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Are boundary conditions in surface productivity at the Southern Polar Front reflected in benthic activity?

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ABSTRACT

In austral summer 2012, during the expedition ANT-XXVIII/3 on board RV *Polarstern*, two sites were sampled 1600 km apart in the South Polar Front area (52°S) at the boundary of different productivity regimes for meio- and macrobenthos using a multiple-corer and an epibenthic sledge, respectively. Patterns in density and abundance data were compared between different size classes of the benthos and interpreted in relation to surface primary productivity data and sediment oxygen consumption. We tested the hypothesis that long-term satellite-derived surface phytoplankton biomass, in situ real time biomass, and productivity measurements at the surface and throughout the euphotic zone are reflected in abyssal benthos densities, abundances and activity. Specifically, we investigated the effect of boundary conditions for lower and higher surface productivity. Surface and integrated to 100 m depth biomass and primary productivity measurements vary stations, with the lowest values at station 85 (0.083 mg Chl-*a* m^{-3} at surface, 9 mg Chl-*a* m^{-2} and 161 mg C m^{-2} d^{-1-} integrated over the first 100 m depth), and the highest values at station 86 (2.231 mg Chl-*a* m^{-3} at surface, 180 mg Chl-*a* m^{-2} and 2587 mg C m^{-2} d^{-1} integrated over first 100 m depth). Total meiofaunal densities varied between 102 and 335 individuals/10 cm^2. Densities were the highest at station 86-30 (335 individuals) and lowest at station 81-13 (102 individuals). Total macrofaunal densities (individuals/1000 m^2) varied between 26 individuals at station 81-17 and 194 individuals at station 86-24. However, three EBS hauls were taken at station 86 with a minimum of 80 and a maximum of 194 individuals. Sediment oxygen consumption did not vary significantly between stations from east to west. Bentho-pelagic coupling of meio- and macrobenthic communities could not be observed in the South Polar Front at the boundary conditions from low to high surface productivity between stations 81 and 86.

1. Introduction

Seasonal productivity influences benthic species composition and life cycles (e.g. Abem et al., 1997; Brandt, 1995, 1996, 1997; Gaston and Blackburn, 2000; Ormond et al., 1997), but can also influence species' reproductive pattern in the deep sea, as documented in the North Atlantic (Brandt et al., 1994). These processes also imply responses of the benthos to fluctuations in the food supply (Gooday and Thurley, 1990). Graf (1989, 1992) published the first evidence of a deep-sea benthic community response to a pulse of natural organic matter, which occurred in less than eight days and down to nine cm in the sediment. Later, the importance of biologically mediated fluxes from the benthic nepheloid layer across the sediment–water interface into the sediment and vice versa was underpinned, and it was described how changes of the physical properties of the sediment (e.g., tubes, pits, burrows) influence hydrodynamic conditions and processes such as bioresuspension and biodeposition (Graf and Rosenberg, 1997). Moreover, sediment topography influence interfacial flows which are important for the uptake of particulate organic matter into permeable shelf sediments (Huettel et al., 1996). Piepenburg et al. (1997) uncovered that benthic community pattern in the Northeast Water polynya (Greenland) reflects water column processes. These authors explained that the profound impact of water column processes on the benthos in this area is influenced by many factors, including microbial activity, total phytoplankton production, zooplankton grazing and lateral advection.

These results were obtained in upper bathyal water depths, while, roughly 70% of the Earth's surface is abyssal seafloor ≥4000 m depth (Gage and Tyler, 1991). Phytodetritus is one of

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the major food sources for abyssal benthic communities which can also arrive in pulses within a few days (Billett et al., 1983; Graf, 1989; Lampitt, 1985).

Witte et al. (2003a) performed an in situ experiment and quantified the abyssal benthic community response to a phytodetritus pulse over a period of 2.5–23 days. In contrast to previous publications (e.g. Graf, 1989; Smith and Baldwin, 1984; Smith and Kaufmann, 1999), Witte et al. (2003a, 2003b) could demonstrate that the sediment community oxygen consumption doubled immediately and that the macrofauna was most important for initial carbon degradation, while responses of bacteria and foraminiferans occurred retardedly. Tracer experiments with ^{13}C-labeled diatoms (*Thalassiosira rotula* Meunier, 1910) in the Porcupine Abyssal Plain underpinned the fast response of the macrofauna, as only after 2.5 days, 77% of the macrofauna displayed tracer uptake (Aberle and Witte, 2003). The response of the metazoan meiofauna to pulses of phytodetritus is often less obvious and in several cases limited to shifts in vertical distributions rather than variation in total density or biomass (Galéron et al., 2001; Guilini et al., 2011, 2013).

The Southern Ocean is the largest water mass on Earth. It is the central connection between Atlantic, Pacific and Indian ocean basins as well as between upper and lower layers of the global ocean circulation (Meredith et al., 2013; Rintoul et al., 2001, 2012; Van Sebille et al., 2013). Carbon fixation, through phytoplankton and the subsequent pathways of the "biological pump" (grazing, export into deep-water layers, sedimentation to the sea floor) (e.g. Longhurst and Harrison, 1989), represents one of the major CO_2 sinks on Earth (Falkowski et al., 2000) and is the primary energy source for abyssal life (e.g. Smith et al., 2008). However, it is almost unknown whether the benthos shows a clear reaction to primary productivity processes at the surface of the ocean, as reported for the initial processing of fresh phytoplankton from the water column through the macrofauna (as explained above, Witte et al., 2003a, 2003b).

