance with the Weddell Gyre.

4.2 Habitat distribution characterisation and distribution

Seabed classes, substrate types and benthic communities are crucial for defining benthic habitats (Dolan et al., 2008; Wienberg et al., 2008). Additional factors that control habitats are light penetration (depth of the photic zone), disturbance (iceberg scouring and slope collapse) (e.g. Gutt, 2000), bottom currents and the availability of nutrients. The first two factors can be derived from bathymetric seabed image data. Light levels are a function of the water depth and turbidity and, in polar regions, also of ice cover. In addition, the presence of macroalgae can be used to indicate the light level critical for photosynthesis. With regards to disturbance, iceberg scouring is the dominant process on the upper slope (although also deeper iceberg scours occur in the study area). Seabed traces of disturbances and erosion cannot always be linked to a specific process but coarse scour tails associated with boulder size IRD (Fig. 3) suggest that bottom currents can be at least temporarily erosive. Nutrient levels are another important factor for habitat characterisation. Unfortunately, no direct nutrient measurements are available for this study. However, the enhanced number of animal phyla and organism abundances on the hill slope (Fig. 5) is likely to indicate areas of enhanced nutrient levels.

The results from analyses of the terrain (Fig. 2) and the seabed imagery (Fig. 4) both show that, in addition to the broad depth-related classification of the site in plateau, upper slope, foot and background setting, the hill is highly complex in terms of small-scale geo-morphology, seabed classes, substrate and benthic communities distribution. This complexity is captured in the seabed classification due to the incorporation of the fine scale BPI in the BTM.

In terms of habitat characterisation, the plateau is completely in the photic zone, hence the presence of macroalgae and diatom layers (Fig. 5). The overlying water mass is well mixed and homogenous. It, however, did not have a typical warm surface layer during the investigations in the middle of the austral summer (Fig. 6). Due to the shallow water depth, the impact of iceberg scouring is the dominant control on habitat distribution. Thus, the strongest contrast is between elevations exposed to frequent iceberg scouring and areas sheltered by elevations and ridges. In addition, wave action is another disturbance that potentially affects the fauna living on the plateau. It can, however, not directly be measured or observed and separated from icebergs disturbance. Although, the BTM classifies the central part of the plateau as "flat plateau", the "local ridges on broad flats" and "local depressions" reflect the fine-scale structure of habitat distribution (Fig. 2) seen in the seabed images. Accordingly, in the sheltered depressions, the seabed is covered by abundant IRD often in the form of boulder and gravel pavements. On the ridges and in less sheltered areas, consolidated sediments are exposed (Fig. 3). Towards the rim of the plateau, IRD becomes less abundant and consolidated sediments prevail (Fig. 3). Also ther, algae and sessile organisms are limited to sheltered areas. Sessile organisms generally only occur in low abundance and only a small proportion of the available hard substrate is colonised. In the exposed habitats, only mobile fauna can be found.

The hill slopes cross several environmental gradients. The presences of algae down to 56 m wd on the northern transect and down to 72 m wd on the southern transect (brown attached to boulders found at 240 m wd must have been displaced by icebergs, Fig. 5a) indicate that the uppermost parts of the slopes are still within the photic zone.

Across the slope, the potential bottom water temperature and salinity are rather constant and only rise by ~0.15 °C and 0.16 psu.

Geo-morphologically, the hill slopes show even more complex patterns than the plateau. In addition to the general terrace structure (flat areas separated by steeper areas, Fig. 2), small ridges and troughs create a very rugged heterogeneous terrain. These patterns are also reflected in the seabed classification where the slopes are characterised by the seabed classes "broad slopes" and "flat terrain" (Fig. 2). The steps between the terraces are classified as "steep slopes" and on the upper slopes as "escarpment, cliff" (Fig. 2). Some areas with distinct broad scale concave morphology are classified by the BTM as "current scoured depression" (Fig. 2).

