Benthic communities of the Filchner Region (Weddell Sea, Antarctica)

Santiago E. A. Pineda-Metz[1,2,*], Enrique Isla[3], Dieter Gerdes[1]

[1]**Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, 27568 Bremerhaven, Germany**
[2]**Fachbereich 2 Biologie/Chemie, Universität Bremen, 28334 Bremen, Germany**
[3]**Institut de Ciències del Mar – CSIC, 08003 Barcelona, Spain**

ABSTRACT: Due to extreme pack ice, the Filchner Region in the southern Weddell Sea is one of the least studied regions on the planet. Here, we provide a detailed description of the benthic communities of this high-Antarctic ecosystem, and assess the relationship between environmental factors and benthic distribution patterns. Fieldwork was performed in the austral summers of 2013–14 and 2015–16 during the R/V 'Polarstern' cruises PS82 and PS96. Using a combination of multibox corer (MBC) and seabed image data from 37 stations (water depths 243–1217 m), we differentiated 6 station groups. While 1 of these groups was comprised of a single station, the other 5 groups represented distinct benthic communities. Three of these correspond to the previously described Eastern Shelf, Southern Shelf, and Southern Trench communities. However, we found distribution shifts and MBC abundance and biomass reductions when comparing our results with earlier studies. The other 2 groups have novel characteristics and are presented here as an Ice/Ice Shelf Water-related community and a Continental slope community. Water depth in combination with 2 or 3 other environmental variables (out of 7 available) explained <30% of the benthic distribution and composition. We found a tighter relationship between water mass circulation and spatial distribution of the communities; we suggest using water-mass-related characteristics (e.g. productivity regimes, water currents) to better explain benthic spatial distribution patterns.

KEY WORDS: Southern Ocean · Infaunal benthos · Epifaunal benthos · Mega- and macrofauna · Zoobenthic distribution patterns · Sediment cores · Seabed images · Environment-benthic relationships

1. INTRODUCTION

The Antarctic benthos has been studied for over a century (e.g. Spry 1877). In the Weddell Sea, quantitative studies have focused more on the northwestern and eastern shelf areas (e.g. Gerdes et al. 2003, Sañé et al. 2012, Gutt et al. 2013). In contrast, the pack-ice-covered southern Weddell Sea is difficult to access and remains poorly studied (e.g. Voß 1988, Gerdes et al. 1992, Gutt & Starmans 1998). The present study attempts to reduce this gap by providing benthic community data from an area of ~476 000 km², covering the Filchner Trough and the adjacent continental shelf at the southern margin of the Weddell Sea (see Fig. 1).

The study area hereinafter referred to as the Filchner Region is characterized by heterogeneous topography, hydrography, and sea-ice conditions. The continental shelf in front of the Filchner Ice Shelf is incised by the Filchner Trough with water depths >1000 m (Arndt et al. 2013). The Filchner Trough is considered the main conduit for Ice Shelf Water (ISW) from underneath the Filchner-Rønne Ice Shelf towards the continental slope where it mixes with open ocean waters forming the deep and bottom waters of the Weddell Sea (Schröder 2016), making the Filchner Region key for the formation of Antarctic bottom water and the regulation of global water mass circulation (Gammelsrod et al. 1994, Foldvik et al. 2004, Ryan et al. 2017). Some key drivers of benthic

*Corresponding author: santiago.pineda.metz@gmail.com

distribution and composition, such as primary productivity, particle flux, and current regimes (Pineda-Metz in press), are characteristics which can be regarded as water-mass-specific (e.g. Barry 1988, Barry & Dayton 1988). Thus, we could expect the heterogeneous water mass circulation, in combination with e.g. the increased depth range in the Filchner Region, to cause benthos to be equally heterogeneous.

Another conspicuous characteristic of the Filchner Region is the presence of the grounded iceberg A23-A. Iceberg A23-A is located on the Berkner Bank on the western shelf of the Filchner Region. The iceberg separated from the Filchner Ice Shelf in April 1986 and changed the circulation of High Salinity Shelf Water (HSSW) in the Filchner Region (Grosfeld et al. 2001). Previous to the calving of iceberg A23-A, HSSW flowed directly from the Berkner Bank into the Filchner Trough; after this event, HSSW started to flow southwards to the Rønne Ice Shelf before entering the Filchner Trough as ISW (Grosfeld et al. 2001, Ryan et al. 2017).

The Filchner Region is characterized by 2 main sea-ice regimes (see Fig. 2). On the shelf east of the Filchner Trough and in front of the Rønne Ice Shelf, sea-ice cover is seasonal, i.e. during summer, open water conditions prevail, and during winter, the sea surface is sea-ice-covered. In contrast, over the Filchner Trough and the continental shelf west of it, heavy year-round sea-ice cover dominates, as reported from previous campaigns to the Filchner Region (Knust & Schröder 2014, Schröder 2016). Sea ice not only directly regulates primary production (Arrigo et al. 2015) but also the particle flux from the euphotic zone to the benthic realm (Isla 2016, Pineda-Metz in press), especially in the marginal sea-ice zones, where primary and secondary planktonic production are enhanced and higher than in open water areas (e.g. Bathmann et al. 1991, Isla et al. 2009, Isla 2016). Due to the opening of a polynya during summer, productivity on the eastern shelf of the Filchner Region should be considerably higher than productivity at the heavy year-round sea-ice-covered Filchner Trough and the continental shelf west of it. Based on these productivity differences, benthic abundance and biomass should be higher in high-productivity regions compared to those with lower productivity. The composition of infaunal and epifaunal communities should also reflect such local productivity regimes. However, advection of primary-produced carbon to areas adjacent to polynyas here could support benthic communities similar to those within the polynyas with high benthic abundance and biomass (e.g. Grebmeier & Cooper 1995, Smith et al. 2006, Jansen et al. 2018).

Changes in sea-ice cover and volume directly affect water mass characteristics and planktonic productivity, thus affecting benthos. During recent decades, sea-ice cover in the eastern Weddell Sea, including a large part of our study area in the Filchner Region, has increased (see our Fig. 2; Turner et al. 2016, S.E.A.P.M. & D.G. unpubl. data), in response to a decrease in surface water temperatures and a stronger positive Southern Annular Mode (Liu et al. 2004, Turner et al. 2016, Comiso et al. 2017). Thus, distinct differences in spatial and temporal scales of sea ice and productivity regimes should be expected on the eastern shelf of the Filchner Region, in the Filchner Trough, and on the shelf west of the trough.

The first description of the benthic fauna in this region was published in the late 1980s (Voß 1988). It differentiated among 3 community types: (1) a highly abundant and diverse Eastern Shelf community dominated by suspension feeders, especially sponges; (2) a Southern Shelf community, less diverse and abundant than the Eastern Shelf community, dominated by bryozoans; and (3) a Southern Trench community, with low diversity, high abundances, and a clear dominance of holothurians. This description was, however, exclusively based on trawl catches. Later campaigns on the eastern shelf collected quantitative data on benthic assemblages by means of a multibox corer (MBC; Gerdes et al. 1992) and seabed images (SBIs; Gutt & Starmans 1998). Based on benthic abundance and biomass data, these studies reported assemblages that resembled the Eastern Shelf and Southern Trench communities sensu Voß (1988). These descriptions encompassed either only infaunal (based on MBC data) or only epifaunal benthos (based on SBI data), while an approach combining both benthic faunal compartments and in addition, integrating the whole study area, is still missing.

A recent study in the Filchner Trough and its adjacent shelves, based on MBC and SBI samples, concluded that both methods should be used in combination whenever possible to allow a more comprehensive representation of the benthic fauna, including both infaunal and epifaunal benthos (Pineda-Metz & Gerdes 2018). Due to a focus on the methodological approach, this recent description of the benthic fauna lacked the detail of previous studies. Here, we attempted to provide a detailed description of the benthic communities in the Filchner Region along with their distribution by using a comprehensive methodological approach which considers both infaunal and epifaunal benthos. In a further step, we related the observed benthic distribution with environmental factors which have already been affected

by climate change and which are predicted to change in the future. These include e.g. near-seabed water temperature and salinity, and sea-ice cover (Timmermann & Hellmer 2013, Turner et al. 2016, Hellmer et al. 2017), but also other factors which are considered to be important for the benthos, e.g. sediment organic carbon (OC) content as food source, and e.g. water depth and sediment grain size (Cummings et al. 2010) as regulators for benthic distribution. Based on this approach, we aimed to observe how the different environmental parameters drive the structure, composition, and distribution of the benthic communities of the Filchner Region.

2. MATERIALS AND METHODS

Fieldwork was performed in the austral summers of 2013–14 and 2015–16 during the R/V 'Polarstern' (AWI 2017) cruises PS82 (ANT-XXIX/9; Knust & Schröder 2014) and PS96 (ANT-XXXI/2; Schröder 2016). At 37 stations with water depths ranging from 243 to 1217 m, the benthos fauna was investigated by means of MBC (Gerdes 1990) and SBI (Table S1 in the Supplement at www.int-res.com/articles/suppl/m628p037_supp.pdf; Fig. 1).

A 10 cm diameter multicorer (MUC) was deployed at 22 stations (Table S1) to obtain data on sediment grain size, OC, and biogenic silica (bSi). The upper 9 cm of the sediment cores were subsampled on board and frozen at −20 °C in darkness until further treatment in the laboratory. Sediment grain size was measured with laser diffraction in a Horiba Partica LA950V2 laser scattering particle-size distribution analyzer after removal of organic matter in a 20% hydrogen peroxide solution. The fine sediment fraction, expressed in weight %, is equal to the combined proportion of silt- and clay-sized material, while the coarse fraction represents the combination of the sand and gravel fractions. OC was measured in a LECO Truspec CN analyzer, and expressed as weight %. bSi was calculated following sequential alkaline extractions with Na_2CO_3 (DeMaster 1981, Mortlock & Froelich 1989, DeMaster 1991) to distinguish the biogenic and lithogenic silica fractions, both also expressed as weight %.

