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Composition and abundance of epibenthic-sledge catches in the South Polar Front of the Atlantic

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ABSTRACT

An epibenthic sledge (EBS) was deployed at seven different deep-sea stations along the South Polar Front of the Atlantic in order to explore the composition and abundance of macrofaunal organisms and to identify the most abundant taxa in this transition zone to the Southern Ocean. In total 3,130 specimens were sampled by means of the EBS on board of RV *Polarstern* during the expedition ANT-XXVIII/3 in the austral summer of 2012. Benthic and suprabenthic Crustacea occurred to be most frequent in the samples. Among those, copepods were by far most numerous, with 1,585 specimens followed by the peracarid taxa Isopoda (236 ind.), Amphipoda (103 ind.), Tanaidacea (78 ind.) and Cumacea (50 ind.). Annelida were represented by a high number of specimens belonging to different polychaete taxa (404 ind.). The molluscan fauna was clearly dominated by Bivalvia (255 ind.), followed in numbers of specimens by Gastropoda (47 ind.). The deep-sea benthos sampled along the Southern Polar Front occurred in surprisingly low abundances, contrasting the largely high surface productivity of the area. Numbers of specimens across different macrofaunal taxa and especially of peracarid crustaceans underscored by far those from South Ocean sites at higher latitudes in the Weddell Sea.

1. Introduction

Different apparati were used in the past for catching macrofaunal taxa (organisms $>63\ \mu m$, but mostly several mm–cm in size) (see Eleftheriou (2013) for a summary). Among the variety of available gears, epibenthic sledges (EBS) proved to be the most efficient and a reliable device for macrofauna due to the comparatively small mesh sizes of 300 μm (Rothlisberg and Pearcy, 1977). This type of sledge was modified by Brandt and Barthel (1995) and later by Brenke (2005). Investigations on supra- and epibenthic macroorganisms are still limited for bathyal and especially abyssal environments, although during the last decades an increasing number of publications dealt with the results of a variety of epibenthic sledge types in different regions of the world (e.g., Brandt, 1995; Brandt et al., 1996; Brattegard and Fosså, 1991). Few investigations were performed in polar seas with different epibenthic samplers (e.g. San Vicente et al., 1997; Brandt, 2001) prior to the ANDEEP (ANtarctic benthic DEEP-sea biodiversity, colonization history and recent community patterns) expeditions with RV *Polarstern*. An EBS was deployed within the framework of the ANDEEP project in the Southern Ocean deep sea (Brandt et al., 2007a, 2007b, 2007c), from the Ross Sea (Lörz et al., 2013) and from the Scotia and Amundsen Sea (Kaiser et al., 2007, 2009). This EBS is comparable to the Rothlisberg and Pearcy (1977), Brandt and Barthel (1995) and Brenke (2005) model, which was subsequently equipped with additional camera systems and a CTD (Brandt et al., 2013).

Based on the data gained within the frame of the ANDEEP I–III expeditions in 2002 and 2005, high macrofaunal biodiversity from the Southern Ocean deep sea was reported (Brandt et al., 2007a, 2012).

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Kaiser et al. (2013) described pattern, process and vulnerability of Southern Ocean benthos and summarized these and other results from the Census of the Antarctic Marine Life (http://www.caml.aq/). The ANDEEP expeditions focused on biodiversity patterns. The follow-up project SYSTCO (SYSTem COupling) has been designed to understand processes driving the patterns observed (Brandt and Würzberg, 2014). The very high abundances and high biodiversity reported in the southern Weddell Sea (Brandt et al., 2007a, 2007b, 2007c) challenged the hypotheses of latitudinal gradients in the deep sea (Rex et al., 1993; Poore and Wilson, 1993). Graf (1989, 1992) published first evidence of a response of a deep-sea benthic community to a pulse of natural organic matter and the importance of ecosystem engineers for coupling processes (Graf and Rosenberg, 1997). Since then, the influence of fluxes of organic carbon to deep-sea benthos abundance and diversity has been consolidated (e.g. Ruhl and Smith, 2004; Ruhl et al., 2008). Accordingly, results from iron fertilization experiments triggering primary productivity in the Southern Indian Ocean revealed greater densities and biomasses as well as impacts on deep-sea faunal composition (Wolff et al., 2011). For the Atlantic sector of the South Polar Front (SPF), high primary production rates have been reported (e.g. Tréguer and Jacques, 1992; Schlitzer, 2002). We were therefore interested to investigate the abyssal macrobenthic fauna within this high productivity area. Assuming that the high food input in this region provides energy sources for all fauna, from water surface down to the deep ocean floor, we hypothesized that benthic organisms benefit from such an input, and consequently to report high macrobenthic abundances in the EBS catches. Until now our knowledge of the benthic fauna in the SPF is still too limited and fragmentary to support this theory (Brandt and Ebbe, 2011; Brandt and Würzberg, 2014).