Very steep and rugged terrain just below the rim of the plateau, are likely formed by continuous icebergs scouring. By the BTM, these areas with the highest ruggedness are classified as "rock outcrops" (Fig. 2). This classification is in good accordance with the data from the seabed imaged analyses that show common erosion features and escarpments (Fig. 3). Areas classified as "current scoured depression" are another geo-morphological feature on the upper slope are. In this setting they probably also indicate slope failures and small slides. This interpretation is supported by seabed imagery showing slide structures from the upper slopes (Fig. 4c). With these slides limited to the upper slopes, it is probable that they have been triggered by iceberg scouring. At the time of the survey several icebergs were grounded on the upper slope of the hill. In terms of habitat distribution, the entire upper slope can be interpreted as a complex heterogeneous habitat. The delineation of smaller sub-units based on seabed classification and imagery was mere possible as these parameters show no distinct spatial correlation and often vary from image to image which would mean from pixel to pixel in the classification raster. This complexity is also apparent in the correlation of biological and environmental parameters later in the text. On the upper slopes, hard substrate is abundant in the form of consolidated sediment and IRD (Fig. 3). The available hard substrate is, however, not fully colonised.

In comparison with the upper slope, the terrain of the lower slope is less rugged with more gradual changes between "broad slopes" and "flat plains" (Fig. 2). In addition to the dominant classes, long elongated depressions (seabed class"local depression, current scour") were found on the lower slope, in the north and west of the hill (Fig. 2). They are probably the result of enhanced bottom current activity as they coincide well with the depth range in which current indication have been identified on seabed images (Fig. 3). On the lower slope, the high variability in habitats is not so much the result of rugged and complex terrain but of varying abundance of hard substrate. Hard substrate occurs in the form of IRD and also broken off rocks from the hill. Available hard substrate shows high levels of colonisation.

For the entire slope area, it can be said that in all biological parameters, except for those referring to organisms living exclusively on the plateau and the very upper slope (the algae), the slope shows the highest biological heterogeneity within and between taxa as well as within and between transects. With minor exceptions and with the background of the taxa being generally present in the area: all combinations of taxa can be encountered everywhere.

Although geo-morphologically distinguishable from the background shelf setting (the maximal spatial extent of the hill is delimited by the "broad slope" class), no sedimentological differences can be identified between the hill foot and the background setting. Both settings are characterised by bioturbated soft sediments. Hard substrate only occurs in the form of IRD. Predicted by the BTM and supported by the seabed images, rock outcrops and escarpments are absent. Small areas of "current scoured depressions" are supported by scoured IRD in the vicinity (Figs. 2 and 3) indicating that least temporarily enhanced bottom currents in this area. In terms of habitat characterization, the hill foot and the background setting represent a soft bottom habitat typical for the western Weddell Sea shelf (Fillinger et al., 2013; Gutt, 2006). Hard substrate (IRD) is mostly densely colonized and appears to be the limiting factor for the occurrence of sessile epibenthic organisms. The limited availability of hard substrate is also reflected in generally reduced abundances of epibenthos in these areas. Also the ophiuroids (the only abundant mobile taxon) were less abundant at the hill foot.

On a site note, high abundances of krill have been observed at 3 locations on the shelf to the northeast of the hill at 400–420 m wd. The phenomenon, that krill can regionally aggregate at unusually deep sites close to the sea-floor is known to occur at some sites on the Antarctic shelf (e.g. west of the Antarctic Peninsula as well as in the Eastern and Western Weddell Sea (Schmidt et al., 2011)). Along the remaining transects, krill has only occurred sporadically and in low numbers.

4.3 Environmental control on the distribution of benthos communities

We have assessed the relationships between geo-environmental and epibenthic biological patterns in order to identify environmental drivers that shape high latitude Antarctic benthic communities in general and under the specific environmental settings of this site. The calculations have, however, not provided clear and convincing results. In the cases of relatively high ρ values (0.6–0.7), the slightest decrease of the correlation coefficients with changing environmental factor combinations shows that a variety of such combinations can explain the biological patterns. This is especially obvious for a merged data set. To improve the situation, calculations for single OFOS transects (transects 186 and 188 considered separately and pooled) have been carried out. It is possible that different factors have different effects at different stations thus causing the weak results.