The OC and bSi inventories for the upper 9 cm of the sediment column were calculated as the product of their concentrations, dry bulk density (mg cm^{-3}), and the height of the subsample sediment layer, and expressed as mg cm^{-2}. Based on the homogeneous ^{210}Pb activity in Antarctic sediment cores, we considered that the upper 5–9 cm is the section of the sediment column most susceptible to be reworked by benthic organisms (e.g. Isla et al. 2004, Isla 2016, E. I.
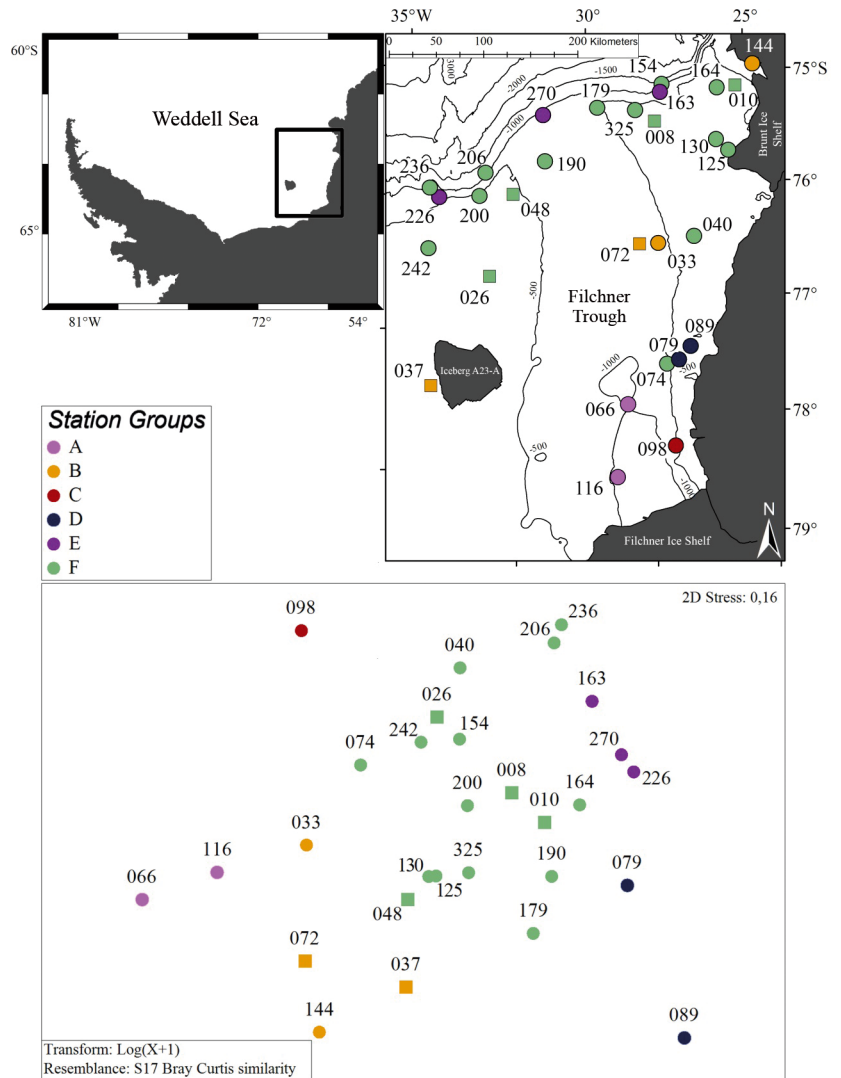

Fig. 1. Stations (numbered; see Table S1 in the Supplement) where multi-box corer (MBC) and seabed images (SBI) data were collected in the Filchner Region (Southern Weddell Sea; upper-left inset) during R/V 'Polarstern' cruises PS82 (circles) and PS96 (squares). Bathymetric data from IBCSO chart (Arndt et al. 2013). Lower graph: 2-dimensional MDS plot visualizing the among-station resemblance pattern of the benthic fauna identified in MBC and SBI samples collected during the cruises. The pattern is based on between-station Bray-Curtis similarities calculated from MBC biomass and SBI abundance data. Grouping obtained from Cluster and SIMPROF analyses and its distribution in the Filchner Region is shown (colors correspond to color key for station groups; numbers are Stn identification numbers)

unpubl. data). Furthermore, we found a high correlation between OC and bSi inventories of the upper 1 cm and those of the upper 5–9 cm. Thus, only the inventories of the upper 9 cm of the sediment column were considered. Additional to MUC grain size data (especially from areas where this gear could not be deployed), areal cover (%) of fine sediments, gravel, and rocks/stones were estimated at each SBI station (Table S2 in the Supplement).

To assess the effect of sea ice on benthic distribution and composition, we first collected monthly sea-ice cover data from the Sea Ice Index provided by the National Snow and Ice Data Center (NSIDC) for the period 1979–2017 (Fetterer et al. 2018). Monthly data were used to calculate summer and yearly sea-ice cover averages, and the temporal trends of sea-ice cover per year and per summer. These temporal trends were calculated as the slope of the linear function of sea-ice cover over time for the period 1979–2017.

Additional to MUC samples and sea-ice cover, a CTD (Seabird SBE-911 plus) was deployed at 201 stations to obtain oceanographic data on water column parameters (Schröder & Wisotzki 2014, Schröder et al. 2016). From these data, we extracted near-seabed water temperature, salinity, density, and dissolved oxygen to use in the correlation analyses.

While sea-ice data were already in raster format, CTD and sediment data were first imported to the GIS environment and interpolated for the study area with the Kriging method of ArcMap 10 (ESRI). The 'extract multi values to points' toolbox of ArcMap was used to extract environmental data from each raster derived from CTD, MUC, and sea-ice cover at all stations where both SBI and MBC benthic data were obtained (Tables S1 & S2). The extracted environmental data were used to assemble an environmental data matrix consisting of 20 environmental variables. To avoid co-correlation when conducting a BEST test (see later in this section), the environmental variables were correlated with each other. We then selected against environmental variables with significant correlations. The final environmental matrix consisted of 7 of the 20 environmental variables (Table S3 in the Supplement).

Sediment cores for benthic analyses were sieved on deck over a 500 μm mesh. Material retained on the sieves was fixed in a 5% seawater-formaldehyde solution buffered with borax. In the laboratory, benthic organisms were sorted, identified to the lowest identifiable taxonomic level (ITL) via a stereomicroscope, and classified into taxonomic units (TUs) similar to those used in previous MBC studies, in order to enable a comparison with previous data obtained in the Filchner Region (Gerdes et al. 1992) and other areas of the Weddell Sea (Gerdes 2014a–h). Although the use of larger TUs such as e.g. class or order is not common, other studies have shown little loss of statistical resolution regardless of the low taxonomic resolution (e.g. Warwick 1988). Abundance (ind. m^{-2}) and wet-weight biomass (g ww m^{-2}) values were calculated for each TU and sample. Abundance of colonial (e.g. bryozoans and hydrozoans) and large benthic organisms (e.g. sponges) was counted as presence only.

MBC abundance and biomass data were 4th-root-transformed and used to calculate between-station Bray-Curtis (Bray & Curtis 1957) similarity matrices. These MBC matrices were used in a PERMANOVA (Anderson 2001) to test for differences with older comparable MBC benthic abundance and biomass data from the Filchner Region (Gerdes et al. 1992) and other regions of the Weddell Sea (Gerdes 2014a–h). These multivariate statistics were performed by means of the software package PRIMERv6 with its PERMANOVA+ add on (Clarke & Gorley 2006, Anderson et al. 2008).

A RELATE test between MBC abundance and biomass data showed benthic distribution patterns derived from abundance and biomass to be significantly correlated (Spearman rank correlation, rho = 0.893; p < 0.001). Based on this result, we only used MBC biomass values in combination with SBI abundance values for the subsequent statistical analysis. All TUs from this benthic matrix were classified into 4 feeding guilds: deposit feeders, suspension feeders, scavengers, and predators (Table S4 in the Supplement). The classification of taxonomic groups into feeding guilds followed the recommendations in Yonge (1928), Hansen (1978), Fauchald & Jumars (1979), Montiel et al. (2005), and Macdonald et al. (2010). In cases where different feeding types occurred parallel in 1 taxonomic group, the percentage of contribution of the respective guild was estimated following the detailed classification scheme presented by Macdonald et al. (2010).

During cruise PS82, SBIs were taken every 15 s during a 15 min drift phase with a camera (Canon EOS D100) installed in an underwater housing attached to the MBC, resulting in an average of 55 images per station. Before treating SBIs for analyses, all images out of focus or blurred by suspended particles were discarded, resulting in an average of 35 usable images per station (for more details on SBI sampling and treatment previous to the analyses, see Pineda-Metz & Gerdes 2018). At 4 stations (Stns 033, 040, 052, and 206), all SBIs were analyzed to calcu-

late the number of images per station sufficient to identify ≥75% of all TUs differentiated. These curves were extrapolated to 35 images whenever necessary to reach the mean number of SBIs per station. All taxon accumulation curves were calculated using the EstimateS software (Colwell 2013). The taxon accumulation curves at these 4 stations clearly indicated that the analysis of 15 images was sufficient for this purpose (Fig. S1 in the Supplement). For this reason, at all other stations, a subset of 15 randomly selected SBIs was used to describe epifaunal benthos. During cruise PS96, SBIs were obtained by means of the Ocean Floor Observation System (OFOS; for details of the gear, see Piepenburg et al. 2017). From each OFOS transect, 50 SBIs taken on the closest position to the corresponding MBC station were selected, and a subset of 15 randomly selected SBIs was analyzed and used to calculate the taxon cumulative curve, as described above (earlier in this paragraph) for the SBIs obtained with the underwater camera attached to the MBC. All images obtained by means of the OFOS can be found in the PANGAEA virtual database (Piepenburg 2016).

In the laboratory, all organisms visible in the images were counted, and identified to the lowest ITL, to TUs similar to those defined for MBC samples. Whenever possible, TUs lower than those defined for the MBC were used. Organism counts were standardized to abundance (ind. m^{-2}). The abundance of colonial organisms (e.g. bryozoans, gorgonians, and hydrozoans) was calculated as the area covered by the colonies (m^2).

Previous to multivariate analysis and to eliminate the influence of different units in the benthic data matrix (i.e. ind. m^{-2}, m^2, and g ww m^{-2}), all data were first pre-treated to conform a benthic data matrix of the SBI abundance ratios and MBC biomass ratios of each TU at every station. Ratios were calculated by dividing TU abundance/biomass values at each station by the corresponding total abundance/biomass value of the station (Text S1 in the Supplement).

Multivariate statistics were applied by means of the software package PRIMERv6 with PERM-ANOVA+ (Clarke & Gorley 2006, Anderson et al. 2008). Prior to analysis, benthic data were log(x+1)-transformed. Between-station similarities were calculated using the Bray-Curtis index (Bray & Curtis 1957). The benthic data matrix was used in a Cluster and SIMPROF analysis (Clarke & Gorley 2006) to differentiate and define station groups, and the resemblance pattern was visualized using 2-d multidimensional scaling (MDS) plots. Additionally, 1-way PERMANOVA (Anderson 2001) and SIMPER analyses (Clarke & Warwick 1994) were performed to test for significant differences among and between station groups, to establish the mean dissimilarity between groups, and to determine which TUs mainly contributed to these between-group differences.

Additional to these tests, the similarity matrix derived from the benthic data matrix was used in a BEST analysis (Clarke & Gorley 2006) to test for correlations with the environmental data matrix, and thus the influence of environmental variables over benthic distribution patterns. This exploratory test was followed by a BEST analysis with 999 permutations to test for significant correlations.