In the framework of three ANDEEP (ANtarctic benthic DEEP-sea biodiversity: colonization history and recent community patterns) expeditions to the southern ocean, deep sea high biodiversity and distinct patterns of species richness and distribution within meio-, macro and megafauna (Brandt et al., 2007a, 2007b, 2007c, 2009, 2012) have been revealed depending on taxon and reproductive mode. On the background of this baseline project, SYSTCO (SYSTem COupling) project was designed to investigate the processes that drive the pattern observed. Research questions of SYSTCO included the investigation of the trophic structure and functioning of abyssal communities. The first SYSTCO I expedition on board of research vessel *Polarstern* took place in 2008/2009 (ANT-XXIV/2) (Brandt and Ebbe, 2011). During this expedition, a reaction of southern ocean deep-sea bacteria and meiofauna to the deposition of particulate organic matter could be observed after a phytoplankton bloom (Veit-Köhler et al., 2011). For the seamount Maud Rise it could be demonstrated that "downward transport of the organic matter produced in the pelagic realm may be more constant than elsewhere due to low lateral drift over the seamount" (Brandt et al., 2011: 1962) and that the biological prosperity can be related to both oceanographic and sea-ice processes in this area.

Based on our present knowledge on bentho-pelagic coupling processes in the southern ocean, we wanted to test whether meio- and macrofaunal organisms reflect primary productivity further north in the south polar front (SPF), where phytoplankton blooms occur frequently during austral summer (e.g. Bracher et al., 1999; Moore and Abbott, 2000; Arrigo et al., 2008). To this end, two areas in the SPF at roughly 52°S 10°E (stations 81 and 84) and 52°S 12°W (stations 85 and 86) (Fig. 1) were compared with regard to surface phytoplankton biomass (Chl-*a* conc.) and productivity, meiofaunal and macrofaunal densities and sediment properties. Almost all stations were abyssal stations (with the exception of the lower bathyal station 85-15 at 2752 m depth) and ranged between 2570 and 4320 m depth. We focused this comparison on the area characterized by the strongest spatial shifts from high to low surface productivity, hypothesizing that vertical transport of particulate organic carbon (POC) would reflect in similar patterns in different size fractions of the benthos.

2. Material and methods

Data and specimens were collected during the SYSTCO II (SYSTem COupling) expedition (ANT-XXVIII/3) with RV *Polarstern* in the South Atlantic during the austral summer between 7 January and 11 March of 2012 (Fig. 1; Tables 1–4, Wolf-Gladrow, 2013).

2.1. Primary productivity

Water samples were obtained from Niskin bottles attached to the conductivity temperature depth (CTD) rosette at different depths (10, 20, 40, 60, 80 and 100 m) from six stations. Net primary production (NPP) rates were determined in duplicate by the incubation of 20 mL seawater sample spiked with 20 μCi $NaH^{14}CO_3$ (53.1 mCi mmol^{-1}; Perkin-Elmer) in a 20 mL glass scintillation vial for 24 h in a seawater cooled on-deck incubator. Seawater samples were incubated at different irradiances for 24 h on-deck. Irradiance levels were achieved with neutral density filters decreasing incoming photosynthetic active radiation (PAR) to 25%, 12.5%, 6.3%, 3.1%, 1.6% and 0.8%.

After the addition of the $NaH^{14}CO_3$ spike, 0.1 mL aliquots were immediately removed and mixed with 10 mL of scintillation cocktail (Ultima Gold AB, PerkinElmer). After 2 h, these samples were counted with a liquid scintillation counter (Tri-Carb 2900TR, Perkin-Elmer) to determine the total amount of added $NaH^{14}CO_3$ (100%). For blank determination, one additional replicate per sample was immediately acidified with 0.5 mL 6 N HCl. After the outdoor incubation of the samples over 24 h, ^{14}C incorporation was stopped by adding 0.5 mL 6 N HCl to each vial. The vials were then left to degas overnight, thereafter 15 mL of scintillation cocktail (Ultima Gold AB) was added and samples were measured after 2 h with the same liquid scintillation counter. NPP rates [mg C m^{-3} d^{-1}] at each sample depth were calculated as follows:

$$\mathrm{NPP}\left[\mathrm{mg\ C\ m^{-3}d^{-1}}\right] = \left(\mathrm{DIC}\left(\mathrm{DPM}_{sample}-\mathrm{DPM}_{blank}\right)1.05\right)/\mathrm{DPM}_{100\%}t$$

where DIC is the concentration of dissolved inorganic carbon [μmol kg^{-1}], t is the incubation time [h], DPM_{blank}, DPM_{sample} and $DPM_{100\%}$ are the disintegration per minute measured by the scintillation counter for the blank, the sample and the determination of the total amount of added $NaH^{14}CO_3$, respectively. Column-integrated NPP [mg C m^{-2} d^{-1}] were derived by integrating values for 100 m depth.