A first observation is, however, that the number of phyla rarely shows a good ($\rho > 0.5$) correlation with the environment factors. Hence, additional overall and station-specific analyses are not promising. As expected, among the total of the results with good correlations factors, IRD and depth best explained the biological patterns when using the community data. IRD is a proxy for hard substrate which is especially important for sessile but also for mobile animals. Depth must be considered as a proxy for a variety of relevant ecological factors. All other environmental factors have only weakly influences on the correlations. Environmental factors that are not among the best correlations are

assumed to have no influence on the epibenthos distribution patterns. Surprisingly, among these factors are some that are a priori assumed to be most promising as they are either very distinct or more obvious at the Nachtigaller Hill and, hence, ecologically more effective than the same factors in a more homogenous environment.

For example, proxies for enhanced bottom current (ripples marks, current and to some extend erosion) are considered indicators for important ecological factors. Higher energetic environments should have a significant effect on the epibenthos especially since bottom-near currents provide an advective food transport for filter feeders. Ripple marks are five times among the relevant sediment parameters but other current indicators appear completely irrelevant. Additional proxies for highly dynamic environments are ruggedness (as result of erosion processes), striation primarily caused by iceberg scouring, small-scale erosive escarpments, and general erosion. Amongst these, striation and erosion represent weak parameters rarely occurring among the best environmental factors, while ruggedness and escarpments turned out to be never really relevant.

Other "classical" sedimentological parameters such as sand, consolidated sediment and soft sediment could affect the benthos distribution patterns in two ways. They represent proxies for higher energetic environments and hence advective food transport (sand, consolidated sediment) or for low energetic environments (soft sediment) in which finer sediments deposit thus also supporting the deposition and vertical flux of phytodetritus. Like IRD, these sedimentological factors might be important for a successful recruitment of early life stages as well as a successful survival and growth for sessile adult organisms. All these sedimentological factors have, only weak influences on the biological data. Surprisingly, also the clear impression from Fig. 5d that the number of phyla is highest at the slope analysed by GIS technics is not confirmed by the statistical correlation method. This parameter became, however, more relevant when 10 photographs were pooled. This indicates that the large-scale bottom topography is more relevant for the biological patterns than local individual images.

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The seabed classification results from the BTM are another GIS-derived factor. This factor has only been used in the single-photograph-approach as the data represent non-continuous classes. It does not explain any of the biological patters well. This means that, according to the applied statistical methods, for the distribution of the epibenthos at the Nachtigaller Hill the three-dimensional small-scale bottom morphology and resulting other potential drivers (e.g. small-scale current regimes) appear not play an important role. The statistical approach to merge all stations in one data set indicates the search for more general correlations patterns between the environment and the epibenthos, rather than local phenomena.

The generally weak correlations between environmental and biological data can have different reasons:

(1) Environmental factors others that those used in this study mainly drive the biological patterns. Sediment and bottom topography is quite well known in this study. The applied methods also provide valuable information on the generally relevant near-bottom current patterns. However, it cannot be excluded that the very obvious morphological structure of the Nachtigaller Hill acts as an obstacle for the currents on an otherwise flat shelf and causes current peculiarities such as turbulences and lee-situations. Finally, possible superimposed tidal effects are not found.

(2) In combination with large-scale effects, small-scale phenomena are of high relevance. The photograph-wise analyses accommodate this option and the number of photographs is generally high enough to decipher small-scale phenomena. However, some of the observed factors (e.g. current ripples, sand, escarpments, striations, current indicators) only occur very rarely (less than 50 of a total of 1730 photographs). Consequently, the sample size of these specific parameters might be too small to discover statistically significant biota-environment relationships.

(3) Computations with 10-binned photographs generally resulted in higher correlations. This indicates that environmental factors affect the benthos on a larger (~100 m) rather than a smaller scale (single photograph). This explanation does not exclude that, for the benthos local (here single photographs) and possible regional factors (here the

entire investigation area) are also relevant. It is plausible that both scales have their specific significance (e.g., current patterns may primarily act on a larger scale while small-scale sediment variations result in local biological patchiness).

(4) The investigated environmental factors are not the main drivers of the biotic patterns. Instead biological characteristics and interactions may play the dominant role in shaping the benthic communities.

