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Marine microbial ecology off East Antarctica (30 - 80°E): Rates of bacterial and phytoplankton growth and grazing by heterotrophic protists

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ABSTRACT

Marine microbes ($<200\,\mu m$) contribute most of the living matter and carbon flow in the Southern Ocean, yet the factors that control the composition and function of these microbial communities are not well understood. To determine the importance of microbial grazers in controlling microbial abundance, we determined microbial standing stocks and rates of herbivory and bacterivory in relation to the physical environment off East Antarctica during the Baseline Research on Oceanography, Krill and the Environment: West (BROKE-West) survey, which covered waters from the Polar Front to the coast between 30 and 80°E. Concentrations of heterotrophic nanoflagellates (HNF) ($\sim$2 to $20\,\mu m$), microzooplankton ($\sim$20 to $200\,\mu m$), bacteria, and chlorophyll *a* (Chl *a*) were determined and the growth and grazing mortality of phytoplankton and bacteria were estimated using the grazing dilution technique at 22 sites along the survey. Results showed that microzooplankton and HNF consumed on average 52% of bacterial production d^{-1} and 62% primary production d^{-1} but consumed $>100\%\ d^{-1}$ at the western ice-edge sites. Rates of bacterivory ranged from 0.4 - 2.6 d^{-1} and were correlated with bacterial concentrations, bacterial growth rates and longitude. Rates were highest in the eastern-most part of the survey, which was sampled last, reflecting the transition along the successional continuum toward a respiration-based, senescent, microbial community. Rates of herbivory ranged from 0.3 to 2.4 d^{-1} and were correlated with concentrations of microzooplankton and HNF combined, rates of phytoplankton growth, and latitude. Rates were highest at southern ice edge sites where concentrations of prey (as represented by Chl *a*) and microzooplankton were also highest. Cluster analysis of the concentrations of marine microbes and their rates of growth and grazing mortality identified 5 groups of sample sites that conveniently summarised the variability in the composition and function of the microbial community. Cluster groups differentiated between low Chl *a* ($\sim 0.3\,\mu g\,l^{-1}$) open ocean Antarctic Circumpolar Current (ACC) communities; and high Chl *a* ($\sim 2.4\,\mu g\,l^{-1}$) ice-associated coastal blooms at various stages between bloom formation and senescence. This partitioning of cluster groups can be used to determine spatial and temporal patterns of carbon transfer by the microbial loop within the BROKE-West survey area.

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1. Introduction

Grazing by both micro- (20-200 μm) and nano- (2-20 μm) heterotrophs is a vital determinant of productivity in the Southern Ocean and is integral to modelling the Antarctic marine ecosystem. While the Southern Ocean is regarded as one of the world's most productive marine ecosystems (Busalacchi, 2004), this productivity is restricted in space and time and controlled by factors that are not yet fully understood. It is now recognised that the contribution of nano- (2-20 μm) and picoplankton ($<2\,\mu m$) to microbial communities within the Southern Ocean can equal or exceed that of the micro-sized (20-200 μm) fraction depending on regional and seasonal variation (Mengesha et al., 1998). The importance of 'top-down' vs. 'bottom-up' control of this productivity has been a topic of debate over the last few decades (Smith and Lancelot, 2004). Some authors propose that phytoplankton abundance and distribution is controlled by 'bottom-up' environmental factors including iron, light, silicic acid and nitrate (Smith and Lancelot, 2004). Others suggest that high productivity is restricted to the iron-sufficient waters of the marginal ice zone and occurs when environmental perturbations allow large or grazer-resistant phytoplankton such as *Phaeocystis*, to escape top-down grazing control (Smith and Nelson, 1986;

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Smetacek et al., 2004). *Phaeocystis* is considered one of the most important phytoplanktonic organisms in Antarctic waters (Davidson and Marchant, 1992) and large blooms are common at ice edge sites. Grazer resistance has been variously attributed to colony size; deterrence by prolific synthesis of volatile sulphur compounds such as dimethylsulfoniopropionate (DMSP); and clogging of the feeding apparatus with mucilaginous colony matrix (Davidson and Marchant, 1992; Caron et al., 2000; Safi et al., 2007).

Grazing exerts top-down control on phytoplankton and bacterial biomass and community composition; remineralises nutrients; releases dissolved organic matter (DOM); and mediates carbon transfer to higher trophic levels (Azam et al., 1983; Fenchel, 1988; Burkill et al., 1995; Froneman and Perissinotto, 1996;Strom et al., 1997; Li et al., 2001; Calbet and Landry, 2004). In the Southern Ocean micro- and nanoheterotrophs consume a diverse range of prey ranging from DOM and sub-micrometre sized particles to large chain forming diatoms (Sherr and Sherr, 1994; Sherr, 1988) and are considered to exert more predatory pressure on phytoplankton than larger grazers such as salps, copepods or krill (Burkill et al., 1995; Becquevort, 1997). However these grazers are not necessarily competitors for the same resources as some consume DOM directly or graze the bacteria that consume DOM, thereby returning carbon that would otherwise be unavailable to the food web (Sherr, 1988). They are also an important link between pico- and nanophytoplankton and mesozooplankton as microzooplankton such as ciliates and copepod nauplii are grazed by krill and can comprise a larger proportion of their diet than phytoplankton (Price et al., 1988; Froneman et al., 1996; Wickham and Berninger, 2007). Thus grazing plays a pivotal role in regulating carbon flux in Antarctic waters, respiring carbon substrates in near-surface waters and transferring carbon to higher trophic levels.