2.2. Phytoplankton biomass

Water samples for pigment analysis were collected from CTD Niskin bottles at the same depths as for the primary production measurements. Samples were filtered with 25 mm diameter GF/F filters, shock-frozen in liquid nitrogen and stored at −80 °C for later analysis at the laboratory in Germany. The pigments were analyzed using the high performance liquid chromatography (HPLC) technique, following the method Barlow et al. (1997) modified by Hoffmann et al. (2006) and adjusted to our instruments as presented in Taylor et al. (2011). We determined the total chlorophyll-*a* concentration (Chl-*a*) taking the sum of concentrations of monovinyl- and divinyl

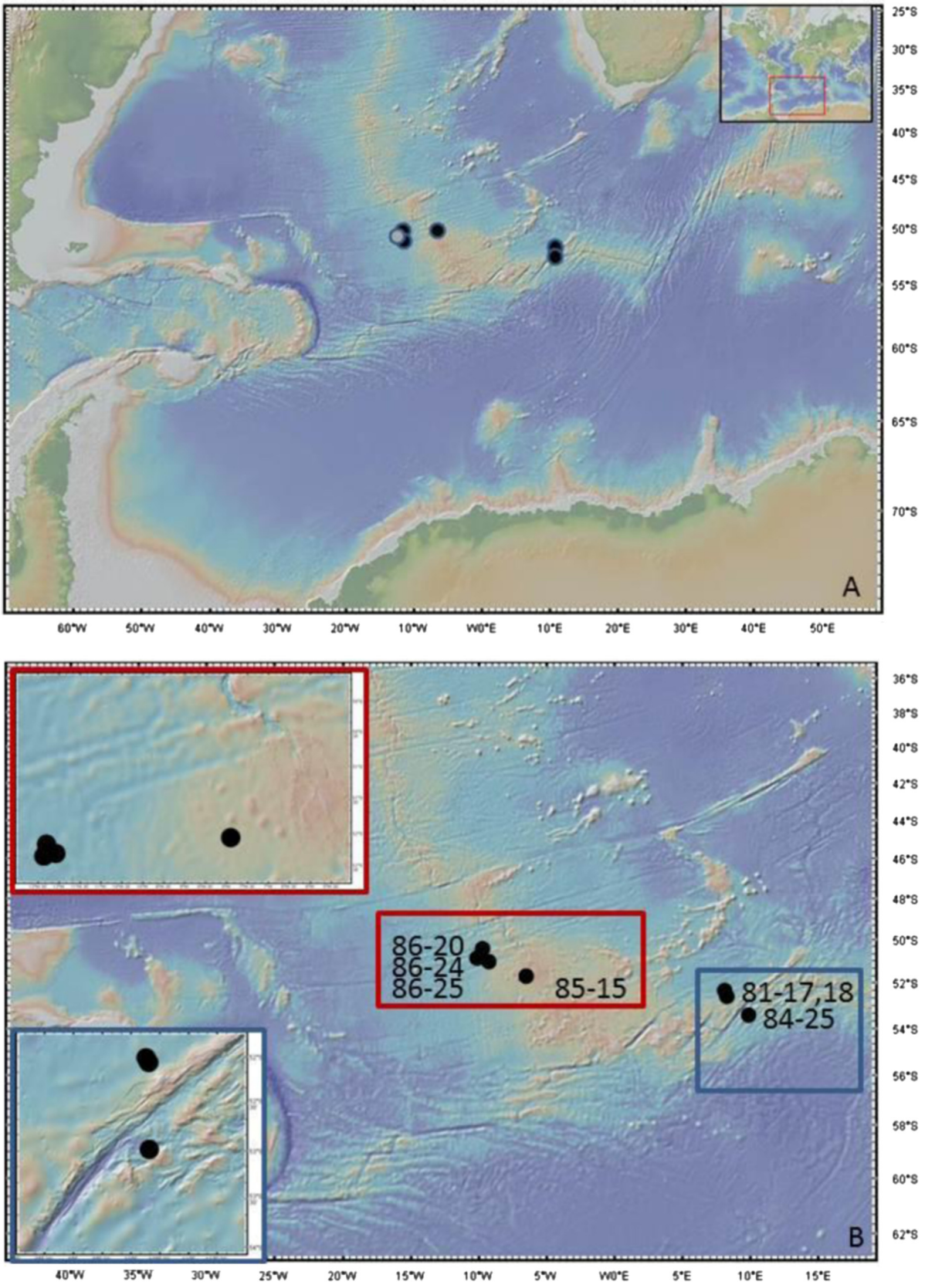

Fig. 1. Location of stations sampled in the southern Polar Front during SYSTCO II cruise. Replicate stations were taken roughly at 52°S 10°E (station 81) and 52°S 12°W (station 86). (A) Overview of the area sampled in the South Atlantic and (B) station numbers and enlarged topography (red and blue frames represent enlarged stations) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

Table 1
100 m-integrated net primary production (NPP [mg C m^{-2} d^{-1}]) and Chl-*a* (surface [mg Chl-*a* m^{-3}] and integrated for 100 m [mg Chl-*a* m^{-2} d^{-1}]) as well as 1-year and 3-year averaged GlobColour satellite-based surface layer Chl-*a* estimates [mg Chl-*a* m^{-3}] for sampled stations in the southern Polar Front during SYSTCO II cruise.