5 Conclusions

Even for the complex morphology encountered at the Nachtigaller Hill, the seabed classification calculated by the BTM returned meaningful patterns. The general geomorphological structure of the hill was well captured, while local features were also represented. Solely derived from bathymetry, the BTM represents a strong tool even for the classification of complex terrains. The geo-morphology of the Nachtigaller Hill was characterised by complex and rugged terrain resulting in highly structured, complex heterogeneous habitat distribution. This variability was also represented in the species abundances. Hard substrate for sessile epibenthos is abundant at the hill plateau and slope but rare at the hill foot and in the background deep-shelf setting. The distribution patterns of sessile epibenthos were characterised by highly variable small-scale variability rather than broad distribution zones, reflecting the importance of the heterogeneous geo-morphology rather than the influence of more continuous environmental parameters such as water depth or water mass. Most likely it reflects the small elevated areas on the hill slope in combination with patchy distributions of hard substrate. In contrast, the less location-dependent mobile fauna showed broader distribution patterns. The statistical correlation between biota and the analysed environmental factors was, however, generally weak.

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Table 1. Seabed classification catalogue modified after Erdey-Heydorn (2008). "100" represents one standard deviation of the standardised BPI.

Class	Zone	Fine BPI		Broad BPI		Slope in degree		Depth in metre	
		Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper
1	Flat Plains	−100	100	−100	100		5		−60
2	Broad Slopes	−100	100	−100	100	5	10		
3	Steep Slopes	−100	100	−100	100	10			
4	Current Scoured Depressions	−100	100		−100				
5	Scarp, Cliff		−100	−100	100	10			
6	Depression		−100		−100				
7	Crevices, NarrowGullies over elevated terrain		−100	100					
8	Flat Ridge Tops	−100	100	100					
9	Rock Outcrop High, Narrow Ridge	100		100					
10	Local Ridge, Boulders, Pinnacles in Depression	100			−100				
11	Local Ridge, Boulders, Pinnacles on Broad Flats	100		−100	100		5		
12	Local Ridge, Boulders, Pinnacles on Slopes	100		−100	100	5			
13	Local Depression, Current Scours		−100	−100	100		10		
14	Plateau	−100	100	−100	100		5	−60	

Table 2. Calculations of correlation between environmental factors and epibenthic taxa. Results in grey not considered for further analyses or detailed interpretation due to low (<0.5) ρ values. Abbreviations for environmental factorsare biot: bioturbation, BTM: benthic terrain modeler seabed classification, cons: consolidated sediment, depth: water depth, eros: erosion (e.g. disturbed seabed, scours), esca: escarpment (steeply inclined seabed, cliff), IRD: ice rafted detritus, ripl: ripple marks due to bottom current activity, rug: ruggedness of the seabed, sand: sandy surface sediments, slope: seabed inclination, stri: striation on the seabed due to iceberg scouring. In the "approach" column, 1 stands for the analyses of single, 10 for pooled 10 photographs. COM stands for the analyses considering abundance classes of all higher benthic taxa, the community; DIV for "biodiversity", here defined by the no. of phyla.

OFOS transect	approach	ρ	Environmental factors that explain best benthic patterns (1st and 2nd best)	Transformation Log (IRD+1) Log (rugg) Log (slope)	No. of env. factors
185	1_COM	0.640	IRD, depth	Slope, rugg	13
		0.634	IRD, sand, depth		
186	1_COM	0.516	IRD, cons, sand, ripl, depth	IRD, rugg	13
		0.514	IRD, cons, sand, depth		
189	1_COM	0.656	IRD, stri, ripl	Rugg	10
		0.654	IRD, ripl		
185	10_COM	0.718	IRD, biot, stri	Slope, rugg	13
		0.712	IRD, biot, stri, depth		
186	10_COM	0.725	IRD, cons, sand, soft, ripl	Slope, rugg	13
		0.721	IRD, cons, soft, ripl		
189	10_COM	0.705	IRD, soft, eros, stri, depth, slope	IRD, rugg, slope	10
		0.704	IRD, eros, stri, depth, slope		
186 and 188	10_COM	0.722	IRD, cons, sand., soft, biot, ripl, slope	IRD, slope, rugg	13
		0.720	IRD, cons, soft, biot, ripl, slope		
189	1_DIV	0.675	IRD, stri, ripl	Rugg	10
		0.656	IRD, stri		
189	10_DIV	0.675	IRD, stri	IRD, Rugg, slope	9
		0.672	IRD, stri, slope		
186 and 188	10_DIV	0.519	Sand, ripl	IRD, slope, rugg	13
All	10_COM	0.714	IRD, cons, sand, soft, stri, ripl, depth, rugg	IRD, slope, rugg	13
		0.714	IRD, cons, sand, soft, stri, ripl, depth, slope		
All	10_DIV	0.506	IRD, cons, sand, stri, ripl, slope	IRD, slope, rugg	13
		0.504	IRD, cons, stri, ripl, slope		