2. Material and methods

The data were collected during the SYSTCO II expedition (ANT-XXVIII/3) with RV *Polarstern* in the South Atlantic (Fig. 1; Table 1). Samples were taken by means of an EBS (modified after Rothlisberg and Pearcy, 1977; Brandt and Barthel, 1995; Brenke, 2005) at depths from 2,752 to 4,327 m. Stations were located in the SPF, where the EBS was successfully deployed at seven stations (Table 1). Numbers 81, 84, 85 and 86 of this table are station numbers, the numbers after the hyphen reflect the haul numbers of the respective stations (e.g. 86-20, 86-26).

The EBS consists of a supra- and epibenthic net equipped with cod ends of 300 μm each with an opening- and closing mechanism. It was lowered with 0.7 m/s to the seafloor and then with 0.5 m/s (ship speed compensates for the lowering in order to lay the wire straight in front of the gear on the ground) to 1.5 times wire length to water depth. It was then hauled over the ground for 10 min at a mean velocity of 1 knot. Afterwards the ship stopped and heaving was done with 0.5 m/s until the EBS had left the ground, then it was heaved with 0.7–1 m/s until it reached the ship's deck. The haul distances were calculated from the time the sledge traveled on the ground until the moment when it had left the ground, which was clearly indicated by the tension meter. Haul lengths varied from 2,586 m to 4,789 m; for the comparative analysis between sampling stations the data are therefore standardized to 1,000 m hauls, equivalent to a bottom area of 1,000 m² sampled by the sledge (according to Brenke, 2005; Brandt et al., 2004a, 2007c). In total, 29,090 m² of seafloor were sampled. On deck the samples were immediately transferred into pre-cooled 96% ethanol and kept for at least 48 h at −20 °C. Further, the samples were rotated every two hours in order to ensure that the ethanol is equally distributed throughout the whole samples and thus obtain a thorough fixation. Moreover, ethanol was renewed after 24 h.

The samples were sorted first on board and later in the laboratories of the Zoological Museum of the University of Hamburg and the Bavarian State collection of Zoology, Munich into the major taxonomic groups. Samples from the cod ends of epi- and supra-net were pooled for the analysis and the complete samples were analyzed (there was no protrusion of sediment above the cod ends).

Foraminifera were very numerous, therefore a subsample was individually collected on board and not quantitatively analyzed. Furthermore, only living specimens of shell bearing organisms (e.g. Ostracoda, Mollusca) or body parts relevant for identification in damaged organisms (e.g. pieces with heads in cases of crustaceans and polychaets) were counted.

All the obtained data is listed in Table 1. Benthic and suprabenthic Copepoda and Ostracoda, however, were not included in Figs. 2 and 3, because both taxa are still under study. Moreover, the high number of copepods would be blurring the graphical presentation. Also excluded from further analyses are the chaetognaths. Differences in the standardized abundance of macrofaunal taxa (accounting for the ten most abundant taxa) between the different stations were calculated via a Kruskal–Wallis test (for not normally distributed data) with subsequent post-hoc analysis using the statistic software R (Version 3.0.2, Development Core Team, 2011).

3. Results

Of macrofaunal taxa 3,130 specimens were sampled (raw data are reported here, while in the table specimens/1,000 m² trawled distance are listed) (Table 2, Figs. 2 and 3). The faunal composition was dominated by Crustacea and among those by calanoid Copepoda (1,585 ind.). The peracarid taxa Isopoda (236 ind.), Amphipoda (103 ind.), Tanaidacea (78 ind.) and Cumacea (50 ind.) were less numerous. Annelida were represented by a high number of polychaetes (404 ind.), with the dominating families Ampharetidae, Syllidae, Paraonidae and Spionidae (Appendix Table 1). Among molluscs, Bivalvia occurred most frequently (255 ind.), followed in numbers by Gastropoda (47 ind.). Abundances of Echinodermata were very low in the samples.