Station	81-11	84-17	85-3	86-2	141	175*
Surface mg Chl *a* m^{-3}	0.531	0.326	0.083	2.231	1.148	2.086
100 m integrated mg Chl *a* m^{-2}	55	29	9	180	187	100
100 m integrated net primary productivity [mg C m^{-2} d^{-1}]	791	1.023	161	2.587	–	1.575
1 year average Chl *a* (mg/m^3) from GlobColour	0.236	0.366	0.163	0.270	0.396	1.228
3 years average Chl *a* (mg/m^3) from GlobColour	0.231	0.261	0.260	0.444	0.445	1.113

–: Data not available.
* Samples were taken with the MUC, but not with EBS which was lost at station 141-4.

Table 2
EBS data (macrofaunal densities per 1000 m²/station).

Station no. EBS	Date	Latitude	Longitude	Depth (m)	Haul length (m)	Total macrofauna
81-17	20.01.2012	52°00.18′ S	010°00.72′ E	3744	3926	26
81-18	20.01.2012	52°00.36′ S	010°01.47′ E	3706	4789	96
84-25	23.01.2012	53°00.89′ S	010°03.55′ E	4327	4525	101
85-15	27.01.2012	51°59.88′ S	007°59.73′ W	2752	2586	87
86-20	31.01.2012	51°59.83′ S	012°03.17′ W	3935	4442	80
86-24	01.02.2012	52°00.07′ S	012°02.94′ W	3934	4319	194
86-25	01.02.2012	52°00.49′ S	012°02.05′ W	3936	4503	105
141-4	17.02.2012	51°11.97′ S	012°37.06′ W	3913	EBS lost	–

Table 3
MUC data (meiofaunal densities per 10 cm²/station).

Station no. MUC	Date	Latitude	Longitude	Depth (m)	Total meiofauna
PS79/081-08	19.01.2012	51° 59.99′ S	09° 59.99′ E	3761	209
PS79/081-09	19.01.2012	52° 00.01′ S	10° 00.05′ E	3761	271
PS79/081-12	19.01.2012	51° 59.93′ S	10° 00.06′ E	3758	295
PS79/081-13	19.01.2012	52° 0.042′ S	09° 59.90′ E	3761	102
PS79/084-24	23.01.2012	53° 00.67′ S	10° 03.00′ E	4320	–
PS79/085-14	27.01.2012	51° 59.98′ S	07° 59.99′ W	2749	–
PS79/086-26	01.02.2012	51° 58.87′ S	12° 03.76′ W	3966	335
PS79/086-28	01.02.2012	51° 58.74′ S	12° 02.11′ W	3968	141
PS79/086-29	01.02.2012	51° 58.78′ S	12° 01.95′ W	3971	260
PS79/086-30	01.02.2012	51° 58.91′ S	12° 02.16′ W	3965	319

chlorophyll-*a* and chlorophyllide-*a* (divinyl chlorophyll-*a* was not detected in our samples). We derived surface Chl-*a* [mg Chl-*a* m^{-3}] from the 10 m depth samples and column-integrated Chl-*a* [mg Chl-*a* m^{-2}] by integrating values for 100 m depth.We derived maps showing the average Chl-*a* for January and February 2012 from the POLYMER level-3 product of the Medium Resolution Imaging Spectrometer (MERIS) data at 0.02° spatial resolution (Steinmetz et al., 2011). POLYMER is an atmospheric correction algorithm developed to improve pixels contaminated by sun glint, thin clouds or heavy aerosol plumes, providing much better spatial coverage than operational data products. The Chl-*a* concentration is derived using the standard OC4Me algorithm (Morel et al., 2007) (Figs. 2A and 3). We also assessed the mean, median and standard deviation of Chl-*a* for the year (2011) and for the three years (2009–2011) before the cruise for the grid point of each station from the merged daily Full Product Set of the GlobColour Archive (http://hermes.acri.fr). This level-3 Chl-a data set is gridded at 4.6 km resolution.

2.3. Meiofaunal and macrofaunal samples

Samples for meiofauna were obtained using a multiple-corer (MUC) (Eleftheriou, 2013), while samples for macrofauna by means of an epibenthic sledge (EBS) (after Brandt and Barthel, 1995; Brenke, 2005; Rothlisberg and Pearcy, 1977) at depths from 2570 to 4320 m. Stations were located at the South Polar Front (SPF). The EBS was successfully deployed at seven stations before it got unfortunately lost in a submarine crevice at station 141-4 (Table 2). At all deep benthic stations (ten MUC and seven EBS hauls), and for each MUC deployment, two cores were selected for meiofaunal analyses (Table 3). The cores were sliced in slices of 1 cm for the first 5 cm's. All separate sediment slices were stored in 4–7% buffered formalin until further analysis. Organisms were later sorted and counted on major taxon level following Higgins and Thiel (1988) at the laboratory of the Marine Biology Research Group of Ghent University. In the present analysis, however, total meiofaunal density from MUC cores was used. Density was expressed as number of individuals per 10 cm^2.