3. RESULTS

Fine (clay and silt) and coarse (sand and gravel) sediments were unevenly distributed among stations in the Filchner Region (Table S1). Shelf and trough stations were characterized by high (>50%) proportions of fine sediments, whereas coarse sediments prevailed (>50%) at slope stations (Fig. 3, Table S1). In the SBIs, >50% of the seabed of most stations was covered by fine sediments (Fig. 3, Table S1). OC inventories varied from 8.0 to 70.4 mg cm^{-2}, with higher OC concentrations along the northern slope of the Filchner Region and lower concentrations on some parts of the eastern and western shelves of the region (Fig. 4). The bSi inventories ranged from 50.7 to 560.6 mg cm^{-2}; lower bSi concentrations were found at the western shelf stations, while higher values were observed in the deep trough and along the eastern shelf (Fig. 4).

Near-seabed water temperatures in the Filchner Region varied between −1.98 and −0.33°C (Fig. 5; Table S2). Lower temperatures were recorded in the southern Filchner Trough and at the southernmost stations on the eastern and western shelves, while higher temperatures were recorded on the northern slope of the Filchner Region (Fig. 5). Stations within the Filchner Trough were characterized by the highest salinity values (Fig. 5).

The highest average summer and yearly sea-ice cover occurred over the Filchner Trough (Fig. 2A,B). The sea-ice cover temporal trend over the years 1979–2017 showed similar patterns for summer and yearly averages, with gain of sea-ice cover especially in the trough area and loss of cover in the direct vicinity west of the A23-A iceberg and on the eastern shelf close to the shelf ice edge (Fig. 2C,D). Average loss of sea-ice cover on the eastern shelf was greater
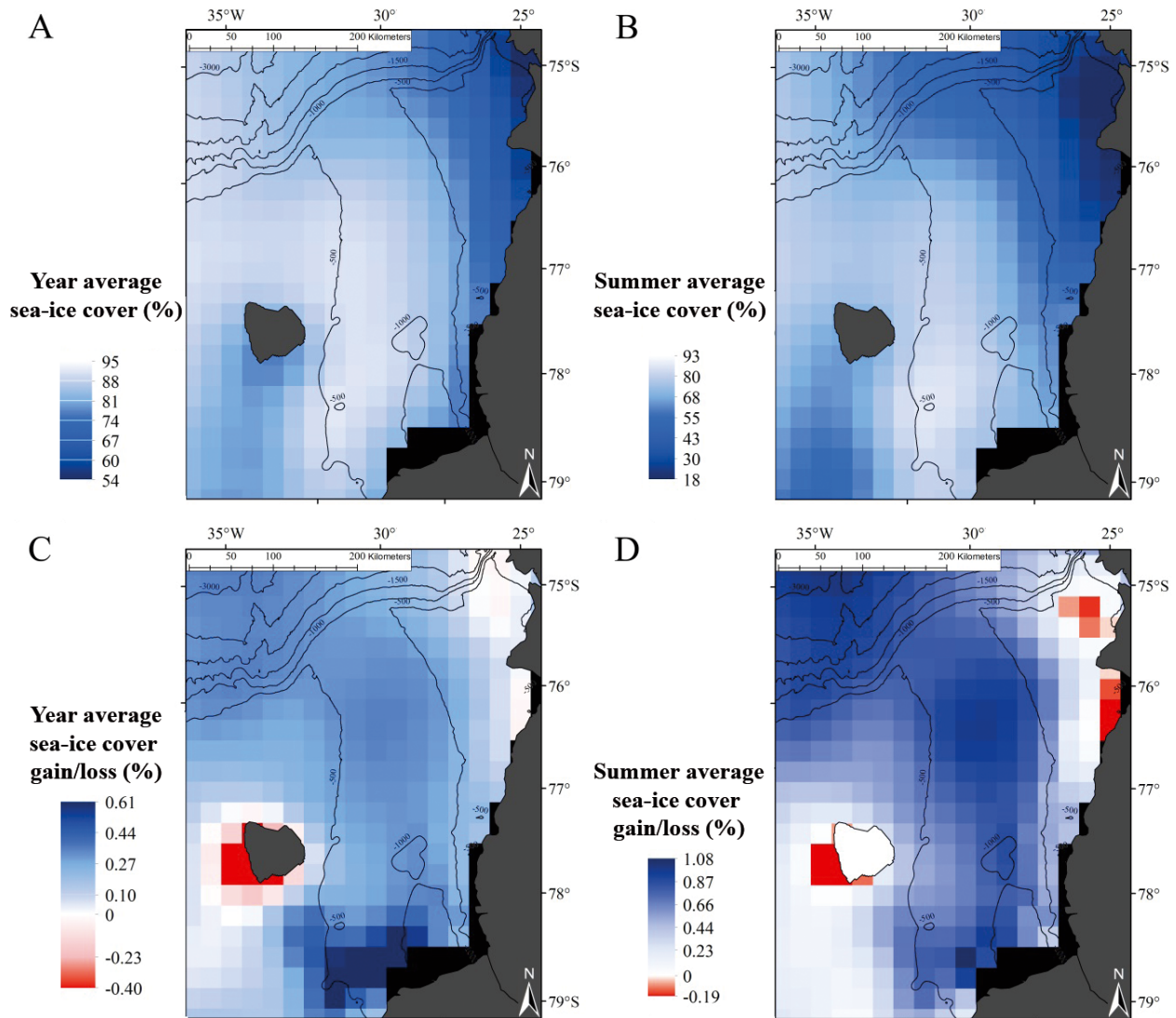
Fig. 2. (A) Yearly and (B) summer average sea-ice cover, and average (C) yearly and (D) summer sea-ice cover gain/loss for the period 1979–2017 in the study area in the Filchner Region. Note that each plot has its own color scale. Black: cells with no values. Modified after Fetterer et al. (2018)

in summer (-0.19% yr^{-1}) than over the year (slightly less than 0% yr^{-1}; Fig. 2C,D), whereas west of the A23-A iceberg, the average loss in summer (-0.19% yr^{-1}) was smaller than over the year (-0.4% yr^{-1}; Fig. 2C,D).

Thirty-five TUs were distinguished in the MBC samples at the Filchner Region stations (Table S5 in the Supplement). The number of TUs at MBC stations ranged from 3 (Stn 066) to 26 (Stns 163 and 164); only at 6 MBC stations <10 TUs were found. In the SBI analysis, a total of 31 TUs were distinguished. The number of TUs per SBI station ranged from 6 (Stn 144) to 23 (Stns 164, 179, and 190); in all but 1 station, >10 TUs were identified. Combining MBC

and SBI data, a total of 46 benthic TUs were distinguished (Table S5). Fifteen TUs were exclusively found in MBC samples (unidentified anthozoans, sipunculids, flatworms, nemerteans, priapulids, aplacophorans, scaphopods, clitellate worms, echiurids, acari, cumaceans, harpacticoid copepods, cirripeds, tanaids, and ostracods), and 11 TUs were exclusively found in SBIs (unidentified medusae, stauromedusae, gorgonians, pennatulaceans, actinarians, scleractinians, nudibranchs, cephalopods, mysids, serolids, and decapods).

The mean total benthic abundances at the 31 MBC stations ranged from 104 to 4627 ind. m^{-2}, with an overall mean of 1526 ind. m^{-2} and an overall
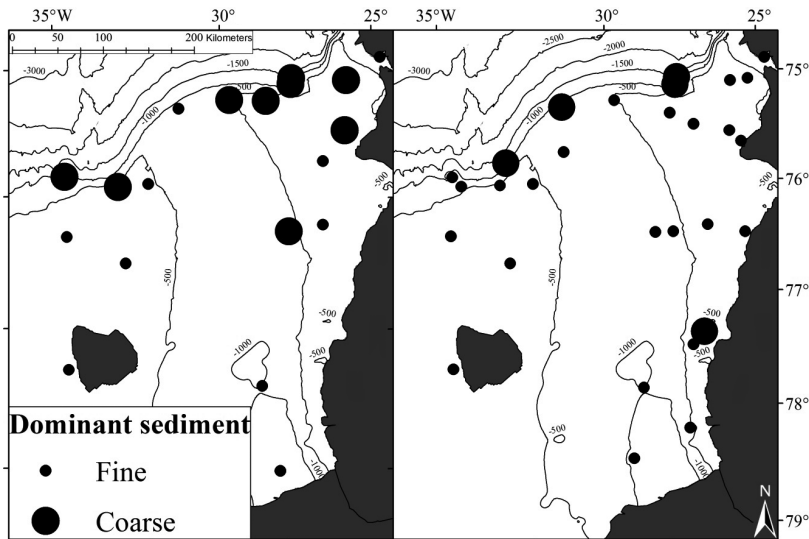
Fig. 3. Dominant sediment (proportion > 50%) in the sediment column calculated from multicorer stations (left), and at the seabed surface (derived from seabed images) for all stations where multibox corer and seabed images data were collected (right) in the Filchner Region during R/V 'Polarstern' cruises PS82 and PS96

The mean benthic biomass ranged from 1.31 to 335.47 g ww m^{-2}, with an overall mean of 51.08 g ww m^{-2} and an overall median of 23.85 g ww m^{-2}. Following the criteria given for MBC abundance data, bryozoans, sponges, polychaetes, ophiuroids, and tunicates were identified as the dominant TUs (Table 1). Suspension feeders contributed most to biomass, with an overall mean of 33.04 g ww m^{-2} (range: 0.38–321.49 g ww m^{-2}), followed by deposit feeders (10.81 g ww m^{-2}; range: 0.47–56.06 g ww m^{-2}), predators (6.89 g ww m^{-2}; range: 0.23–37.07 g ww m^{-2}), and scavengers (0.34 g ww m^{-2}; range: 0.01–2.20 g ww m^{-2}).