Relative Abundance of the ten most abundant taxa differed significantly between stations (Kruskal–Wallis $p=0.029$). Multiple pairwise comparisons during post-hoc analysis using Bonferroni correction showed no obvious significant differences. However, using a non-conservative correction method (false discovery range method), significant differences became apparent between station 86-24 and 81-17 as well as 86-24 and 86-20 (Wilcoxon rang sum test, $p=0.037$).

In fact, abundances were patchy as observed in the area of station 86, where the highest and lowest abundances were collected at almost the same depths. The more abundant stations had unproportionally higher numbers of polychaetes and isopods, while bivalves were more abundant at stations 86-24 and 86-25. Abundances were highest at station 86-24 and lowest at station 86-20, followed by station 81-17 in numbers of macrofaunal organisms (Fig. 3). Polychaetes were most abundant at stations 81-18, 84-25 and 86-24, followed in numbers by isopods and bivalves. At station 85-15 polychaetes and isopods were almost equally abundant (Fig. 3).

Relative abundance of the 10 most abundant taxa was compared in Figs. 2 and 3. Relative abundance of polychaetes was highest at stations 84-25 and 86-24, whereas it was lowest at station 86-25 demonstrating the high differences among nearby stations and the patchiness of the occurrence (Fig. 2). Amphipoda were most prevalent at station 81-17 and occurred with lowest relative abundance at station 86-25. Isopoda and Tanaidacea were relatively evenly distributed. The highest relative isopod abundance occurred at station 81-18 and lowest at station 86-20, highest relative tanaidacean abundance was observed at station