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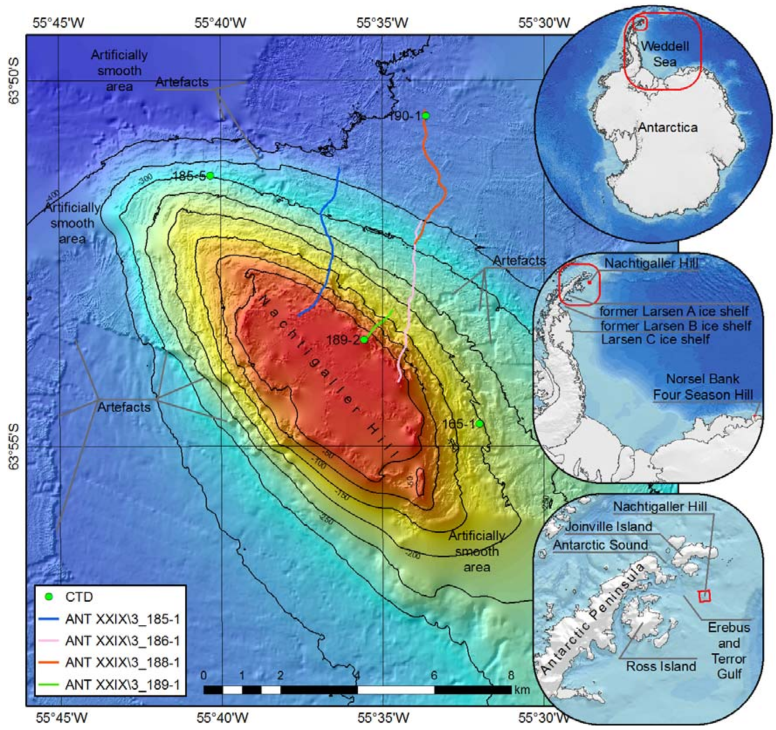

Fig. 1. Overview of the research area in the North-Western Weddell Sea in the Erebus and Terror Gulf on the over-deepened shelf east off the Antarctic Peninsula. Smooth areas and steps at the sides of the multibeam coverage are artefacts generated by the integration of different bathymetric data sets.

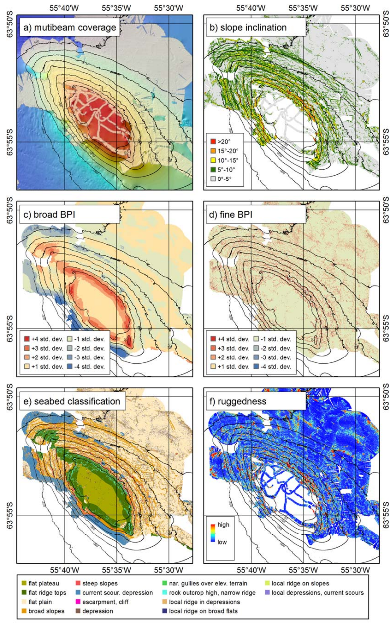

Fig. 2. Bathymetry-derived parameters used for seabed classification. **(a)** Shaded area indicates the extent of the multibeam coverage recorded during cruise ANT XXIX/3 of the R/V *Polarstern*. **(b)** Slope inclination in degree (1st derivate of the bathymetry). **(c)** and **(d)** Focal statistic raster (the basis for the seabed classification) **(e)** BTM seabed classification **(f)** Ruggedness (the amount of variability (or bumpiness) of the seabed). Being very sensitive to outer beam variability, the ruggedness shows in addition to real data also artificially high values in the flat area off the hill.

