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Physical and biological control of protistan community composition, distribution and abundance in the seasonal ice zone of the Southern Ocean between 30 and 80°E

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ABSTRACT

Protists are critical components of the Antarctic marine ecosystem as they comprise most of the living carbon and are the base of the Antarctic food web. They are also key determinants of vertical carbon flux and mediate draw-down of atmospheric CO_2 by the ocean. The community composition, abundance and distribution of marine protists (phytoplankton and protozoa) was studied during the Baseline Research on Oceanography, Krill and the Environment-West (BROKE-West) survey, in the seasonal ice zone during the 2005-2006 austral summer between 30°E and 80°E. Light and electron microscopy were used to determine the protistan composition and abundance in samples obtained at 30 sites from surface waters and at 26 sites from the depth of the maximum *in situ* chlorophyll fluorescence (Chl max). Cluster analysis was used to identify 5 groups of sample sites at the surface and 5 at the Chl max that were of similar protist composition and abundance. The physical characteristics, taxonomic composition, indicator taxa, and taxonomic diversity were determined for each group. In the southwest, a bloom of colonial *Phaeocystis antarctica* dominated the protistan community composition and biomass amongst the receding ice, but this was replaced by the flagellate life stage/s of this haptophyte in waters to the north. In the southeast, a diatom bloom had the highest diversity of protist taxa observed during the survey and centric diatoms dominated the biomass. Outside these blooms, grazing by krill probably reduced the composition and abundance of large diatoms and autotrophic dinoflagellates in coastal to mid-inshore waters. Only in offshore waters did large diatoms and dinoflagellates increase in abundance and diversity, despite low concentrations of iron and silicate at many of these sites. This increase was probably due to reduced top-down control by krill and other large zooplankton. Large diatoms dominated in offshore waters, despite other coincident studies showing that the trophic structure and function of the microbial community was frequently typical of nanoflagellate-dominated systems in high-nutrient low-chlorophyll waters. Nanoflagellate abundances were low during the survey and were either poorly resolved by our study or limited by microheterotrophic grazing. We propose that protistan abundance and composition in the sea-ice zone of the Indian Sector were determined by synoptic-scale oceanographic features, meso-scale changes caused by sea-ice retreat and meso- to nano- scale interactions between grazers and the composition and abundance of their protistan prey.

1. Introduction

The Southern Ocean comprises 20% of the world's ocean and is recognised as the most important region in the global marine carbon cycle and regulation of global climate (Sarmiento and LeQuéré, 1996; Sarmiento et al., 1998). In 2006, a survey (BROKE-West) was undertaken to carry out a broad-scale stock assessment of marine living organisms in the western zone of the Indian Sector of the Southern Ocean. Antarctic marine protists were studied as part of this survey. Protists are the largest contributors to living matter in the ocean and a major determinant of the structure and efficiency of Antarctic marine food webs and the flux of particles to deep water (Smith and Sakshaug, 1990; Priddle et al., 1992). However, the fate of this production is determined to a large extent by the composition of the protistan community due to interspecific differences in rates of grazing mortality and vertical flux (Smith and Sakshaug, 1990; Priddle et al., 1992; Moline & Prézelin, 1996; Mengesha et al., 1998; Smetacek et al., 2002). Despite its importance, most studies do not report species information or fail to interpret their distribution patterns (Smetacek et al., 2002). Consequently, little is known about the factors determining the distribution and abundance of protistan

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taxa in the Southern Ocean (Kang and Fryxell, 1993; Boyd, 2002; Smetacek et al., 2002; Garibotti et al., 2005).

Information about the distribution and abundance of Antarctic protist taxa is urgently required. Climate models predict that the Southern Ocean will experience marked changes in temperature, stratification, mixed-layer depth and acidity in association with global warming. As a consequence, light climate and nutrient availability will be affected, and carbonate deposition by organisms reduced. These effects will have major ramifications for the composition, abundance and trophodynamics of the Antarctic marine ecosystem (Sarmiento et al., 1998; Bopp et al., 2001; Boyd, 2002; Orr et al., 2005; Tortell et al., 2008). Already some regions of the Southern Ocean have become warmer and fresher, probably due to climate change (Wong et al., 1999; Gille, 2002). Without information describing the current distributions and abundances of protists it will not be possible to detect changes in marine microbial communities that are the base of the Antarctic food web.