The EBS consists of a supra- and epibenthic net equipped with cod ends of 300 μm. The haul distances were calculated from the time the sledge traveled on the ground until to the moment when it had left the ground, which was indicated by the tension meter. Haul lengths varied from 2586 m to 4789 m; for the comparative analysis between sampling stations the data were therefore standardized to 1000 m hauls, equivalent to a bottom area of 1000 m² sampled by the sledge (according to Brenke, 2005; Brandt et al., 2007c). In total, 29,090 m² 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.

Table 4
Main sediment characteristic of the stations sampled during SYSTCO II cruise in the southern Polar Front (Meyer-Löbbecke, 2013). SOC: μM O_2 m^2 d^{-1}. SOC=sediment oxygen consumption (all gear have different station-haul numbers, therefore station 86-20 equals 86-26, 81-18 equals 81-13 and 81-17 equals 81-8).

Station	86-20	85-15	84-25	81-18	81-17
SOC (μM O_2 m^2d^{-1})	373.5 ± 216.5	276.5 ± 187.3	209.2 ± 134.9	395.95 ± 243.2	395.95 ± 243.2
Silt-clay	91.53	–	–	92.207	91.992
Very fine sand	8.47	–	–	7.793	7.996
Fine sand	–	–	–	–	0.012

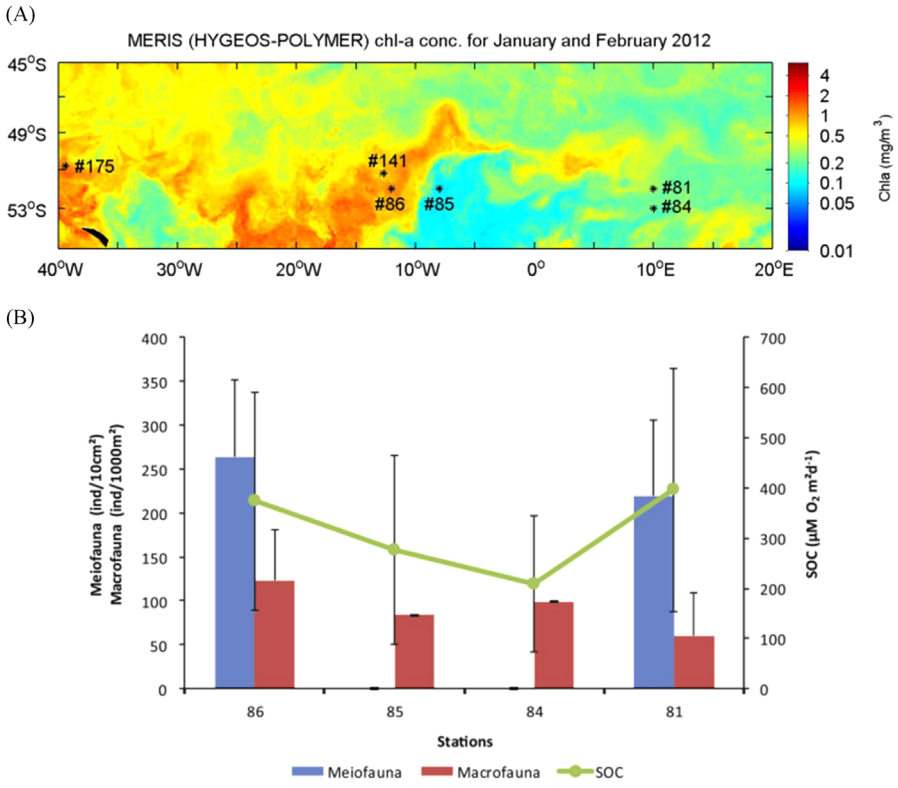

Fig. 2. (A) Sampling stations positions plotted on top of the average Chl-*a* conc. for January and February 2012 derived from the polymer product using satellite observations from MERIS. (B) Meiofaunal densities (ind./10 cm²; mean surface values), macrofaunal densities (ind./1000 m) and sediment oxygen consumption at stations in the SPF.

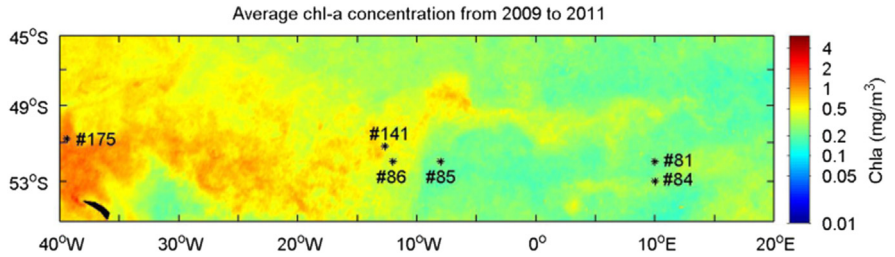

Fig. 3. Sampling stations plotted on top of the mean Chl-*a* conc. in the surface layer for 2009–2011 derived from the merged SeaWifS, MERIS and MODIS GlobColour data set.