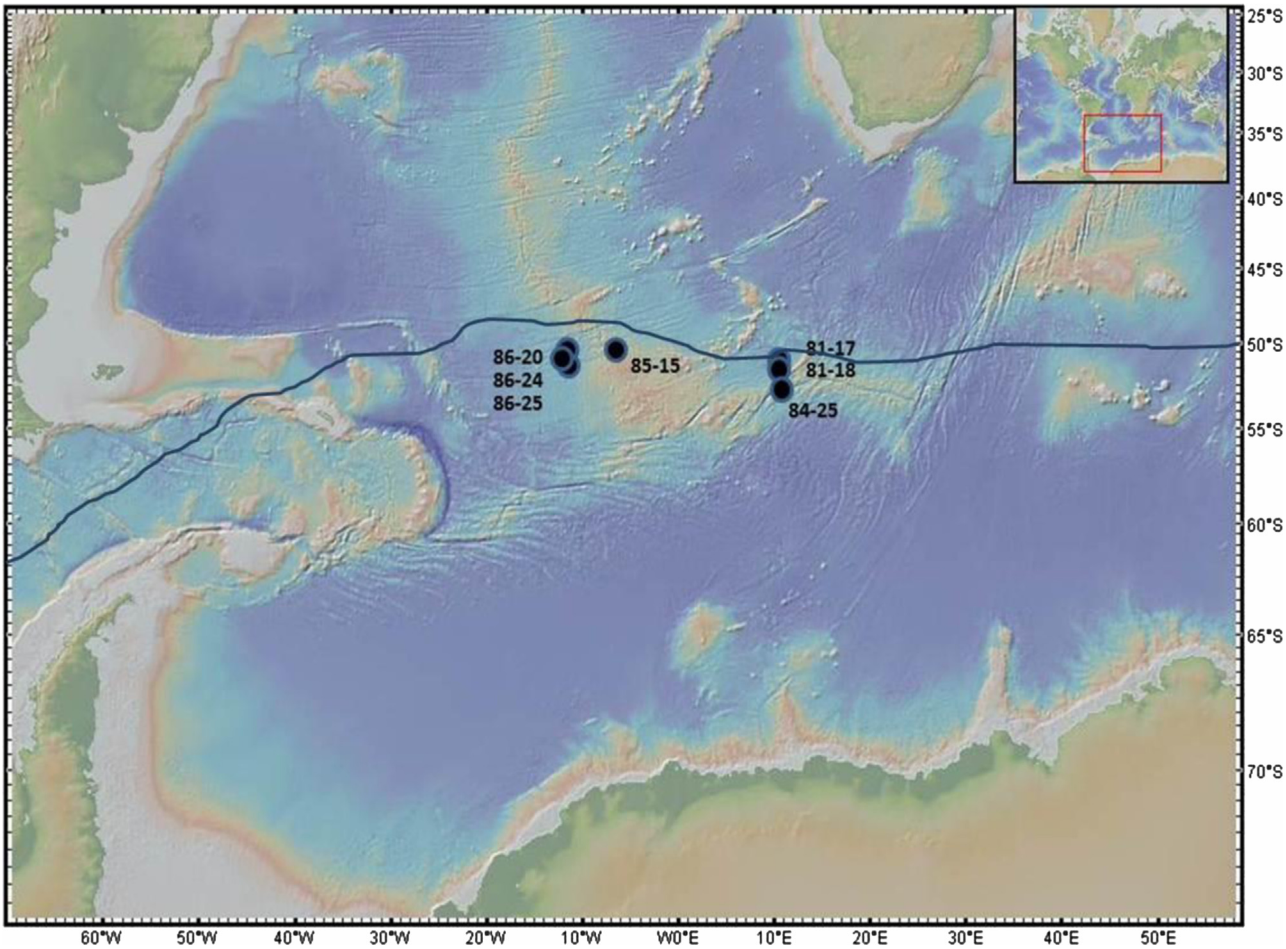

Fig. 1. Positions of the EBS stations in the SPF (Map source: GeoMapApp). The blue line represents the position of the SPF. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Station list of EBS samples from the expedition ANT-XXVIII/3.

Station	Date	Start	End	Depth (m)	Haul distance (m)
PS79/081-17	20.01.2012	52°0.18'S 10°0.72'E	51°59.61'S 9°59.10'E	3,744–3,763	3,926
PS79/081-18	20.01.2012	52°0.36'S 10°1.47'E	51°59.89'S 9°59.55'E	3,706–3,757	4,789
PS79/084-25	23.01.2012	53°0.89'S 10°3.55'E	53°0.22'S 10°2.12'E	4,327–4,046	4,525
PS79/085-15	27.01.2012	52°0.23'S 8°0.48'W	52°0.56'S 8°0.55'W	2,736–2,732	2,586
PS79/086-20	31.01.2012	51°59.83'S 12°3.17'W	51°59.58'S 12°4.13'W	3,935–3,959	4,442
PS79/086-24	01.02.2012	52°0.07'S 12°2.94'W	51°59.21'S 12°4.52'W	3,934–3,994	4,319
PS79/086-25	01.02.2012	52°0.49'S 12°2.05'W	51°59.31'S 12°3.70'W	3,936–3,945	4,503

86-20. Bivalves occurred with highest relative abundance at station 86-25 and were lowest abundant at station 85-15 (Fig. 2).

The analysis of relative abundance within the Peracarida (Fig. 4) documents that Isopoda occurred with the highest percentage (49%), followed by Amhipoda (23%), Tanaidacea (16%), Cumacea (11%) and Mysidacea (1%) (Table 1, Figs. 3 and 4). The relative abundance of Isopoda was highest at all stations, with an exception at station 86-20. The relative abundance of Amphipoda was second highest and showed its highest abundance at station 81-17, where also Mysidacea occurred with its highest relative abundance. Cumacea's relative abundance was high at stations 86-20, 86-24, and 86-25 and relative abundance of Tanaidacea was relatively constant at all stations (Fig. 4). Peracarida were most numerous at station 81-18, and almost as abundant at the stations 86-24 and 85-15. Their abundance was lowest at station 86-20, but it was also low at stations 87-17 and 86-25 (Fig. 3).

4. Discussion

Small macrofaunal organisms have been sampled successfully with the EBS in the recent decades, as it yields more organisms than other samplers, for example the box corer or multiple corer (Brandt, 1993, 1995; Brandt and Barthel, 1995; Brandt et al., 1998, 2004a, b, 2005, 2007a, b, c, 2012; Brenke, 2005; Brökeland et al., 2007; Linse et al., 2002). It has been shown that the faunistic composition between sampling gears can differ greatly, as observed for example for the composition of sponges (megafauna) (Janussen and Tendal, 2007). The tiny and light sponges, e.g. Cladorhizidae (notably *Asbestopluma* Topsent, 1901) and deep-sea Calcarea, are more likely taken by EBS than by larger bottom trawls like the Agassiz trawl, as the larger net size of the latter cannot prevent a wash-out of smaller organisms. Thus, for comparability of the data, only macrofaunal data obtained with this or rather similar and comparable EBS types are discussed in the following.