Before combining MBC and SBI data (see Section 2), we considered only benthic data obtained from the MBC samples in our Filchner Region study (present study) and compared it with the MBC data obtained at the Tip of the Antarctic Peninsula (TAP), the Larsen embayments (LA), and the South-Eastern Weddell Sea Shelf (SEWSS; cf. Gerdes 2014a–h). Benthic abundance and biomass, as well as faunal community composition, differed significantly among regions (PERMANOVA, pseudo-F = 5.549; p < 0.001) and between regions (pairwise PERMANOVA, p-values < 0.05; Table S6 in the Supplement). In terms of abundance, the dominant taxa were polychaetes, bivalves, amphipods,

median of 1270 ind. m^{-2}. Dominant TUs, which together contributed >75% to overall mean abundance, were polychaetes, bivalves, ophiuroids, clitellate worms, and amphipods (Table 1). Deposit feeders were the most abundant feeding guild, with an overall mean of 672 ind. m^{-2} (range: 44–2229 ind. m^{-2}), followed by predators (460 ind. m^{-2}; range: 20–1532 ind. m^{-2}), suspension feeders (344 ind. m^{-2}; range: 20–1090 ind. m^{-2}), and scavengers (34 ind. m^{-2}; range: 1–117 ind. m^{-2}).
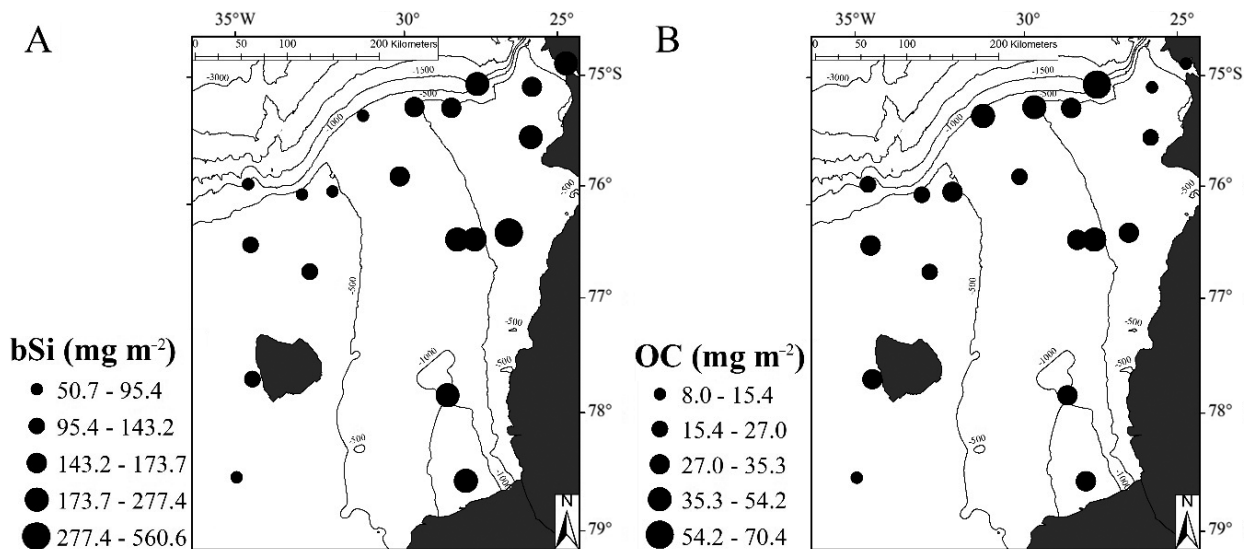

Fig. 4. (A) Biogenic silica (bSi) inventory and (B) organic carbon (OC) inventory for all stations where multibox corer and seabed images data were collected in the Filchner Region during R/V 'Polarstern' cruises PS82 and PS96. Value breaks based on the Jenks natural breaks criterion
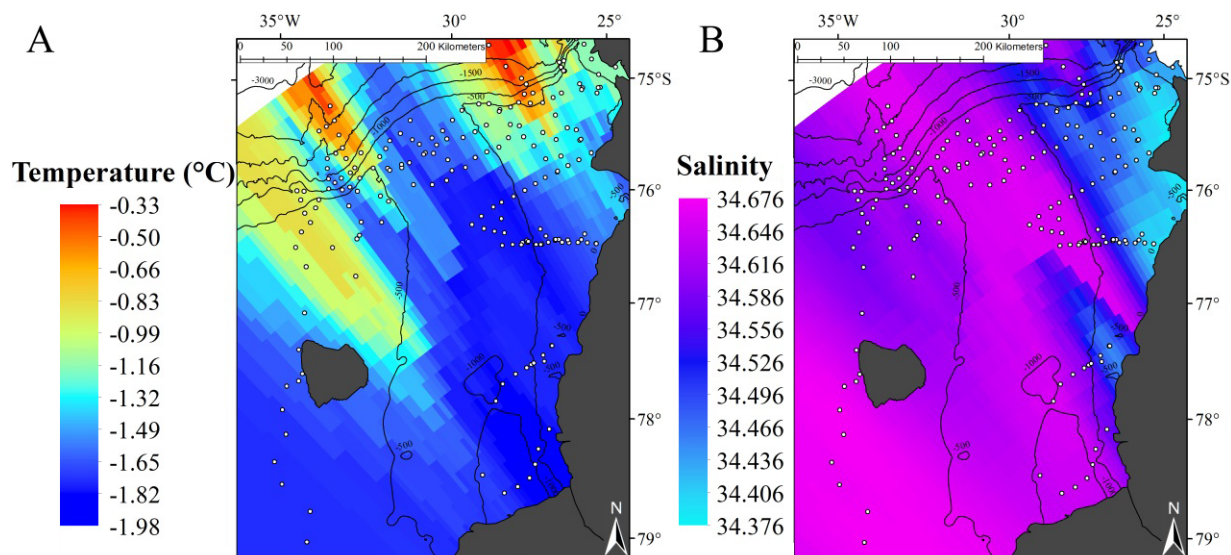
Fig. 5. (A) Near-seabed temperature and (B) salinity in the Filchner Region during R/V 'Polarstern' cruises PS82 and PS96. Modified from Schröder & Wisotzki (2014) and Schröder et al. (2016). White dots: CTD cast locations

Table 1. Abundances derived from all seabed images (SBIs), abundances and biomass derived from all multibox corer (MBC) samples, and their respective dominance and frequency of occurrence for the dominant taxonomic units (TUs). Data are mean ± SD; parentheses: minimum and maximum; dominance calculated from mean abundance/biomass values; (−) not found in images; Freq.occ.: frequency of occurrence; ww: wet weight

| TUs | SBI (n = 35) | | | MBC (n = 31) | | | | |
	Mean abundance (ind m^{-2})	Domi-nance (%)	Freq. occ. (%)	Mean abundance (ind m^{-2})	Mean biomass (g ww m^{-2})	Dominance (%) Abundance	Biomass	Freq. occ. (%)
Porifera	3 ± 7 (0–38)	3.3 ± 4.9 (0–25.8)	80	1[a]	11.3 ± 23.4 (0–87.7)	0.1 (0–0.3)	15.2 ± 23.2 (0–81.1)	71
Bryozoa	0.045 ± 0.111 (0–0.569)[b]	22.2 ± 25.3 (0–98.3)[c]	83	1[a]	13.6 ± 56.8 (0–315.4)	<0.1 (0–0.3)	7.3 ± 18.7 (0–94.0)	55
Bivalvia	<1 ± <1 (0–5)	0.3 ± 1.4 (0–8.5)	17	101 ± 131 (0–542)	0.5 ± 0.5 (0–1.9)	7.6 ± 8.2 (0–40.4)	3.8 ± 7.4 (0–31.7)	97
Polychaeta	11 ± 18 (<1–95)	15.6 ± 15.5 (0.5–65.2)	100	763 ± 580 (57–2181)	11.3 ± 18.6 (0.4–101.9)	55.3 ± 13.2 (33.3–82.7)	38.2 ± 28.2 (2.0–92.3)	100
Clitellata	−	−	−	143 ± 296 (0–1292)	0.2 ± 0.5 (0–2.1)	6.0 ± 7.8 (0–29.4)	0.5 ± 1.0 (0–4.6)	74
Amphipoda	<1 ± <1 (0–3)	0.5 ± 0.7 (0–4.8)	74	108 ± 151 (0–750)	0.4 ± 0.5 (0–1.9)	5.8 ± 5.2 (0–20.6)	1.3 ± 2.2 (0–10.4)	84
Holothuroidea	8 ± 29 (0–166)	9.7 ± 23.0 (0–97.4)	97	9 ± 16 (0–73)	1.3 ± 3.3 (0–15.3)	0.5 ± 0.8 (0–2.9)	3.0 ± 7.2 (0–31.9)	48
Ophiuroidea	24 ± 24 (<1–95)	40.7 ± 27.7 (0.2–88.5)	100	100 ± 121 (0–573)	4.8 ± 9.5 (0–39.3)	7.0 ± 7.0 (0–28.9)	10.1 ± 14.2 (0–56.4)	81
Tunicata	7 ± 14 (0–76)	10.2 ± 13.7 (0–57.1)	89	8 ± 15 (0–73)	2.4 ± 7.6 (0–38.0)	0.8 ± 2.0 (0–10.8)	3.6 ± 11.6 (0–61.2)	45
Unidentified	3 ± 3 (0–16)	4.7 ± 10.5 (0–47.4)	97	2 ± 5 (0–28)	<0.1 ± 0.1 (0–0.4)	0.2 ± 0.7 (0–3.9)	0.1 ± 0.5 (0–2.8)	16

[a]Abundance recorded as presence/absence (see Section 2)
[b]Abundance given in m^2
[c]Dominance based on organism coverage in SBI

and ophiuroids. Polychaetes contributed the most to abundance in all 4 regions, but their dominance declined from west to east (Table 2). Composition based on biomass data clearly showed that sponges dominated in TAP and especially the SEWSS, where they contributed 57.5 and 80.5% to total benthic biomass, respectively; in the Filchner Region, sponges contributed 22.2% of the biomass. In the LA, echiurids dominated (71% of the total biomass) and sponges represented only <2% of the total benthic biomass (Table 2). Further comparison of our MBC data set with previous data from the Filchner Region (Gerdes et al. 1992) also showed significant differences on a temporal scale (PERMANOVA, pseudo-F = 6.289; p < 0.001). The mean abundance (1539 ind. m^{-2}) and biomass (52.76 g ww m^{-2}) resulting from the 2013–14 and 2015–16 Filchner Region cruises were almost half the values (2758 ind. m^{-2} and 108.13 g ww m^{-2}) recorded in the late 1980s (Gerdes et al. 1992). In terms of abundance, polychaetes, bivalves, amphipods, tanaids, and isopods were the most abundant in the late 1980s, while sponges contributed most to biomass, followed by holothurians, polychaetes, priapulids, and ascidians.

For the Filchner Region, mean total benthic abundance at the 35 SBI stations ranged from 2 to 170 ind. m^{-2}, with an overall mean of 61 ind. m^{-2} and an overall median of 55 ind. m^{-2}. Dominant TUs were ophiuroids, polychaetes, holothurians, tunicates, and unidentified organisms, constituting >75% of the overall abundance (Table 1). Suspension feeders were the most abundant feeding guild, with an overall mean of 28 ind. m^{-2} (range: <1–124 ind. m^{-2}), followed by deposit feeders (22 ind. m^{-2}; range: 1–106 ind. m^{-2}), predators (10 ind. m^{-2}; range: <1–31 ind. m^{-2}), and scavengers (1 ind. m^{-2}; range: <1–5 ind, m^{-2}).

