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Indications for algae-degrading benthic microbial communities in deep-sea sediments along the Antarctic Polar Front

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ABSTRACT

Phytoplankton blooms in surface waters of the oceans are known to influence the food web and impact microbial as well as zooplankton communities. Numerous studies have investigated the fate of phytoplankton-derived organic matter in surface waters and shelf sediments, however, little is known about the effect of sinking algal biomass on microbial communities in deep-sea sediments. Here, we analyzed sediments of four regions in the Southern Atlantic Ocean along the Antarctic Polar Front that had different exposures to phytoplankton bloom derived organic matter. We investigated the microbial communities in these sediments using high-throughput sequencing of 16S rRNA molecules to determine microorganisms that were active and catalyzed reporter deposition fluorescence in situ hybridization to infer their abundance and distribution. The sediments along the Antarctic Polar Front harbored microbial communities that were highly diverse and contained microbial clades that seem to preferably occur in regions of high primary productivity. We showed that organisms affiliated with the gammaproteobacterial clade NOR5/OM60, which is known from surface waters and coastal sediments, thrive in the deep-sea. Benthic deep-sea NOR5 were abundant, diverse, distinct from pelagic NOR5 and likely specialized on the degradation of phytoplankton-derived organic matter, occupying a similar niche as their pelagic relatives. Algal detritus seemed to not only fuel the benthic microbial communities of large areas in the deep-sea, but also to influence communities locally, as we found a peak in *Flavobacteriaceae*-related clades that also include degraders of algal biomass. The results strongly suggest that phytoplankton-derived organic matter was rapidly exported to the deep-sea, nourished distinct benthic microbial communities and seemed to be the main energy source for microbial life in the seafloor of vast abyssal regions along the Antarctic Polar Front.

1. Introduction

The extent of primary productivity and the availability of organic matter greatly influence the structure of heterotrophic communities in the oceans, including both macrofauna (Levin and Gage, 1998) and microorganisms (Horner-Devine et al., 2003). Phytoplankton blooms in the euphotic zone of the oceans serve as a food source for zooplankton (Löder et al., 2011) and pelagic communities (Pinhassi et al., 2004; Teeling et al., 2012). These blooms can shift entire planktonic microbial communities from being dominated by oligotrophic *Alphaproteobacteria* to being dominated by copiotrophic *Flavobacteria* that grow on decaying algae and *Gammaproteobacteria* that profit from products released by the degradation of algal biomass (Teeling et al., 2012). Some genera of *Flavobacteria*, such as *Polaribacter*, *Formosa* and *Ulvibacter*, are known to specialize on the degradation of complex polysaccharides that are characteristic for diatoms, such as laminarin, fucan and sulfated polysaccharides in the cell wall. They access these large molecules through specific transport systems, carbohydrate-active enzymes, including glycoside hydrolases and

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sulfatases, which are typically encoded in so-called polysaccharide utilization loci (Mann et al., 2013; Teeling et al., 2012).

Although most of the bloom biomass is remineralized in the food web of the euphotic zone, some of the organic matter escapes degradation in the surface waters and is exported to the meso- and bathypelagial. Estimates on the amount of exported biomass range from around 2% (Fischer et al., 2000) to up to 50% (Smetacek et al., 2012), while only less than 2% of the primary produced organic carbon might actually reach the seafloor (Schlüter et al., 2000). Due to permanent darkness most of the life in the abyssal seafloor is dependent on this input of photosynthesis-derived particulate organic carbon (POC) from the ocean surface (Jørgensen and Boetius, 2007; Sevastou et al., 2013). It was shown that settled POC is taken up by meio- and macrofaunal benthic communities as well as further utilized by microorganisms (Moodley et al., 2002; Witte et al., 2003). POC mainly occurs as algal detritus and fecal pellets (Boyd and Trull, 2007) that have varying sinking speeds between 35 m day^{-1} for copepod fecal pellets (Ploug et al., 2008), to around 200 m day^{-1} for aggregated diatoms (Scharek et al., 1999), to above 2000 m day^{-1} for salp fecal pellets (Bruland and Silver, 1981). Regional studies provided evidence that the size-structure of the phytoplankton community, rather than primary productivity, may be the dominant control on the flux of organic matter to the deep sea (Boyd and Newton, 1995, 1999).

Fischer et al. (2000) proposed that in the Southern Ocean, in particular in the Polar Front area, the organic matter produced during phytoplankton blooms might be more rapidly transported downward due to the formation of large particles or mass sedimentation of diatoms. The standing stocks of benthic meio- and macrofaunal assemblages of the Southern Ocean further suggest a relatively high supply of POC to the sediments (Brandt et al., 2007). Interestingly, in the Southern Ocean, benthic communities of regions with high surface water productivity were found to be similar to those in low productivity regions (Jamieson et al., 2013) and in sediments below the Ross ice-shelf (Carr et al., 2013), indicating that other factors than just the extent of primary productivity play a role. However, as research focused on macrofaunal benthic communities, little is known about microbial communities in sediments along the Antarctic Polar Front. Thus, it is still unclear whether phytodetritus pulses might also induce rapid shifts in microbial community structure, activity or biomass and whether certain microbial groups benefit more from this input than others on a long term.