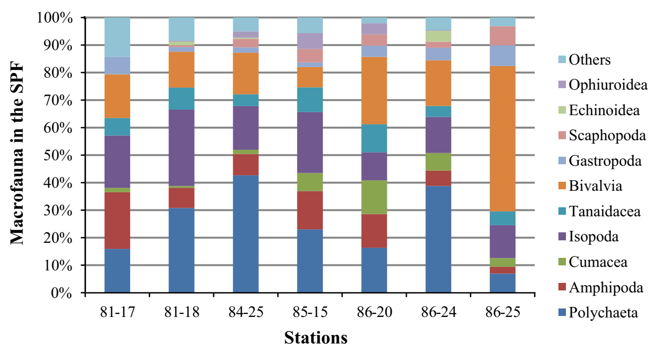

Fig. 2. Relative percentage of macrofauna of taxa in the SPF/1,000 m².

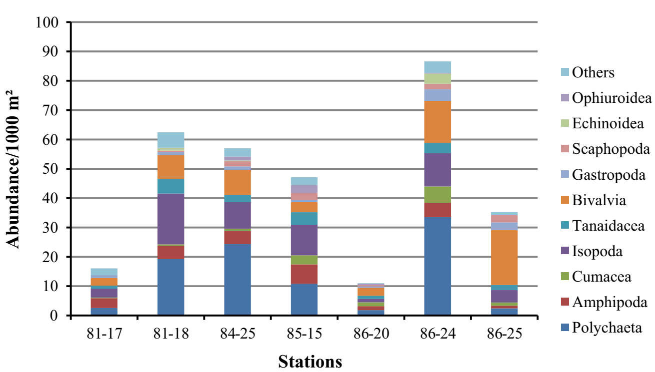

Fig. 3. Abundances of taxa in the SPF/1,000 m².

4.1. *Macrofaunal abundance and composition*

Generally, the macrofauna composition of the EBS catches found in this study is typical for abyssal regions with polychaetes, peracarid crustaceans and bivalve molluscs being the dominant groups (e.g. Brandt et al., 2004a, b, 2007a, b, c). As molluscs and the most abundant peracarid taxon, Isopoda, are outlined in detail in other publications of this volume (Jörger et al., 2014; Meyer-Löbbecke et al., 2014), we decided to only present some details on polychaete family composition at this point. The specimens which could be identified to date belong to 21 families (Table A1). Most abundant were the Ampharetidae, followed by the Syllidae, Paraonidae, and Spionidae.

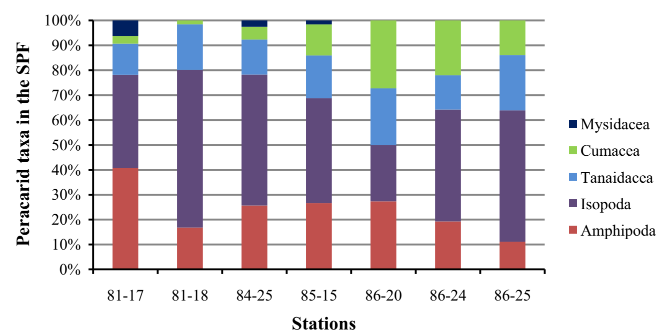

Fig. 4. Relative abundances of Peracarida in the SPF/1,000 m².

Table 2
Faunal composition supra- and epibenthic organisms of the epibenthic sledge catches.

Abundances/1,000 m²	Station	81-17	81-18	84-25	85-15	86-20	86-24	86-25
Phylum	Taxon							
Porifera		0.51	0	0.66	0.73	0	0.23	0
Cnidaria		0	0.21	0.44	0	0	0	0
Nemertini		0	0	0.22	0	0	0	0
Sipunculida		0	0	0.44	1.16	0	0.46	0.22
Annelida	Polychaeta	2.55	19.21	24.31	10.83	1.80	33.57	2.44
Crustacea	Copepoda	10.19	33.41	43.76	40.22	68.89	106.97	69.95
	Ostracoda	5.86	2.51	4.2	8.12	3.6	12.5	12.44
	Branchiopoda	0	0.21	0	0	0	0	0
	Phyllocarida	0.25	0	0	0	0.23	0.23	0.22
	Euphausiacea	0	0	0	0	0	0.23	0
	Mysidacea	0.51	0	0.44	0.39	0	0	0
	Amphipoda	3.31	4.59	4.42	6.574	1.35	4.86	0.89
	Cumacea	0.25	0.42	0.88	3.1	1.35	5.56	1.11
	Isopoda	3.05	17.33	9.06	10.44	1.12	11.34	4.21
	Tanaidacea	1.02	5.01	2.43	4.25	1.13	3.47	1.78
	Decapoda	0	4	0	0	0	0	0
Mollusca	Bivalvia	2.55	8.14	7.39	3.48	2.7	14.12	18.21
	Gastropoda	1.02	1.04	1.1	0.77	0.45	4.17	3.33
	Scaphopoda	0	0.42	1.77	2.32	0.45	1.85	2.66
	Solenogastres	0	0	0	0.39	0	0.23	0
	Caudofoveata	0.51	0.21	0	0	0	0.23	0.44
Bryozoa		0	0.42	0	0	0	0	0
Chaetognatha		0.51	0	0.44	0	0	1.62	0
Chordata	Ascidia	0	0.21	0.22	0	0	0.23	0
Echinodermata	Asteroidea	0	0	0	0	0	0.46	0.22
	Echinoidea	0	0.84	0.22	0	0	3.47	0
	Ophiuroidea	0	0.21	1.33	2.71	0.45	0.23	0
	Total	32.09	98.38	104.97	95.48	83.51	206.09	116.12