Colonial organisms were not recorded at 6 SBI stations, and at the other SBI stations, their coverage ranged from 0 to 0.585 m^2, with an overall mean of 0.051 m^2 and an overall median of 0.012 m^2. Bryozoans were the most abundant colonial TU, with an overall mean coverage of 0.045 m^2

Table 2. Multibox corer (MBC) data of each sub-region of the Weddell Sea: Tip of the Antarctic Peninsula (TAP), Larsen embayments (LA), Filchner Region (FR), and South-Eastern Weddell Sea Shelf (SEWSS). MBC data of TAP, LA, and SEWSS modified after Gerdes (2014a–h). TU: taxonomic unit; ww: wet weight

| Sub-region (no. of samples) | Depth range (m) | No. of TUs | Abundance (ind. m^{-2}) | | | | Biomass (g ww m^{-2}) | | | |
			Range	Mean ± SD	Median	Dominant TUs	Range	Mean ± SD	Median	Dominant TUs
TAP (15)	187–934	34	608–16894	3784 ± 3953	2723	Polychaeta (62.2%), Bivalvia (10.9%), Clitellata (7.2%), Polychaeta (13.8%), Anthozoa (10.1%)	30.11–3484.53	422.98 ± 862.77	223.30	Porifera (57.9%)
LA (21)	202–850	32	129–2016	682 ± 499	568	Polychaeta (59.2%), Bivalvia (8.7%), Isopoda (4.3%), Sipuncula (4.1%)	1.64–785.70	77.73 ± 176.52	16.00	Echiurida (70.6%), Echinoidea (8.3%)
FR (31)	254–1217	33	104–4627	1526 ± 1526	1270	Polychaeta (50.0%), Clitellata (9.4%), Amphipoda (7.1%), Bivalvia (6.6%), Ophiuroidea (6.6%)	1.31–335.47	51.08 ± 68.74	23.85	Bryozoa (26.7%), Porifera (22.2%), Polychaeta (22.0%), Ophiuroidea (9.3%)
SEWSS (41)	248–1486	35	29–6220	2133 ± 1451	1786	Polychaeta (36.1%), Amphipoda (10.8%), Ophiuroidea (10.5%), Bivalvia (9.9%), Sipuncula (4.7%), Isopoda (4.0%)	1.07–103234.71	4810.75 ± 17469.74	134.24	Porifera (80.5%)

(range: 0–0.569 m²), followed by hydrozoans (0.003 m²; range: 0–0.045 m²), and gorgonians (0.003 m²; range: 0–0.045 m²).

Based on the matrix constructed by combining MBC and SBI data obtained in parallel at 29 stations (see Section 2), the Cluster and SIMPROF analyses differentiated 6 station groups, which we named A to F (Fig. S2 in the Supplement). A summarized description of these groups and their composition is given in Table 3, and 1 representative SBI picture of each station group is shown in Fig. 6. The composition in these 6 station groups differed significantly among them (PERMANOVA, pseudo-F = 4.69; p < 0.001). A pairwise PERMANOVA showed almost all groups to be significantly different from each other. Group C as a 1-station group was significantly different only from group F (Table 4). In the SIMPER test, within-group similarities ranged from 50 to 71%, while between-group dissimilarities ranged from 56 to 85%. SBI abundance of holothurians, ophiuroids, bryozoans, and polychaete MBC biomass contributed the most to the between-group dissimilarities (Table 4).

Based on the PERMANOVA among- and between-group comparisons, we differentiated between the 1-station group C and all other groups. We considered the later groups to represent distinct benthic communities in the Filchner Region. Group A consisted of 2 stations (Stns 066 and 116) located close to each other in the deep southern Filchner Trough (Fig. 1). This group represents a deposit-feeding epifauna-dominated community, characterized by a relatively low number of taxa, high epifaunal abundance (though not as high as group D), and low infaunal abundance and biomass. Holothurians contributed most to epifaunal abundance, whereas the infauna was dominated by polychaetes. Group B consisted of 4 stations (Fig. 1), 1 located on the western shelf near iceberg A23-A (Stn 037), 2 at the eastern slope of the Filchner Trough (Stns 033 and 072), and 1 off the Brunt Ice Shelf (Stn 144). This group represents a mixed community, with suspension- and deposit-feeding epifauna and a predator/deposit-feeding-dominated infauna (Table 3). Abundance, biomass, and colonial organism cover showed low values. The number of taxa was intermediate (Table 3), and ophiuroids

Table 3. Standardized group parameters for station groups defined after the Cluster and SIMPROF analyses. Abundances, biomasses, and coverage are given as average ± SD (range in parentheses) for the station group. Main seabed image (SBI) taxonomic units (TUs) and feeding guilds are based on abundance in ind. m⁻², whereas main multibox corer (MBC) TUs and feeding guilds are based on biomass data. ww: wet weight

| Station Group (Stations per Group)	Number of TUs (SBI/MBC)	SBI Abundance (ind. m⁻²)	SBI Colonial coverage (%)	Main TUs	Main feeding guild(s)	MBC Abundance (ind. m⁻²)	MBC Biomass (g ww m⁻²)	Main TUs	Main feeding guild(s)
A (2)	21 (14/10)	95 ± 106 (21–170)	0	Holothuroidea	Deposit feeders (58 %)	220 ± 164 (104–341)	2.4 ± 1.55 (1.31–3.50)	Polychaeta	Deposit (44 %) and suspension feeders (31 %)
B (4)	26 (23/19)	11 ± 8 (2–22)	2.7 ± 28.3 (0.0–59.0)	Ophiuroidea	Deposit (38 %) and suspension feeders (37 %)	373 ± 315 (146–839)	4.6 ± 3.30 (2.51–7.40)	Polychaeta	Predators (42 %) and deposit feeders (39 %)
C (1)	25 (11/17)	28	03. Apr	Ophiuroidea	Deposit (48 %) and suspension feeders (41 %)	1352	50.0		Anthozoa Predators (74 %)
D (2)	32 (20/29)	114 ± 46 (82–147)	84.1 ± 22.4 (68.3–99.0)	Polychaeta	Deposit (42 %) and suspension feeders (34 %)	2281 ± 560 (1894–2766)	204.5 ± 185.28 (73.44–335.47)	Bryozoa	Suspension feeders (92 %)
E (3)	37 (23/27)	81 ± 57 (16–123)	46.0 ± 20.8 (23.5–64.5)	Ophiuroidea	Suspension feeders (52 %)	3079 ± 1560 (1449–4627)	83.0 ± 57.67 (20.43–134.06)	Ophiuroidea	Suspension feeders (46 %)
F (17)	43 (30/27)	60 ± 34 (4–131)	33.3 ± 19.2 (5.3–69.1)	Ophiuroidea	Suspension (45 %) and deposit feeders (35 %)	1593 ± 1217 (306–4474)	47.0 ± 47.29 (3.70–160.14)	Porifera	Suspension feeders (57 %)
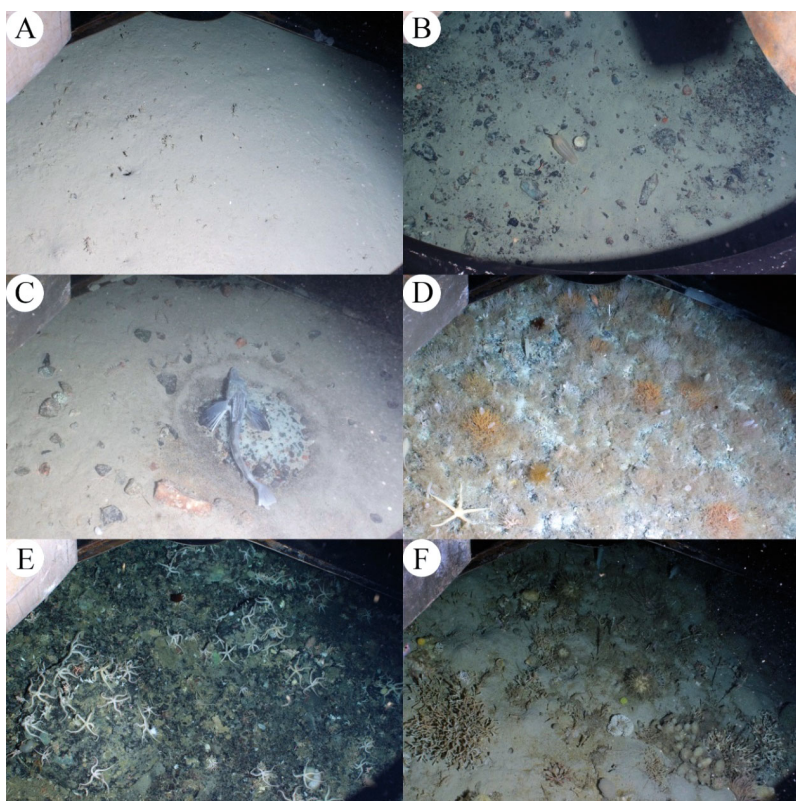
Fig. 6. Seabed images representing the typical appearance of the benthic fauna for station groups A–F defined by the Cluster and SIMPROF analyses. Except for group C, each seabed image includes representatives of the dominant TUs for each group (see Table 3)

and polychaetes were the main TUs in terms of abundance and biomass, respectively. Group C was comprised of only 1 station (Stn 098) located at the eastern slope of the trough (Fig. 1), dominated by ophiuroids and anthozoans (Table 3), and characterized by an intermediate number of TUs; MBC abundance and biomass were higher compared to groups A and B. Group D consisted of 2 stations (Stns 079 and 089) located close to each other (Fig. 1) on the eastern shelf, inhabited by a sessile suspension-feeder community dominated, in terms of biomass and organism cover, by bryozoans. The number of TUs was intermediate, and biomass, colonial organism coverage, and epifaunal abundance were high (Table 3). Group E was formed by 3 stations (Stns 163, 226, and 270) on the shelf break of the Filchner Region (Fig. 1). This group represents a sessile suspension-feeder community with a high number of TUs, high abundance and biomass, and intermediate colonial organism cover, mainly hydrozoans. Ophiuroids showed the highest abundance and biomass values (Table 3), followed by a combination of suspension-feeding tunicates, bryozoans, and sponges. Group F was the biggest group,

spread with 17 stations especially over the northern parts of the Filchner Region. This group is dominated by a mixture of suspension- and deposit-feeders, which accounted for up to 80% of abundance and 57% of biomass (Table 3). This community was characterized by the highest number of TUs and by intermediate abundance, biomass, and colonial organism coverage. Ophiuroids dominated in terms of SBI abundance, while sponges and polychaetes contributed most to MBC biomass.