2.4. Sediment analyses

Sediment cores were collected using a MUC. Undisturbed cores were selected for oxygen micro profiles at temperature control laboratory (2–3 °C). Two sediment cores were analyzed for oxygen (six microprofiles per core) using UNISENSE electrodes. The microprofiles were done at 200 μm intervals. Sediment oxygen consumption (SOC) values reflect the oxygen consumption by bacteria, protists and the fauna (Table 4). Once the profiles were performed, each sediment core was sectioned every 5 mm down to 1 cm and thereafter every 10 mm until the bottom of the sediment core is reached. Grain size distribution per core (each core sectioned per cm down to 5 cm) was measured using a Malvern Mastersizer 2000 (0.02–2000 μm size range).

3. Results

3.1. Surface productivity measures

Surface and integrated to 100 m depth biomass and primary productivity measurements (Table 1) show similar patterns for the

stations, with the lowest values at station 85 (0.083 mg Chl-*a* m^{-3} at surface, 9 mg Chl-*a* m^{-2} and 161 mg C m^{-2} d^{-1-} integrated over the first 100 m depth), and the highest values at station 86 (2.231 mg Chl-*a* m^{-3} at surface, 180 mg Chl-*a* m^{-2} and 2587 mg C m^{-2} d^{-1}). Estimates from the eastern stations (stations 81, 84 and 85) were generally lower than those further west (stations 86) (Lins et al., 2014).

GlobColour satellite data integrated over the year 2011 revealed the highest estimates for mean Chl-*a* concentrations above the station 84 (0.366 mg Chl-*a* m^{-3}), followed by station 86 (0.270 mg Chl-*a* m^{-3}), station 81 (0.236 mg Chl-*a* m^{-3}) and station 85 (0.163 mg Chl-*a* m^{-3}), see Table 1. Differences were more pronounced when GlobColour satellite data were integrated over 3 years, then values at stations 81, 84 and 85 were much lower (with 0.231, 0.261 and 0.260 mg Chl-*a* m^{-3}, respectively) than at station 86 (0.444 mg Chl-*a* m^{-3}) (Table 1 and Fig. 3). The same trends were seen for the median data (data not shown). However, differences between stations were not significant. One has to keep in mind that according to Gordon and McCluney (1975) the satellite ocean color sensors provide only information on the average Chl-*a* within about the first penetration depth, i.e. the depth to which 90% of the water leaving radiance has penetrated to (in our area probably between 5 and 30 m).

The satellite Chl-*a* from the MERIS Polymer-Chl-product and the GlobColour product have been validated globally and regionally within the current ESA Climate Change Initiative for Ocean color. Polymer was chosen as the best algorithm for MERIS data processing (Brewin et al., 2014; Müller and Krasemann 2012). We used for the long-term satellite Chl-*a* data analysis the GlobColour product because until today Polymer has not been processed for the entire MERIS data set. The GlobColour product is therefore for this analysis the best choice because it gives us the best coverage by satellite data for this region. By comparing total Chl-*a* concentrations obtained from surface (<10 m) HPLC measurements during our cruise collocated (same day and within the satellite pixel) to MERIS Polymer, and GlobColour Chl *a*, we revealed a reasonable correlation coefficient ($r^2=0.67$ and 0.65, respectively), low bias (0.17 and 0.21 mg m^{-3}, respectively) and percent error (33% and 37%, repectively) between the satellite and in-situ data sets. Therefore, both satellite Chl *a* data set seem to be of reasonable good quality to reconstruct the temporal and spatial development of phytoplankton at the surface.

3.2. Benthos densities (meio- and macrofauna)

Meiofauna occurred in the MUC samples with a broad range of taxa in lower densities including Rotifera, Kinorhyncha, Gastrotricha, Nematoda, Tardigrada, Aplacophora, Bivalvia, Polychaeta, Acari, Copepoda, Ostracoda, Cumacea, Isopoda, Amphipoda, Tanaidacea, and Holothuroidea. Nematoda were by far most frequently in the samples with relative abundance from 84.4% to 91.7%, followed by Copepoda (3.8–8.2%). Total meiofaunal densities (Table 3) varied between 102 individuals (ind.)/10 cm^2 and 335 ind./10 cm^2. Densities were highest at station 86-30 (335 ind./10 cm^2) and lowest at station 81-13 (102 ind./10 cm^2). However, at haul 86-28 densities were also low (141 ind.). On average the densities were very similar at both areas (Table 3; Fig. 2).

Macrofaunal taxa sampled with the EBS included Cnidaria, Nemertini, Sipunculida, Polychaeta, Bivalvia, Gastropoda, Scaphopoda, Solenogastres, Caudofoveata, Copepoda, Branchiopoda, Cumacea, Amphipoda, Isopoda, Tanaidacea, Mysida, Phyllocarida, Euphausiacea, Decapoda, Asteroidea, Echinoidea, Ophiuroidea, Chaetognatha, Bryozoa and Ascidiacea (Brandt et al., 2014). Total macrofaunal densities (ind./1000 m^2) (Table 2; Fig. 2) varied between 26 ind. at station 81-17 and 194 ind. at station 86-24. However, different EBS hauls at station 86 varied considerably between a minimum of 80 ind. and a maximum of 194 ind. (Table 2).