All of these families were frequently found to be abundant in the Southern Ocean (Hilbig, 2001; Brandt et al., 2007b, 2009, Schüller et al., 2009).

The composition, abundance and diversity of peracarid crustaceans in the North Atlantic has been examined north of Iceland at the Kolbeinsey Ridge (RV *Meteor*) as well as off East Greenland (RV *Polarstern*) by means of the same type of EBS (Brandt 1993, 1995, 1997a, b; Brandt and Piepenburg, 1994; Brandt et al., 1996; Vassilenko and Brandt, 1996). North of Iceland, Amphipoda and Isopoda were most abundant and diverse, followed by Tanaidacea and Cumacea. Amphipoda were prevalent at the shallower stations down to 500 m and preferred coarse sediment, while Isopoda and Cumacea increased in abundance and diversity with depth and with the occurrence of fine and silty sediment. A very similar pattern was observed at shallow stations in the North East Water polynya (NEW) off East Greenland, where Amphipoda occurred with the highest abundance at almost all stations. At the deepest station in 500 m, however, Isopoda became dominant (Piepenburg et al., 1997). Concerning the peracarid composition the Southern Ocean, Amphipoda have been found to also be dominant in the Ross Sea at most stations (Rehm et al., 2012), followed by Isopoda. However, at some stations Isopoda were slightly more abundant (Lörz et al., 2013). The findings are indicating a relatively high proportion of Amphipoda in samples below 2,000 m the Southern Ocean seem to be a peculiarity of the Southern Ocean deep sea, in contrast with the general decrease of abundance of Amphipoda with increasing depth (Dahl, 1954). Even at the deeper stations (between 4,001 and 5,000 m) abundances were higher (19%) than in the Angola basin (Brandt et al., 2005). This is probably a result of the tremendous evolutionary and ecological success of Amphipoda on the Antarctic shelf (Arntz et al., 1994; De Broyer and Jazdzewski, 1996; De Broyer et al., 2003), the lack of a thermocline and the deep shelf, favouring species submergence. Amphipoda appeared to be the most abundant peracarid taxon in most studies on the Antarctic shelf (Brandt, 2001; Rehm et al., 2006, 2007). Brökeland et al. (2007) observed a very similar pattern in the Southern Ocean deep sea with Amphipoda being most abundant down to 4,000 m but Isopoda becoming most abundant between 4,000 and 5,000 m. In the Angola basin $>$5,000 m depth, abundances of Isopoda were highest followed by Cumacea and Amphipoda (Brandt et al., 2005). Also in the current study Isopoda were found being the dominant group above amphipods. However, overall macrofaunal composition differs for example from data of the Ross Sea shelf where echinoderms were by far the most abundant taxon (Echinodermata (39%), Arthropoda (24%), Polychaeta (14%), and Mollusca (12%); Rehm et al., 2012).

4.2. Low SPF macrofaunal abundances

Compared to many sampling campaigns deploying comparable gear, the specimen numbers found in our study appear to be surprisingly low. The general rule that abundance decreases with depth proves true for most macrobenthic taxa (Dahl, 1954; Gage and Tyler, 1991; Hessler and Sanders, 1967). Accordingly, the overall abundance of macrobenthic taxa is rather low within the investigated area of the SPF (Fig. 1), as usually expected for deep-sea basins. However, based on the previously observed high abundances in the southern Weddell Sea we expected to find higher numbers of organisms SPF. Collaterally, abundances of meiofauna and megafauna from MUC and AGT samples were also low at these stations (Brandt et al., 2014; Lins et al., 2014; Würzberg et al., 2014).