The exploratory BEST analysis indicated only rather weak correlations between the environmental data and the benthic data matrix conformed by MBC biomass and SBI abundances. The combination of the 7 selected environmental parameters explained <30% of the overall benthic variation (Spearman rank correlation, rho = 0.275; p = 0.006). When testing each environmental variable individually, water depth was found to be the best explanatory variable (Spearman rank correlation, rho = 0.264; p = 0.014). Combinations of 2 or 3 environmental parameters with water depth were found to be the best explanatory variable combinations, but even these combinations explained <30% of the benthic variation (Spearman rank correlation, rho = 0.284; p = 0.023; Table 5).

4. DISCUSSION

4.1. Benthic communities in the Filchner Region

Our approach to describe benthic communities by combining corer samples and seabed imagery into a single data matrix, and also including stations in the difficult-to-access sea-ice-covered western shelf of the Filchner Region, has considerably extended and updated the current knowledge of the benthic fauna in this high-Antarctic region. Furthermore, our correlation analyses between benthic distribution and environmental parameters could help us to understand how the benthos in the Filchner Region might be affected by ongoing climate change. Such an analysis enables us to recognize the environmental variables affecting benthic spatial distribution, such as near-

Table 4. Within-group similarities, between-group dissimilarities (**bold**), and taxonomic unit contribution (%) resulting from the SIMPER analysis of benthic station groups A–F based on seabed image abundances (S) and multibox corer biomasses (M). *Significantly different (p < 0.05) in a pairwise PERMANOVA. (–) Not applicable

	A	B	C	D	E	F
Within-group similarity (%)	**70.62** Holothuroidea (S) 42.24 % Polychaeta (M) 40.14 %	**52.20** Polychaeta (M) 54.53 %		**67.84** Bryozoa (S) 32.48 % Polychaeta (S) 28.74 %	**66.67** Ophiuroidea (M) 18.88 % Ophiuroidea (S) 18.06 % Porifera (M) 11.93 % Tunicata (S) 11.03 %	**50.24** Ophiuroidea (S) 35.38 % Polychaeta (M) 20.49 %
Between-group dissimilarity (%)						
A	–					
B	**61.97*** Holothuroidea (S) 27.14 % Bivalvia (M) 8.33 % Crustacea (S) 7.78 % Anthozoa (M) 7.14 %	–				
C	**70.55** Anthozoa (M) 26.28 % Polychaeta (M) 20.01 % Ophiuroidea (M) 16.99 %	**73.43** Polychaeta (M) 20.14 % Anthozoa (M) 18.52 % Ophiuroidea (S) 12.24 %	–			
D	**84.65*** Bryozoa (S) 18.17 % Holothuroidea (S) 16.43 % Polychaeta (S) 13.77 % Polychaeta (M) 13.76 %	**78.61*** Bryozoa (S) 18.29 % Bryozoa (M) 16.32 % Polychaeta (M) 15.60 %	**83.87** Bryozoa (S) 18.18 % Anthozoa (M) 18.14 % Bryozoa (M) 15.57 %	–		
E	**82.94*** Holothuroidea (M) 18.08 % Polychaeta (M) 12.24 % Ophiuroidea (M) 10.82 % Ophiuroidea (M) 9.37 %	**74.33*** Polychaeta (M) 14.57 % Ophiuroidea (M) 11.83 % Hydrozoa (S) 8.89 % Ophiuroidea (S) 8.12 % Porifera (M) 6.61 %	**70.93** Anthozoa (M) 21.29 % Ophiuroidea (S) 12.32 % Holothuroidea (S) 10.72 % Hydrozoa (S) 9.49 %	**67.39*** Bryozoa (S) 18.88 % Polychaeta (S) 15.06 % Bryozoa (M) 14.11 % Hydrozoa (S) 8.09 %	–	
F	**74.41*** Holothuroidea (S) 21.14 % Ophiuroidea (S) 15.04 % Polychaeta (M) 9.05 % Bryozoa (S) 7.15 %	**63.46*** Ophiuroidea (S) 21.14 % Polychaeta (M) 15.04 % Bryozoa (S) 9.05 % Crustacea (S) 6.69 % Porifera (M) 6.67 % Anthozoa (M) 6.29	**66.61*** Anthozoa (M) 23.42 % Holothuroidea (S) 11.89 % Polychaeta (M) 10.15 % Bryozoa (S) 7.93 %	**63.90*** Bryozoa (M) 18.12 % Bryozoa (S) 14.83 % Polychaeta (M) 12.28 % Ophiuroidea (S) 11.37 %	**56.70*** Ophiuroidea (M) 10.82 % Hydrozoa (S) 9.79 % Porifera (M) 8.43 % Polychaeta (M) 8.32 % Bryozoa (S) 7.31 % Ophiuroidea (S) 7.03 %	–

Table 5. Single and combination of variables 'best explaining' distribution patterns of benthic communities. Parentheses: Spearman rank correlation rho values. OC: organic carbon; SBI: seabed images. *Correlation p < 0.05; **correlation p < 0.01

Single variable	Combination of variables
Water depth (0.264)**	Water depth, near-seabed temperature, gravel cover in SBI (0.278)**
Gravel cover in SBI (0.203)*	Water depth, gravel cover in SBI (0.278)**
Near-seabed temperature (0.098)	Water depth, gravel cover in SBI, OC inventory (0.277)**
Coarse sediment (%) in sediment column (0.068)	Water depth, near-seabed temperature, gravel cover in SBI, OC inventory (0.277)**
OC inventory (−0.061)	Water depth, summer sea-ice cover, gravel cover in SBI, OC inventory (0.275)**

seabed temperature and sea-ice cover, which are predicted to change by the end of the century due to climate change (Timmermann & Hellmer 2013, Hellmer et al. 2017).

We differentiated 6 station groups, 5 of which represented distinct communities (see Section 3). We consider group C as a 1-station group separately. In terms of epifaunal benthos, group C appears similar to group B, whereas its infauna was different from other groups (Table 3). Whether the infaunal composition at this station is driven more by local environmental characteristics or by the efficiency of the MBC to catch e.g. few but large anthozoans, which characterize the infauna at this station, remains unclear. Assessing why group C is so peculiar will require further sampling in the southeastern part of the Filchner Region.

For the remaining groups, we assume groups A, D, and F to correspond to the benthic communities previously described for the Filchner Region (Voß 1988, Gerdes et al. 1992, Gutt & Starmans 1998). However, our results point to distribution shifts and expansion of previous distribution ranges. Group A corresponds to the Southern Trench community sensu Voß (1988). In contrast to the original description of the Southern Trench community (Voß 1988), we found this group only in the southern deepest part of the Filchner Trough and not along the whole trough, making it a 'Deep Trough community' rather than a Southern Trench Community (Fig. S3 in the Supplement). Group F corresponds to the Eastern Shelf community sensu Voß (1988). This group was distributed not only on the eastern shelf of the Filchner Region, but also on the western shelf, the continental slope, and the slope of the inner trough, hence extending the distribution borders of this community considerably. This agrees with previous descriptions of the Eastern Shelf community, which also pointed to an extended distribution range of this community (Gerdes et al. 1992, Gutt & Starmans 1998). The extended distribution of the Eastern Shelf community to the deeper continental slope and also to the northern part of the western shelf of the Filchner Region suggests a con-

nection between these shelves. Group D corresponds to the Southern Shelf community sensu Voß (1988). The Southern Shelf community was originally described to be mainly distributed along the ice shelf edge southwest of the Filchner Trough and in one small area on the continental shelf off Halley Bay (our Fig. S3; Voß 1988). According to our results, group D on the continental shelf seems to have shifted southwards on the southeastern shelf. However, heavy sea-ice conditions in the entire southern Filchner Region, especially off the Rønne Ice Shelf, did not allow extensive station work in this area, thus making the confirmation of the original distribution range of this community impossible.

The 2 other communities we differentiated are described for the first time in the Filchner Region. One of these corresponds to group B, defined as a poor and mixed community with low abundance, biomass, and number of taxa. This community was found in 700 m water depth at the inner slope of the continental shelf northeast of Halley Bay, at the inner slope of the central part of the Filchner Trough, and in proximity of the large iceberg A23-A on the western shelf in 380 m water depth. We define the heterogeneous group B as an 'Ice/ISW related community'. Although located in different areas of the Filchner Region (Stns 033, 072, and 037), the stations of this group share hydrographic characteristics, which might explain the benthic similarities among them (Fig. S4 in the Supplement). The second newly defined benthic community was represented by group E and occurred along the continental slope at water depths between 600 and 800 m. This community living on sediments highly covered by gravel was dominated by ophiuroids and defined as the 'Continental Slope community'.

4.2. Filchner Region compared to other Weddell Sea regions

The MBC quantitative benthic data we present for the Filchner Region allows us to compare our results

with other Weddell Sea regions. PERMANOVA ana-
lyses of benthic abundance and biomass as well as
faunal community composition showed significant
differences among these Weddell Sea regions (Sec-
tion 3, Table 2). As a general pattern, high benthic
abundance and biomass prevailed in regions with
low sea-ice cover, such as TAP and the SEWSS, with
a yearly average sea-ice cover of 12 and 58% and
summer averages of 2 and 29%, respectively (Fet-
terer et al. 2018). In contrast, lower abundance and
biomass values were observed in regions with higher
sea-ice cover, e.g. in the Filchner Region and the LA,
where yearly average sea-ice cover reached 76 and
69% and summer sea-ice cover 50 and 75%, respec-
tively (Fetterer et al. 2018). Sea-ice cover, its ex-
tension and persistence, are key factors regulating
primary production (Arrigo et al. 2015). Thus, the
between-region sea-ice regime differences would
imply differences in the primary production regime,
which in turn would cause different particle fluxes
and food input to the benthos (Gutt 2001, Isla 2016).
We therefore suggest regional differences of benthic
abundance, biomass, and composition are due to dif-
ferences in local production and particle flux regimes,
regulated by sea ice (e.g. cover, ice-free days).

4.3. Filchner Region past vs. present

The comparison of the present MBC data set with
previously reported data from the Filchner Region
(Gerdes et al. 1992) showed significant differences,
with reduced abundance and biomass as well as
changes in the faunal composition. The MBC abun-
dance and biomass values we found were half of
those previously recorded in the Filchner Region dur-
ing the late 1980s. In terms of abundance-based com-
position, we found that groups such as tanaids and
isopods lost importance, being 'replaced' by clitellate
worms and ophiuroids. In terms of biomass-based
composition, bryozoans gained in importance, con-
tributing more to overall average biomass than
sponges, which were formerly found to dominate the
fauna (Gerdes et al. 1992). These observations might
already evidence climate-induced changes (sea-ice
cover increase; Fig. 2; Fig. S5 in the Supplement) in
community parameters, also including modifications
in composition patterns of benthic communities. Sim-
ilar benthic abundance and biomass losses following
productivity losses have been found for the Austasen
region (eastern Weddell Sea shelf) in a 26 yr period
(authors' unpubl. data). These productivity losses
were related to an increase in sea-ice cover between

1988 and 2014. Thus, we hypothesize our observed
lower benthic abundance and biomass, compared to
values recorded by Gerdes et al. (1992), to be related
to the increase in sea-ice cover (our Fig. S5; Turner et
al. 2016, Fetterer et al. 2018), which reduces the size
and duration of the summer polynya, thus also reduc-
ing primary productivity in the Filchner Region
(Arrigo et al. 2015, Pineda-Metz in press).