Several techniques have been developed to estimate rates of micro- and nanoheterotrophic grazing, each with their inherent weaknesses and ambiguities (Landry, 1994). Fluorescently labelled or stained ‘prey’ particles are often used to measure uptake, however this requires a great deal of manipulation of the natural community and grazers may preferentially avoid stained prey. The grazing dilution technique of Landry and Hassett (1982) simultaneously estimates rates of phytoplankton growth and micro- and nanoheterotrophic grazing for entire microbial communities; uses natural microbial assemblage; and minimises experimental manipulations that can damage protists (Landry, 1994; Kuipers and Witte, 1999). This technique is now a widely applied and accepted method of determining rates of microzooplankton grazing (e.g., Calbet and Landry, 2004; Dolan and McKeon, 2005). Though originally designed to determine growth and grazing mortality of phytoplankton, the dilution technique has also been successfully applied to the measurement of bacterivory (Tremaine and Mills, 1987; Anderson and Rivkin, 2001; Jacquet et al., 2005). Thus the grazing dilution technique remains one of the most informative yet least invasive and damaging techniques available to estimate rates of phytoplankton and bacterial growth and mortality due to grazing by micro- and nanoheterotrophs.

The results of grazing studies performed in coastal and offshore waters of the Southern Ocean vary considerably. Some authors find that microzooplankton and HNF play a major role in bloom suppression, removing much or all of the phytoplankton and bacterial production (Froneman et al., 1996; Tsuda and Kawaguchi, 1997; Anderson and Rivkin, 2001; Calbet and Landry, 2004; Dolan and McKeon, 2005). Others find grazing does not significantly affect production or standing stocks of prey (e.g., Caron et al., 2000). The apparent conflict between such studies suggests that magnitude and impact of grazing by micro- and nanoheterotrophs varies greatly with place and time (Caron et al., 2000; Calbet and Landry, 2004).

The research presented here was conducted as part of a larger BROKE-West (Baseline Research on Oceanography, Krill and the Environment: West) survey, one of the primary aims of which was to establish a krill biomass estimate for the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). The survey provided an opportunity to determine the oceanographic structure and biogeography of organisms from microbes to whales over waters from the coast (66 to 69°S) to near the northern-most limits of maximum sea ice extent (60 to 62°S) between 30 and 80°E. Using the grazing dilution technique, we determined rates of herbivory and bacterivory by micro- and nanoheterotrophs and examined the associations between rates of grazing, the physical environment and the composition and productivity of the microbial community.

2. Methods

2.1. Field sampling

Sea water for dilution experiments was collected at 22 stations along the BROKE-West cruise track between January 10 and March 3, 2006. The survey consisted of one east-west transect (leg 12) followed by 11 north-south transects between 78°E and 30°E longitude, covering latitudes from 60°S, to waters on the continental shelf (up to 69°S) (Fig. 1). At each station, water was collected using two 30-l Niskin bottles mounted on a CTD rosette frame that were closed simultaneously at 5 to 10 m depth. The coincident oceanographic parameters (temperature, conductivity, oxygen, nutrients and salinity) are reported in Westwood et al. (2010) and Williams et al. (2010) and the position of the voyage track in relation to frontal zones and currents are shown in Fig. 1. The sample stations are shown in Figs. 3–10 and the numbering of stations corresponds to CTD locations published in Westwood et al. (2010) and Thomson et al. (2010). Additional information on surface oceanography including mixed layer depth are reported by Williams et al. (2010) and briefly covered below.

2.2. Large-scale circulation

Our results are presented in relation to the major oceanographic features of the BROKE-West region (Williams et al., 2010).

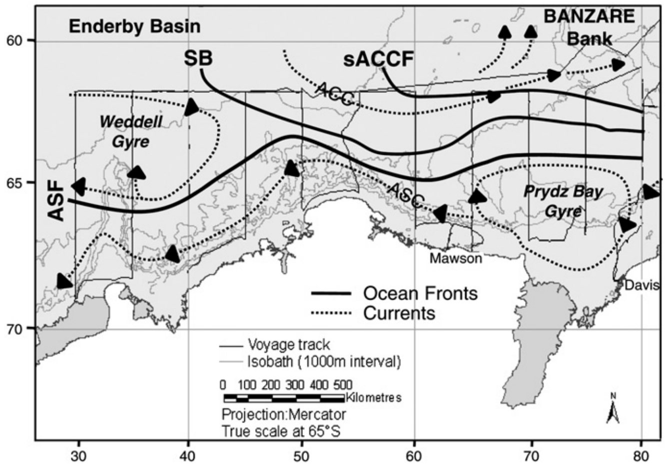

Fig. 1. The major oceanographic features of the BROKE-West region in relation to the BROKE-West voyage track.

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