In detail, the overall abundances of molluscs at all stations of the present study were comparably low. Highest and lowest overall abundances occurred among the different hauls of station 86 (3.60 ind./1,000 m² at 86-20; 24.65 ind./1,000 m² at 86-25), underscoring the notorious patchiness of abyssal molluscs reported previously (Schwabe et al., 2007; Schrödl et al., 2011). In the Beagle Channel from the shelf down to the deep sea in 665 m, Mollusca occurred with 35,087 specimens (equivalent to 107,223 ind./1,000 m²). Here Bivalvia were the most abundant Mollusca with 78,615 individuals followed by Gastropoda (17,289), Aplacophora (4,745), Polyplacophora (4,665) and Scaphopoda (1,909) (Brandt et al., 1997c, 1999; Linse and Brandt, 1998). If we consider only the deep-sea station at 665 m, we found an abundance of 21,244 molluscs of which bivalves comprised 17,605 individuals (Linse and Brandt, 1998). Compared to this, the abundances of molluscs were rather low in the present study with 3.60–24.65 ind./1,000 m² (Table 1). In case of abyssal gastropods, however, the present values exceed those of the EBS catches from the Guinea and Angola basin, ranging among those of the Cape basin most stations (i.e., 81, 84 and 85), while those of station 86 (when pooled between hauls) even reach those of high Antarctic stations (see Schrödl et al., 2011; Jörger et al., 2014). In case of polychaetes, a total of 404 individuals were found at all stations sampled (seven EBS casts). These are rather low numbers compared e.g. with EBS samples from the deep Weddell Sea during the ANDEEP expeditions, where up to over 4000 polychaete specimens were sampled in one EBS cast. However, already during the ANDEEP expeditions two stations located north of and within the SPF also yielded comparably low individual numbers (Schüller et al., 2009).

Also peracarids sampled in the deep sea off Greenland (79°N) showed considerably higher abundances; Cumacea occurred with 32,123 ind./1,000 m², followed by Isopoda with 26,914 ind./1,000 m² and Amphipoda with 20,900 ind./1,000 m² (Brandt and Schnack, 1999). However, these samples are from shallower deep-sea stations from the European Northern Seas. The North Atlantic is much younger than the South Atlantic, thus the European Northern Seas are characterized by high abundances and low species richness (e.g. Brandt, 1993, Brandt et al., 1996). First investigations with an EBS in the Southern Ocean eastern Weddell Sea revealed great differences in peracarid abundances and species richness between the Arctic and Antarctic deep sea (Brandt, 2001), potentially resulting from the different age of the ecosystems and thus the time available for evolution. Abundance of peracarids was lower in the Weddell Sea than in the Arctic off Greenland, but numbers of species were higher in the South Atlantic.

In the southern hemisphere, abundance of peracarid taxa in the Beagle Channel at stations between 25 and 663 m depth yielded 104,618 peracarid individuals (equivalent to 55,633 ind./1,000 m²), comprising/1,000 m²: 15,025 Amphipoda, 28,650 Isopoda, 7,868 Cumacea, 1,636 Mysidacea and 2,454 Tanaidacea (Brandt et al., 1997c; 1998). At abyssal depths (5,125–5,415 m) of the Angola basin, the picture looked different again with Isopoda being most abundant (1,326 ind./1,000 m²), followed by Tanaidacea (194 ind./1,000 m²), Cumacea (479 ind./1,000 m²), Amhipoda (150 ind./1,000 m²) and Mysidacea (34 ind./1,000 m²) (Brandt et al., 2005). Also abundance data from abyssal samples taken in the framework of the ANDEEP expeditions by means of the EBS were magnitudes higher in the abyssal Weddell Sea than the abundances reported from the SPF in the present investigation. Within Peracarida, a total of only 476 specimens of Isopoda have been sampled at seven stations in the SPF during the present study, whereas during the ANDEEP expeditions 13,046 isopod individuals were sampled/1,000 m² (Brandt et al., 2007a, b, c). If we compare numbers of peracarids from our samples with those from ANDEEP, these are also generally lower (Brökeland et al., 2007). For example, in the Powell Basin alone we have sampled at a single EBS station 10,735 peracarids, compared to the small number of specimens (Table 2) of Crustaceans at all seven EBS hauls sampled in the SPF. However, macrofaunal numbers were also comparatively low in the samples from the SYSTCO I expedition in 2008 (Brandt et al., 2011, electronic supplement; Meyer-Löbbecke et al., 2014), indicating that our results are not an annual exception.