Comparing our epifauna results with older data, too,
reveals differences. Previous studies based on SBI
data defined 6 clusters in the Filchner Region. These
assemblages, however, were also found on the SEWSS
and on the Lazarev Sea shelf (Gutt & Starmans 1998).
The holothurian 'deposit-feeder-dominated' cluster
sensu Gutt & Starmans (1998) in the deep southern
Filchner Trough corresponds to our group A. The
'suspension-feeder-rich' and 'suspension-feeder-poor'
clusters (sensu Gutt & Starmans 1998) in the northern
part of the eastern shelf of the Filchner Region par-
tially overlapped with our station groups E and F.
However, while both suspension-feeder clusters were
bryozoan-dominated (Gutt & Starmans 1998), these
were less abundant in our groups E and F. This holds
especially true for group E along the outer slope of the
Filchner Region, where hydrozoans were the domi-
nant TU. Bryozoan dominance in the Filchner Region
appears to have shifted towards the south of the east-
ern shelf, a shift which could be driven by the in-
creased sea-ice cover over the outer slope, and de-
creased sea-ice cover over the eastern shelf.

4.4. Environmental drivers for benthic distribution

Our analyses did not indicate any strong correla-
tion between the assessed set of environmental para-
meters and benthic distribution patterns (all correla-
tion coefficient values of the BEST analyses were <0.3).
This agrees with studies conducted in the Bellings-
hausen, Weddell, and Lazarev Seas, which found rank
correlation coefficients <0.550 by means of an analy-
sis similar to the BEST test (Gutt & Starmans 1998,
Saiz et al. 2008).

Water depth as a single variable showed the
highest correlation value to explain benthic variabil-
ity, although the correlation was weak (Table 5).
Water depth is proposed to regulate benthic food in-
put, its quantity and quality, by modifying particle
residence time in the water column (Smith et al.
2006), thus also regulating benthic distribution. This
could explain why some TUs such as polychaetes,
isopods, amphipods, and bryozoans have been de-
scribed as water-depth-dependent groups on Antarc-

tic shelves (Ellingsen et al. 2007, Saiz et al. 2008, Jaz-dzewska & Sicinski 2017). In contrast, e.g. sponges, ascidians, and bivalves have been proposed to rely on water circulation and re-suspended particle supply instead (McClintock et al. 2005, Ellingsen et al. 2007, Segelken-Voigt et al. 2016), hence being more water-depth-'independent'. The mix of water depth-dependent and -independent TUs could partially explain the low correlation between water depth and benthic spatial distribution patterns. This coincides with benthic distribution patterns described for the Ross Sea (Cummings et al. 2010) and Bellingshausen Sea (Saiz et al. 2008), and would support the proposed capacity of Antarctic benthos to distribute over large depth ranges (Brey et al. 1996).

The content of organic matter in or on the seabed is commonly regarded as an important food source for benthos (Sañé et al. 2011, Zhang & Wirtz 2017). In our study, OC inventories in the sediment were just defined as quantities, and quality was not examined. The OC inventories did not show any correlation with benthic distribution patterns. This lack of correlation between OC as a single variable with benthic distribution would seem to agree with a recent study (Zhang & Wirtz 2017) which said that OC quality was more important than quantity for explaining the structure of benthic communities. Thus, our observations reaffirm the idea that benthos distributes independently of the amount of OC found in the sediment column.

Sea ice affects benthos in an indirect way by regulating primary production (Arrigo et al. 2015, Pineda-Metz in press) and thus the food supply for benthic organisms. Despite these effects on primary production, sea-ice cover or its temporal trend were not listed as variables in our correlation analyses (Table 5). However, we found hints pointing to a combination of polynya location and water mass circulation to be related to benthic spatial distribution, as proposed by bentho-pelagic coupling and benthic distribution studies in other Antarctic regions (Grebmeier & Cooper 1995, Isla et al. 2006, Jansen et al. 2018). The main polynya in the Filchner Region is formed on the eastern shelf (Fetterer et al. 2018), where water from the Weddell Sea Gyre enters and flows southwards towards the Filchner Ice Shelf (Ryan et al. 2017). While the polynya enhances primary production, the water mass circulation distributes this matter towards the south, supporting the presence of suspension feeders even in areas with relatively high sea-ice cover (e.g. southern part of the eastern shelf, where the Southern Shelf community was found). Conversely, water masses in the Filchner Trough origi-

nating from underneath the Filchner Ice Shelf flow northwards towards the continental break (Ryan et al. 2017). Due to its sub-ice shelf origin and heavy ice conditions in the trough, these water masses should be less productive and transport less suspended organic matter, which might explain the high dominance of deposit feeders such as elasipodid holothurians and the concomitant absence of suspension feeders. A similar situation was described for McMurdo Sound in the Ross Sea. Benthos production was higher in the eastern Sound, where water masses flow towards the Ross Ice Shelf, and lower in the western Sound, where water masses come from underneath the Ross Ice Shelf (Barry 1988, Barry & Dayton 1988).

Water mass circulation patterns in the Filchner Region appear to better explain the general benthic distribution pattern than any of our considered parameters or combinations of them (Fig. S4). The 'Deep Trough community' occurs in the deep Filchner Trough, where dense water originating at the Rønne Trough circulates (our Fig. S4; Ryan et al. 2017). The 'Ice/ISW related community' was found outside of the Filchner Trough, either close to the iceberg A-23A on the Berkner Bank, off the Brunt Ice Shelf, or in the ISW flow path (Fig. S4). The influence of water masses on benthic community distribution also becomes evident in the Southern Shelf community, represented in our study by 2 closely located stations in the south of the eastern shelf, likely related to the southern limit of modified Warm Deep Water (WDW; Fig. S4) coming from the north. Furthermore, the Continental Slope and Eastern Shelf communities (groups E and F) appear to live in warmer waters, most likely WDW and modified WDW from the Weddell Gyre. The circulation of WDW along the continental slope of the Filchner Region could also explain the connectivity between the eastern and western shelves of the Filchner Region, which we assume from the distribution of the Eastern Shelf community also on the western shelf.

5. CONCLUSIONS

Our approach using a combination of SBI and MBC data allowed for a comprehensive benthic community description by including data from both infaunal and epifaunal benthos. With this approach, we found the benthos of the Filchner Region to be highly heterogeneous and composed of 5 distinct communities. Comparison of our data with previous benthic studies in the Filchner Region and other areas of the Weddell

Sea show distinct differences among the benthic communities from the Filchner Region, the TAP, the SEWSS, and the LA. We attribute these differences to specific sea-ice and production regimes in these regions. Our results also provide partial evidence that benthos in the Filchner Region underwent changes in terms of abundance, biomass, and composition between the late 1980s and the mid-2010s. In addition, shifts in the distribution ranges of the benthic communities became apparent. These changes are most likely related to water mass circulation patterns and increased sea-ice cover in the area. Our correlation analysis showed that the environmental parameters considered explained <30% of the benthic spatial distribution. These results suggest further drivers for benthic community structure and composition, such as water mass circulation patterns, planktonic productivity, particle flux and lateral transport, and planktonic community abundance and composition. However, due to a lack of data, we could not include these parameters into our analyses. Nevertheless, the results of our correlation analyses can prove useful to further define environmental parameters to be considered for predicting future climate change effects on the Antarctic benthic fauna. Thus, we strongly recommend future studies to take a coordinated multidisciplinary approach. Such an approach should also include comprehensive bentho-pelagic coupling studies, which will provide a better tool to understand how benthos is (and could be) shaped by its environment.

LITERATURE CITED

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth

Arndt JE, Schenke HW, Jakobsson M, Nitsche F and others (2013) The International Bathymetric Chart of the Southern Ocean (IBCSO) version 1.0 – a new bathymetric compilation covering circum-Antarctic water. Geophys Res Lett 40:3111–3117

Arrigo KR, van Dijken GL, Strong AL (2015) Environmental controls of marine productivity hot spots around Antarctica. J Geophys Res Oceans 120:5545–5565

AWI (Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung) (2017) Polar research and supply vessel POLARSTERN operated by the Alfred Wegener Institute. J Large-Scale Res Facil 3:A119

Barry JP (1988) Hydrographic patterns in McMurdo Sound, Antarctica and their relationship to local benthic communities. Polar Biol 8:377–391

Barry JP, Dayton PK (1988) Current patterns in McMurdo Sound, Antarctica and their relationship to local biotic communities. Polar Biol 8:367–376

Bathmann U, Fischer G, Müller PJ, Gerdes D (1991) Short-term variations in particulate matter sedimentation off Kapp Norvegia, Weddell Sea, Antarctica: relation to water mass advection, ice cover, plankton biomass and feeding activity. Polar Biol 11:185–195

Bray JR, Curtis JT (1957) An ordination of upland forest communities of southern Wisconsin. Ecol Monogr 27:325–349

Brey T, Dahm C, Gorny M, Klages M, Stiller M, Arntz WE (1996) Do Antarctic benthic invertebrates show an extended level of eurybathy? Antarct Sci 8:3–6

Clarke KR, Gorley RN (2006) PRIMER 6: user manual/tutorial. PRIMER-E, Plymouth

Clarke KR, Warwick RM (1994) Change in marine communities. Natural Environmental Research Council, Plymouth

Colwell RK (2013) EstimateS: statistical estimation of species richness and shared species from samples. Version 9. User's guide and application. http://purl.oclc.org/estimates (accessed 4 April 2018)

Comiso JC, Gersten RA, Stock LV, Turner J, Perez GJ, Cho K (2017) Positive trend in the Antarctic sea ice cover and associated changes in surface temperature. J Clim 30:2251–2267

Cummings VJ, Thrush SF, Chiantore M, Hewitt JE, Cattaneo-Vietti R (2010) Macrobenthic communities of the northwestern Ross Sea shelf: links to depth, sediment characteristics and latitude. Antarct Sci 22:793–804

DeMaster DJ (1981) The supply and accumulation of silica in the marine environment. Geochim Cosmochim Acta 45:1715–1732

DeMaster DJ (1991) Measuring biogenic silica in marine sediments and suspended matter. Geophys Monogr 63:363–367

Ellingsen KE, Brandt A, Ebbe B (2007) Diversity and species distribution of polychaetes, isopods and bivalves in the Atlantic sector of the deep Southern Ocean. Polar Biol 30:1265–1273