Here, we analyzed the bacterial community structure of four abyssal sediments and one shallow reference site in the Atlantic sector of the Southern Ocean using high-throughput sequencing and fluorescence in situ hybridization. The sediments originated from regions that had different exposures to phytoplankton blooms in order to investigate potential links between the blooms and benthic microorganisms. Our main hypotheses were (i) that the seafloor of this region harbors specific bacterial clades that benefit from the sinking algal-derived matter and (ii) that an extended bloom situation in the surface ocean leads to changes in the benthic microbial communities with short delay times.

2. Materials and methods

2.1. Sampling procedure and sampling sites

The five investigated stations were located along the Antarctic Polar Front between South Africa and Argentina (Fig. 1 and Table 1), of which four stations were abyssal, open ocean sites. Station 81 was sampled around 20 days after the peak of a short phytoplankton bloom (bloom A, duration ~30 days). This station was likely exposed to low amounts of bloom-derived particulate organic carbon (POC, Table 1) and is referred to as $A81_{short}$ (A: bloom A; 81: sampling station 81; $_{short}$: short exposure time to bloom-derived POC). Station 86 was sampled around 10 days after the peak of an extended bloom (bloom B) and was thus also shortly exposed to POC (sample ID: $B86_{short}$). Station 141 (sample ID: $B141_{long}$) was sampled around 30 days after the peak of the same extended bloom B and had a long exposure to bloom-derived POC. Both stations, 86 and 141, were located in the same area, were influenced by the same bloom and seemed to have a similar biogeochemistry. They mainly differed in the time they were exposed to sinking particles. Station 175 (sample ID: $C175_{long}$) was sampled 50 days after the peak of another extended bloom (bloom C). The fifth station (sample ID: R177), taken as a reference, was shallow and located on the South American shelf. The samples were retrieved by multi-coring during cruise ANT-XVIII/3 on the German research vessel "FS Polarstern" in 2012. After retrieval, the cores were transferred to the cold room (4 °C) and sectioned at intervals of 1 cm. For the microbial community analysis, we selected four layers (layer 1: 0–1 cm; layer 2: 1–2 cm; layer 3: 2–3 cm; layer 4: 3–5 cm) of each core. Subsamples for nucleic acid extraction were frozen at −20 °C and subsamples for CARD-FISH were fixed in 3% formaldehyde in sterile sea water for a maximum of 8 h at 4 °C, washed twice with 1× PBS and stored in 1× PBS/absolute ethanol (1:1) at −20 °C.

Settling particles were collected using free-drifting sediment traps (referred to as 'drifting traps') at all open-ocean stations. The drifting traps consisted of a drifting array attached to a surface buoy equipped with a GPS satellite transmitter, two surface floats and 12 small buoyancy balls serving as wave breakers to reduce the hydrodynamic effects on the traps. One gimbal mounted collection cylinder (100 × 10.4 cm), was deployed at 300 m. The collection cylinder was equipped with 200 ml of a viscous gel (Tissue-Tek®, O.C.T.™ COMPOUND, Sakura) to intercept and preserve settling particles without destroying their original size and structure. Upon recovery, the particles settled for 12 h before the gels were removed and photographed using a stereomicroscope.

2.2. Chlorophyll a measurements

Water samples for Chlorophyll *a* (Chl*a*) analysis were collected from Niskin bottles mounted on a CTD rosette and filtered onto 25 mm diameter GF/F filters at pressures not exceeding 200 mbar. Filters were immediately transferred to centrifuge tubes with 10 ml 90% acetone and 1 cm^3 of glass beads. The tubes were sealed and stored at –20 °C for at least 30 min and up to 24 h. Chl*a* was extracted by placing the centrifuge tubes in a grinder for 3 min followed by centrifugation at 0 °C. The supernatant was poured in quartz tubes and measured for Chl*a* content in a Turner 10-AU fluorometer. Calibration of the fluorometer was carried out at the beginning and at the end of the cruise. Results of the fluorometer calibration diverged by 2% between beginning and end of the cruise. Chl*a* content was calculated as described previously (Knap et al., 1996) using average parameter values from the two calibrations.

2.3. Particulate organic carbon (POC) measurements

Water samples for POC analyses were obtained from Niskin bottles attached to a Conductivity Temperature Depth (CTD) rosette from discrete depths between 10 and 150 m depth at each station. Samples (from 1 to 2 l) were filtered onto pre-combusted glass fiber filters (Whatman GF/F) and stored in pre-combusted glass petri dishes. After filtration filters were dried overnight at