In this study ~29 km² of seafloor were sampled and yielded a very low number of invertebrates, as also reported during SYSTCO I in 2008 (Meyer-Löbbecke et al., 2014). The extremely low numbers of specimens observed in the present study might either reflect the truly poor benthic fauna along the South Polar Front or present a sampling artefact caused by incomplete sampling of the EBS over the entire distance. However, in case of gastropods, specimen numbers partly exceeded those found in other deep-sea regions. Furthermore, the presence of benthic fauna in the cod ends confirms that the gear was successfully lowered to the seafloor. Hence, a malfunction of the EBS is considered unlikely, particularly as the gear was deployed in the usual sampling routine successfully undertaken in several previous studies (e.g. Brandt, 1993, 1995, 1997a, b, 2001; Brandt and Barthel, 1995; Brandt et al., 1997, 1999, 2004a, b, 2007a, b, c, 2009, 2011; Brenke 2005; Brökeland et al., 2007, and many more). This type of an EBS has always been deployed in a standardized manner at bathyal and abyssal depths for more than 20 years and due to its opening and closing device no pelagic fauna is collected, the samplers were always closed and never blocked due to stones during the present investigation. Analyses of independent gear from the same stations (AGT and quantitative MUC samples) show similar low species densities and support our conclusions based on EBS hauls (Würzberg et al., 2014; Lins et al., 2014).

We hypothesized to find high numbers of macrobenthic specimens within the SPF, due to the high productivity within the research area. Abundance and composition of for example Arctic benthos have been shown to be largely influenced by mesoscale pelagic processes, which provide evidence for the importance of pelagic-benthic coupling at high latitude seas (Piepenburg et al., 1997). We therefore also expected high abundances at our sampling sites along the SPF. Nevertheless, these were magnitudes lower than those reported in the North Atlantic (Table 2). It is striking that in the SPF the numbers of macrobenthos are much lower than further south (e.g. Arntz et al., 1994; Brandt et al., 2007b, c; Kaiser et al., 2013) despite the high pelagic productivity in this area (Wolf-Gladrow, 2013). One reason could be the influence of pelagic activity, strictly speaking recycling processes throughout the water column, preventing the organic matter from reaching the seafloor (e.g. Delille, 2004). For example, high ratios of biogenic silica to organic carbon (Si:C) in sinking particles might reduce vertical POC fluxes and thus food supply for benthic organisms (Assmy et al., 2013). Alternative scenarios could simply be the influence of strong currents (Rintoul et al., 2001) and the horizontal transport of organic matter through lateral advection (e.g. Tesi et al., 2011; Langone et al., 2012). Contrary to the Arctic Ocean, where the benthos is largely positively influenced by pelagic processes (Piepenburg et al., 1997), bentho-pelagic coupling could not be confirmed at the stations sampled with the EBS in the SPF (Brandt et al., 2014) and our hypothesis to find high abundances of macrobenthic organisms in the SPF has to be rejected.

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Appendix A

See Table A1.

Table A1
Polychaete families and specimen numbers at four areas sampled with the EBS.

	PS79/81	PS79/84	PS79/85	PS79/86	Sum
Ampharetidae	18	14	1	15	48
Amphinomidae	2	0	0	0	2
Capitellidae	2	0	0	3	5
Cirratulidae	3	2	0	4	9
Flabelligeridae	2	1	2	2	7
Glyceridae	2	0	2	3	7
Lumbrineridae	1	8	0	7	16
Maldanidae	1	0	0	4	5
Nephtyidae	5	4	1	1	11
cf. Nereididae	0	0	0	1	1
Opheliidae	6	0	2	6	14
Orbiniidae	3	1	0	3	7
Paraonidae	4	8	6	13	31
Phyllodocidae	3	1	1	1	6
Polynoidae	0	0	5	6	11
Scalibregmatidae	1	1	0	3	5
Sphaerodoridae	2	0	0	2	4
Spionidae	6	8	0	17	31
Syllida	9	8	0	20	37
Terebellidae	3	2	0	0	5
Travisiidae	0	0	0	1	1
Indet.	26	51	12	52	141
Sum	**99**	**109**	**32**	**164**	**404**

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