Fauchald K, Jumars PA (1979) The diet of worms: a study of polychaete feeding guilds. Oceanogr Mar Biol Annu Rev 17:193–284

Fetterer F, Knowles K, Meier W, Savoie M, Windnagel AK (2018) Sea Ice Index, version 3 [01 January 1979 to 31 December 2017]. NSIDC: National Snow and Ice Data Center, Boulder, CO. doi:10.7265/N5K072F8 (accessed 9 January 2018)

Foldvik A, Gammerlsrod T, Osterhus S, Fahrbach E and others (2004) Ice shelf water overflow and bottom water formation in the southern Weddell Sea. J Geophys Res Oceans 109:C02015

Gammelsrod T, Foldvik A, Nost OA, Skagseth O and others (1994) Distribution of water masses on the continental shelf in the southern Weddell Sea. Geophys Monogr Ser 85:159–176

Gerdes D (1990) Antarctic trials of the multi-box corer, a new device for benthos sampling. Polar Rec (Gr Brit) 26: 35–38

Gerdes D (2014a) Abundance of macrozoobenthos in surface sediments sampled during POLARSTERN cruise ANT-XXI/2. Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, Bremerhaven

Gerdes D (2014b) Abundance of macrozoobenthos in surface sediments sampled during POLARSTERN cruise ANT-XXIII/8. Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, Bremerhaven

Gerdes D (2014c) Abundance of macrozoobenthos in surface sediments sampled during POLARSTERN cruise ANT-XXVII/3. Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, Bremerhaven

Gerdes D (2014d) Abundance of macrozoobenthos in surface sediments sampled during POLARSTERN cruise ANT-XVII/3 (EASIZ III). Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, Bremerhaven

Gerdes D (2014e) Biomass of macrozoobenthos in surface sediments sampled during POLARSTERN cruise ANT-XXI/2. Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, Bremerhaven

Gerdes D (2014f) Biomass of macrozoobenthos in surface sediments sampled during POLARSTERN cruise ANT-XXIII/8. Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, Bremerhaven

Gerdes D (2014g) Biomass of macrozoobenthos in surface sediments sampled during POLARSTERN cruise ANT-XXVII/3. Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, Bremerhaven

Gerdes D (2014h) Biomass of macrozoobenthos in surface sediments sampled during POLARSTERN cruise ANT-XVII/3 (EASIZ III). Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, Bremerhaven

Gerdes D, Klages M, Arntz WE, Herman RL, Galéron J, Hain S (1992) Quantitative investigations on macrobenthos communities of the southeastern Weddell Sea shelf based on multibox corer samples. Polar Biol 12:291–301

Gerdes D, Hilbig B, Montiel A (2003) Impact of iceberg scouring on macrobenthic communities in the high-Antarctic Weddell Sea. Polar Biol 26:295–301

Grebmeier JM, Cooper LW (1995) Influence of the St. Lawrence Island polynya upon the Bering Sea benthos. J Geophys Res 100:4439–4460

Grosfeld K, Schröder M, Fahrbach E, Gerdes R, Mackensen A (2001) How iceberg calving and grounding change the circulation and hydrography in the Filchner Ice Shelf-ocean system. J Geophys Res 106:9039–9055

Gutt J (2001) On the direct impact of ice on marine benthic communities, a review. Polar Biol 24:553–564

Gutt J, Starmans A (1998) Structure and biodiversity of megabenthos in the Weddell and Lazarev Seas (Antarctica): ecological role of physical parameters and biological interactions. Polar Biol 20:229–247

Gutt J, Cape M, Dimmler W, Fillinger L and others (2013) Shifts in Antarctic megabenthic structure after ice-shelf disintegration in the Larsen area east of the Antarctic Peninsula. Polar Biol 36:895–906

Hansen MD (1978) Nahrung und Freßverhalten bei Sedimentfressern dargestellt am Beispiel von Sipunculiden und Holothurien. Helgol Wiss Meeresunters 31:191–221

Hellmer HH, Kauker F, Timmermann R, Hattermann T (2017) The fate of the southern Weddell Sea continental shelf in a warming climate. J Clim 30:4337–4350

Isla E (2016) Environmental controls on sediment composition and particle fluxes over the Antarctic continental shelf. In: Beylich A, Dixon J, Zwoliński Z (eds) Source-to-sink fluxes in undisturbed cold environments. Cambridge University Press, Cambridge, p 199–212

Isla E, Masqué P, Palanques A, Guillén J, Puig P, Sánchez-Cabeza JA (2004) Sedimentation of biogenic constituents during the last century in western Bransfield and Gerlache Straits, Antarctica: a relation to currents, primary production, and sea floor relief. Mar Geol 209:265–277

Isla E, Gerdes D, Palanques A, Gili J-M, Arntz W (2006) Particle fluxes and tides near the continental ice edge on the eastern Weddell Sea shelf. Deep Sea Res II 53:866–874

Isla E, Gerdes D, Palanques A, Gili JM, Arntz WE, König-Langalo G (2009) Downward particle fluxes, wind and a phytoplankton bloom over a polar continental shelf: a stormy impulse for the biological pump. Mar Geol 259: 59–72

Jansen J, Hill NA, Dunstan PK, McKinlay J and others (2018) Abundance and richness of key Antarctic seafloor fauna correlates with modelled food availability. Nat Ecol Evol 2:71–80

Jazdzewska AM, Sicinski J (2017) Assemblages and habitat preferences of soft bottom Antarctic Amphipoda: Admiralty Bay case study. Polar Biol 40:1845–1869

Knust R, Schröder M (2014) The expedition PS82 of the research vessel Polarstern to the southern Weddell Sea in 2013/2014. Ber Polarforsch Meeresforsch 680:1–155

Liu J, Curry JA, Marinson DG (2004) Interpretation of recent Antarctic sea ice variability. Geophys Res Lett 31:L02205

Macdonald TA, Burd BJ, Macdonald VI, van Roodselaar A (2010) Taxonomic and feeding guild classification for the marine benthic macroinvertebrates of the Strait of Georgia, British Columbia. Can Tech Rep Fish Aquat Sci 2874: 1–63

McClintock JB, Amsler CD, Baker BJ, van Soest RWM (2005) Ecology of Antarctic marine sponges: an overview. Integr Comp Biol 45:359–368

Montiel A, Chaparro OR, Segura CJ (2005) Changes in feeding mechanisms during early ontogeny in juveniles of *Crepidula fecunda* (Gastropoda, Calyptreidae). Mar Biol 147:1333–1342

Mortlock RA, Froelich PN (1989) A simple method for the rapid determination of biogenic opal in pelagic marine sediments. Deep Sea Res A 36:1415–1426

Piepenburg D (2016) Seabed photographs taken along OFOS profiles during Polarstern cruise PS96 (ANT-XXXI/2 FROSN). Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, Bremerhaven

Piepenburg D, Buschmann A, Driemel A, Grobe H and others (2017) Seabed images from Southern Ocean shelf regions off the northern Antarctic Peninsula and in the southeastern Weddell Sea. Earth Syst Sci Data 9: 461–469

Pineda-Metz SEA (in press) Benthos-pelagos interconnectivity: Antarctic shelf examples. In: Jungblut S, Liebich V, Bode-Dalby M (eds) YOUMARES 9 – the oceans: our research, our future. Proceedings of the 2018 conference for YOUng MARine RESearchers in Oldenburg, Germany. Springer

Pineda-Metz SEA, Gerdes D (2018) Seabed images versus corer sampling: a comparison of two quantitative approaches for the analysis of marine benthic communities in the southern Weddell Sea (Southern Ocean). Polar Biol 41:515–526

Ryan S, Hattermann T, Darelius E, Schröder M (2017) Seasonal cycle of hydrography on the eastern shelf of the Filchner Trough, Weddell Sea, Antarctica. J Geophys Res Oceans 122:6437–6453

Saiz JI, García FJ, Manjón-Cabezo ME, Parapar J and others (2008) Community structure and spatial distribution of benthic fauna in the Bellingshausen Sea (West Antarctica). Polar Biol 31:735–743

Sañé E, Isla E, Grémare A, Gutt J, Vetion G, DeMaster DJ (2011) Pigments in sediments beneath recently collapsed ice shelves: the case of Larsen A and B shelves, Antarctic Peninsula. J Sea Res 65:94–102

Sañé E, Isla E, Gerdes D, Montiel A, Gili GM (2012) Benthic macrofauna assemblages and biochemical properties of sediments in two Antarctic regions differently affected by climate change. Cont Shelf Res 35:53–63

Schröder M (2016) The expedition PS96 of the research vessel Polarstern to the southern Weddell Sea in 2015/2016. Ber Polarforsch Meeresforsch 700:1–142

Schröder M, Wisotzki A (2014) Physical oceanography during POLARSTERN cruise PS82 (ANT-XXIX/9). Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, Bremerhaven

Schröder M, Ryan S, Wisotzki A (2016) Physical oceanography during POLARSTERN cruise PS96 (ANT-XXXI/2 FROSN). Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, Bremerhaven

Segelken-Voigt A, Bracher A, Dorschel B, Gutt J, Huneke W, Link H, Piepenburg D (2016) Spatial distribution patterns of ascidians (Ascidiacea: Tunicata) on the continental shelves off the northern Antarctic Peninsula. Polar Biol 39:863–879

Smith CR, Minks S, DeMaster DJ (2006) A synthesis of bentho-pelagic coupling on the Antarctic shelf: food banks, ecosystem inertia and global climate change. Deep Sea Res II 53:875–894

Spry WJJ (1877) The cruise of Her Majesty's ship 'Challenger': voyage over many seas, scenes in many lands. Belford Brothers, Toronto

Timmermann R, Hellmer HH (2013) Southern Ocean warming and increased ice shelf basal melting in the twenty-first and twenty-second centuries based on coupled ice-ocean finite-element modelling. Ocean Dyn 63:1011–1026

Turner J, Hosking JS, Marsahll GJ, Phillips T, Bracegirdle TJ (2016) Antarctic sea ice increase consistent with intrinsic variability of the Amundsen Sea Low. Clim Dyn 46:2391–2402

Voß J (1988) Zoogeographie und Gemeinschaftsanalyse des Makrozoobenthos des Weddellmeeres (Antarktis). Ber Polarforsch 45:1–145

Warwick RM (1988) Analysis of community attributes of the macrobenthos of Frierfjord/Langesundfjord at taxonomic levels higher than species. Mar Ecol Prog Ser 46:167–170

Yonge CM (1928) Feeding mechanisms in the invertebrates. Biol Rev Camb Philos Soc 3:21–76

Zhang W, Wirtz K (2017) Mutual dependence between sedimentary organic carbon and infaunal macrobenthos resolved by mechanistic modelling. J Geophys Res Biogeosci 122:2509–2526