3.3. Sediment

Sediment grain size was determined from MUC cores (Table 4). Sediment was mainly composed of very fine fractions of silt-clay (91.4–92.5%) and some very fine sand (6.6–8.6%), whereas fractions of fine, medium and coarse sand were absent. There were no significant differences between sampling stations. Sediment oxygen consumption (SOC) ($\mu m\ O_2\ m^2\ d^{-1}$) was measured as a proxy for biological activity. It was lowest at station 84-25 ($209.2 \pm 134.9\ \mu m\ O_2\ m^2\ d^{-1}$), and highest at stations 81-17 and 81-18 with $395.95 \pm 243.2\ \mu m\ O_2\ m^2\ d^{-1}$ (Table 4, Fig. 2B).

4. Discussion

We tested the hypothesis that long term satellite-derived surface phytoplankton biomass (Chl-*a*) data and in situ real time measurements of Chl-*a* and primary production are reflected in abyssal benthos densities and activity at boundary conditions. The results of our analyses did not indicate that bentho-pelagic coupling occurred during the sampling time between January and March 2012 in the two areas investigated (52°S 10°E (st. 81) and 52°S 12°W (st. 86)).

Although ^{14}C-based estimates of primary production and Chl-*a* measured by HPLC technique (Table 1), as well as satellite images on mean Chl-*a* of January and February 2012 (Fig. 2A), document differences in Chl-*a* standing stocks and primary productivity between stations 81 and 86, no significant differences in either meiofaunal or macrofaunal densities could be observed (Fig. 2B). Fig. 2B illustrates that the values of both meiofauna and macrofauna were slightly higher at station 86 than at station 81. However, variability between hauls at station 86 was high (Tables 2 and 3) for meio- (between 141 and 335 ind./10 cm^2) and macrofaunal communities (80–194 ind./1000 m^2) and sediment oxygen consumption showed not much difference between stations, except for stations 84 and 85, were values were somewhat lower. Bottom topography can be excluded as a potential reason for differences between stations, as stations 81 and 86 were both sampled at smooth abyssal plains. Only stations 84 and 85 differed slightly in having a more complex topography (Fig. 1). Sediment properties however did not differ between any of the stations (Table 4) and total microbial cell counts (as determined by DAPI staining [ml-1 sediment]) differed insignificantly (7,48E $\pm$08 at station 81 and 7,69E+08 st station 86; Knittel et al., 2014). These strong variabilities in meio- and macrofaunal communities at stations 81 and 86 did not allow to attribute the slightly higher values at station 86 to coupling with the surface productivity, as these differences might be due to patchiness or rarity of organisms sampled.

Serpetti et al. (2013) investigated spatial distribution and patchiness of deep-sea macrofaunal communities on the basis of three megacores (very similar to MUC) at 900 m depth and about 18 km apart in the Rockall Trough. These authors concluded that macrofaunal communities differed significantly. Differences were mostly driven by changes in densities of polychaetes, crustaceans and nematodes. These groups are in fact also the most important faunal components of abyssal plains (Brandt et al., 2007a, 2007b, 2007c, 2012). Kaiser et al. (2007) documented the complexity of the deep-sea isopod composition. They sampled across three spatial scales and concluded that variability in densities between stations was no greater at sites thousands of km apart than meter tens of km. These authors also showed that most of the studied peracarid families or genera are probably not rare but very patchily distributed, because most peracarid species occur in very few samples and even then in just low numbers or as singletons. Ellingsen et al. (2007) analyzed the importance of depth for the

diversity and species distribution of polychaetes, isopods and bivalves in the Atlantic sector of the deep Southern Ocean and also found that a high proportion of species was restricted to one or two sites. The impact of depth on species richness was not consistent. Polychaetes showed a negative relationship with depth, isopods displayed highest richness at around 3000–4000 m, while bivalves showed no clear relationship with depth. However, depth did not play a role in our deep-sea samples, as all (but one) samples were taken at similar abyssal depths.

It is striking that, despite the relatively high pelagic biomass and productivity in the SPF (Bracher et al., 1999; Moore and Abbott, 2000; Tremblay et al., 2002; Kaiser et al., 2011), the numbers of macrobenthic organisms are much lower than further south (e.g. Arntz et al., 1994; Brandt et al., 2007b, 2007c; Kaiser et al., 2007). Next to effects of lateral transport of sinking organic matter (e.g. Fischer et al., 2000), this apparent mismatch could be explained by the high temporal and spatial inter-annual variability in the occurrence and intensity of phytoplankton blooms in the Atlantic sector of the polar frontal zone (Borrione and Schlitzer, 2013; Park et al., 2010), which may be restricting the potential to sustain benthic communities over longer timespans. Another reason for the observed decoupling could be various recycling processes occurring in the water column, preventing the organic matter from reaching the sea floor (Buesseler and Boyd, 2009; De La Rocha and Passow, 2007). While the largest changes in vertical fluxes occur in the upper part of the water column (<250 m), there are fluxes of particulate organic carbon (POC) to the deep ocean which are usually low and almost constant (Iversen et al., 2010; Iversen and Ploug, 2013). Similar to earlier findings on the polar frontal zone, the fraction of organic matter recycled in the upper mixed layer estimated from nutrient deficits was high for the large-scale phytoplankton bloom occurring around station 86 (C. Hoppe, pers. comm.; Tremblay et al., 2002).