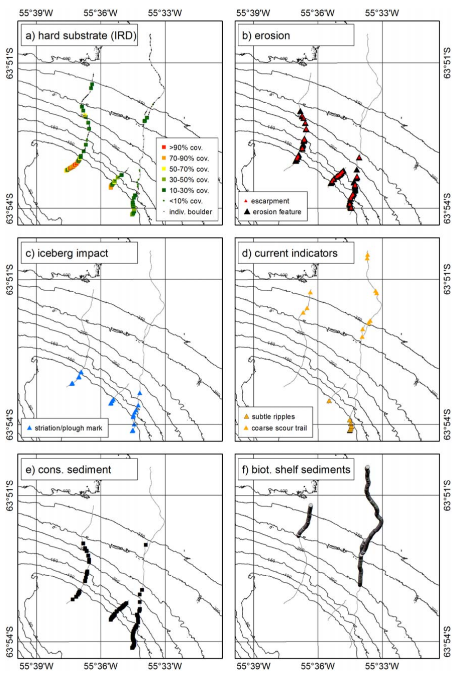

Fig. 3. A selection of environmental parameters and proxies for environmental parameters along the OFOS transects. The coverage of hard substrate **(a)** in the form boulders and pebbles was semi-quantitatively, visually estimated from the seabed images by one observer for consistency. **(b–d)** were qualitatively recorded and **(e)** and **(f)** represent background sediments in the OFOS images. Cons. = consolidated, biot. = bioturbated.

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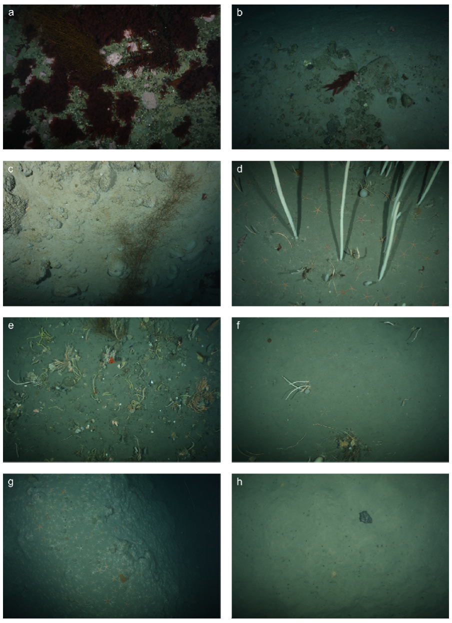

Fig. 4. Selected seabed images of dominant benthic habitats. **(a)** Sheltered area on the plateau (35 m wd), dense boulder and pebble coverage with abundant erect and encrusting red algae. **(b)** Exposed area towards the rim of the plateau (38 m wd). **(c)** Escarpment on the upper slope (56 m wd). **(d–f)** Benthic communities on the slope of the hill in 106 m wd, 308 m wd and 313 m wd. **(g)** Erosional feature with exposed consolidated sediment at 241 m wd with abundant mobile fauna (mostly ophiuroids). **(h)** Background shelf setting at 403 m wd.

