Deep-Sea Research II 108 (2014) 51–59

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

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

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ARTICLE INFO

Available online 8 September 2014

Keywords:
South Atlantic
Polar front
Primary production
Benthos
Meiofauna
Macrofauna
Densities

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.

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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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http://dx.doi.org/10.1016/j.dsr2.2014.09.001
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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

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