Laboratory experiments on temperature effects on carbon-specific respiration rate and sinking velocity of diatom aggregates "using a remineralisation rate measured at 4 °C and an average particle sinking speed of 150 $m d^{-1}$, calculated carbon fluxes were similar to those collected in deep ocean sediment traps from a global data set, indicating that temperature plays a major role for deep ocean fluxes of POC" (Iversen and Ploug, 2013: 4073). Temperature was rather similar between stations. Moreover, differences in sinking velocities of aggregates unlikely influence deep fluxes and benthic densities at stations compared in this investigation (Meyer-Löbbecke et al., 2014).

Densities are low in the abyssal deep sea (Dahl, 1954; Gage and Tyler, 1991). However, there is evidence that macrofauna may play an important role in the initial processing of fresh phytoplankton from the water column (Levin et al., 1999; Witte et al., 2003a, 2003b). Foraminiferans are considered an important intermediate link in the energy flow from phytodetritus to small metazoans (Gooday et al., 1996; Koho et al., 2008; Nomaki et al., 2009; Sibuet et al., 1989; Witte et al., 2003b; Würzberg et al., 2011; Würzberg, 2014). Additionally, deep-sea metazoan meiofauna reacts to food input, as documented in observational and experimental studies (e.g. Gooday et al., 1996; Ingels et al., 2010; Witte et al., 2003b). However, there is a time lag of several days to months between food presentation and measurable reactions on and in the seafloor. Little research, however, analyzed the reaction of metazoan meiofauna to food input at abyssal depths (e.g., Guilini et al., 2011; Ingels et al., 2010; Witte et al., 2003b). For example, Veit-Köhler et al. (2011) investigated sediment from the SYSTCO I expedition with RV *Polarstern* in 2008/2009 at a station in the SPF at 52°S 0°E and 2960 m depth during and after a phytoplankton bloom. These authors observed "significantly higher relative meiofaunal densities at the sediment surface after the remains of the phytoplankton bloom reached the seafloor" and concluded that …" higher oxygen consumption after the phytoplankton bloom may have resulted from an enhanced respiratory activity of the living benthic component" (Veit-Köhler et al., 2011: 1983). In their study also Nematoda were by far the most abundant meiofaunal taxon followed by Copepoda in importance.

Sachs et al. (2009) identified different plankton provinces in the Southern Ocean, which are reflected in the benthic organic carbon flux. Regional pattern of organic carbon fluxes derived from microsensor data furthermore suggests that episodic and seasonal sedimentation pulses are important for the carbon supply to the seafloor of the deep Southern Ocean. Furthermore, Sachs et al. (2009) provided a spatial distribution of the benthic flux of labile organic carbon reaching the seafloors. The spatial map indicates that our stations 81 and 86 are both situated in an area with elevated proportions of *Fragilariopsis kerguelensis* (O'Meara, 1877) frustules. This strongly silicified diatom species leads to high ratio of biogenic silica to organic carbon (Si:C) in sinking particles, restricting the proportion of POC in sinking material (Assmy et al., 2013) and thus food supply for benthic organisms. On the contrary, phytoplankton communities and sediments in the SPF north of South Georgia are dominated by *Chaetoceros* spp. (Sachs et al., 2009: 1326, Fig. 6), a genus being characterized by much lower Si:C ratios and thus serving as a particularly efficient carbon-sinking species (Assmy et al., 2013). Congruently, high surface concentration of Chl-*a* translated to increased densities and response of meiofauna (station 141; see data by Lins et al., 2014). At this station and further to the west in the SPF north of South Georgia, some foraminiferans were found to contain large amounts of pigments (Cedhagen et al., 2014) indicating immediate grazing of the freshly sedimented food pulse. Unfortunately, the EBS was lost at station 141, so that we lack macrofaunal data for this region. In the context of plankton provinces it should furthermore be noted, that differences in dominant species could possibly lead to differences in meio- and macrofaunal communities depending on dietary specializations.

5. Conclusions

Bentho-pelagic coupling of meio- and macrobenthic communities retrieved from EBS and MUC samples could not be observed in the SPF at the boundary conditions from low to high surface productivity. However, this does not necessarily mean that coupling of the benthic communities to surface production does not occur in the SPF at all. On the one hand there are indications of tight linkages between surface primary productivity and meiofaunal densities as well as pigment uptake by foraminiferans (Lins et al., 2014; Cedhagen et al., 2014). On the other hand, high ratios of Si:C in sinking particles might reduce vertical POC fluxes and thus food supply for benthic organisms (Assmy et al., 2013). Due to the loss of the EBS at station 141 we can only compare the data available. Therefore, we need to return to the SPF and sample stations further west at the same season of the year by means of the EBS in order to uncover potential bentho-pelagic coupling processes in this seemingly high productivity area.

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