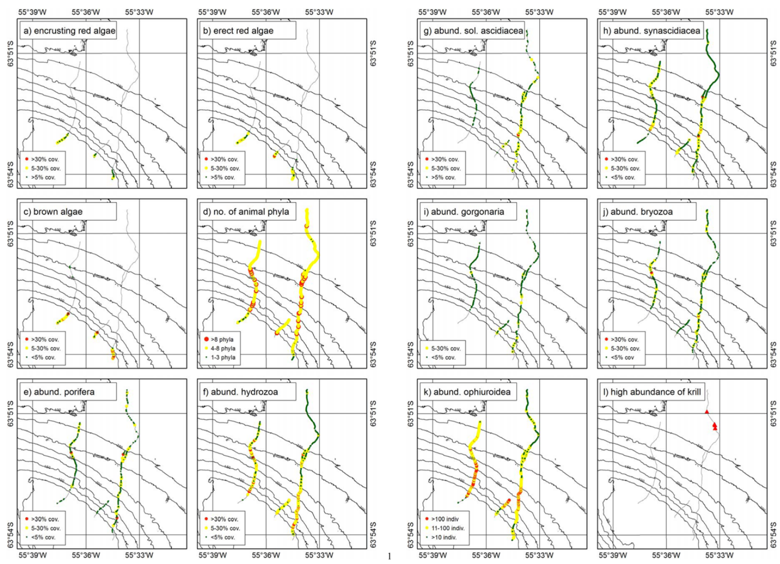

Fig. 5. Abundances of algae **(a–c)** and benthic organism groups **(e–l)** along the OFOS transects. **(d)** Number of animal phyla in each image. This information is an indicator for the distribution of biodiversity on the hill. Abund. = abundance, sol. = solitary.

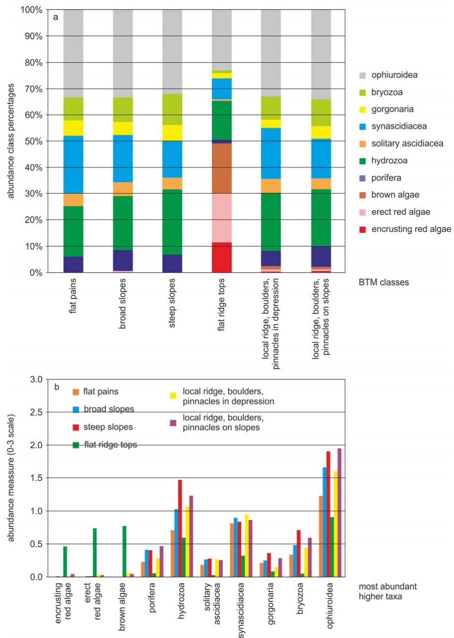

Fig. 6. Relationship between seabed terrain, expressed through the qualitative BTM classification scheme (Table 1), and the abundance and composition of the epibenthos, determined through the semi-quantitative (0–3 scale) abundances of the most common higher taxa. **(a)** Relative proportions of the selected taxa averaged within six selected BTM classes. **(b)** Within-BTM average abundances of the selected taxa, computed for six selected BTM classes.

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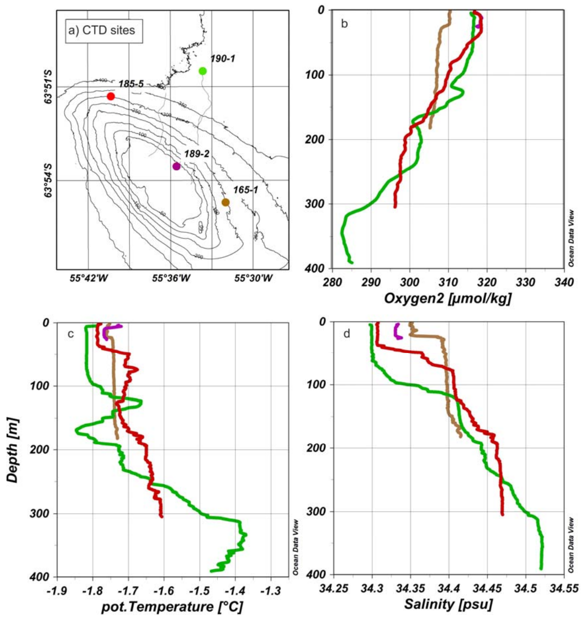

Fig. 7. Water-column profiles of oxygen concentration, potential temperature and salinity from 4 sites on and off the Nachtigaller Hill. The profiles from the hill site show the local hydrographic conditions. Water column profile 190-1 furthest away from the hill already shows the transition from local hill-controlled hydrography to the general oceanographic conditions in the area. This effect is most pronounced in the potential temperature **(c)**.