Various biogeographic provinces have been identified in the Southern Ocean that are occupied by distinct protistan communities due to differences in grazing mortality and the availability of light and nutrients such as iron and silicate (Boyd, 2002; Smetacek et al., 2004; Smith and Lancelot, 2004). In the permanently open-ocean zone (POOZ), phytoplankton biomass is low due to iron and light limitation and the abundance of phytoplankton (predominantly nanoplanktonic flagellates) is controlled by microzooplankton grazing (Garibotti et al., 2003; Smith and Lancelot, 2004). Phytoplankton biomass increases south of the POOZ where iron concentrations are higher. The southward retreat of sea-ice from the seasonal ice zone (SIZ) during spring and summer creates a shallow mixed layer near the ice edge (marginal ice zone, MIZ) that traps phytoplankton in a high-light, high-nutrient environment. The resulting blooms, which are commonly dominated by microplanktonic diatoms or *Phaeocystis antarctica*, contribute 25-67% of phytoplankton production in the Southern Ocean (Smith and Nelson, 1985; Smith and Asper, 2001; Gomi et al., 2007). The meltwater-derived stratification that supports these blooms is continually degraded at the seaward edge by vertical mixing, resulting in a 100 to 250 km wide belt of high protist biomass that parallels the retreating ice edge (Smith and Nelson,1985; Lancelot et al., 1993). Some authors also distinguish the coastal zone (CZ) where high phytoplankton biomass persists during summer (e.g., Gomi et al., 2007). Finally there are zone-independent regions where enrichment of iron in areas of upwelling, at fronts, over continental shelves and in the proximity of islands supports phytoplankton blooms (e.g., Marchant, 1993; Gomi et al., 2007). These aforementioned zones provide an ecological framework that describes the broad-scale changes in microbial communities and the factors that cause them (Pollard et al., 1995). However, they do not aid our understanding of factors determining microbial communities at spatial and temporal scales less than synoptic or seasonal, respectively.

Understanding the processes that determine the distribution and abundance of marine protists at small to medium spatial scales is no trivial task. Some 550 marine protists have been reported from waters south of the polar front (Scott and Marchant, 2005). Changes in this vast diversity of protists can occur over small and large spatial and temporal scales in response to differences in the history and nutrient content of water masses, the maturity of the community, grazing, and the defensive strategies employed by the constituent protistan taxa (Moline and Prézelin, 1996; Smetacek, 2001; Smetacek et al., 2002; Fonda Umani et al., 2005). Recent efforts to integrate physical, chemical and biological data have shed new light on the dynamics of protist blooms. Such studies have shown that similar hydrographic conditions give rise to similar species assemblages and that species associations and successional sequences are repeated interannually (Kang and Fryxell, 1993; Moline and Prézelin, 1996; Kang et al., 2001; Smetacek et al., 2002). Thus, there appear to be widespread and persistent factors that structure protist communities in the Southern Ocean.

Here we report the composition and abundance of marine protists from surface waters and the Chl max in the SIZ off East Antarctica during the BROKE West survey. Results identify the composition of different protistan communities in the SIZ in austral summer, where they occur and the factors that appear to determine their location.

2. Methods

2.1. Sampling and processing procedures

The BROKE-West survey was conducted from 30°E and 80°E between January and March 2006. It consisted of 1 east-west transect at the northernmost limit of the survey between 60°S and 62°S between the 10 and 19 of January, followed by 11 meridional transects separated by 5° of longitude that extended from approximately 62°S to the Antarctic continental shelf between the 19 January and 3 March.

Sea water samples for determining the identity, composition and abundance of protists were obtained using 20-l Niskin bottles (General Oceanics) mounted on a CTD rosette at 30 sites in surface waters (3-12 m depth) and 26 sites at the Chl max (11-80 m) over a total of 34 locations during the BROKE-West survey. At two sites during the survey (10 and 99) the Chl max occurred at the surface. Samples were preserved with 1% vol:vol Lugol's iodine and stored in glass bottles in the dark at 4 °C until processed by light microscopy after the survey.

Permanent slides were prepared from Lugol's fixed material according to the 2-hydroxypropyl methacrylate (HPMA) method of Crumpton (1981), further modified by Sung-Ho Kang (KORDI, pers. comm.). Each sample was filtered at <5 kPa onto a 0.45-μm pore size, 25-mm-diameter, GN-6 cellulosic membrane filter (Gelman). The filter was then rinsed by filtering a further 15 ml of MilliQ water, removed from the filtration apparatus and placed face down on a cover glass. A few drops of HPMA (Sigma) were placed on the back of the filter and the sample then transferred to a 60 °C cabinet for 12 to 24 h to clear the filter and polymerise the HPMA. Further drops of HPMA were then placed on the back of the filter, a slide was placed on top and the sample was again polymerised as above for 6-12 h.

Protistan taxa were identified and counted in 20 randomly chosen quadrats (Whipple grids) for each HPMA slide using a Zeiss Axioskop equipped with Nomarski interference optics and epifluorescence. Counts were performed at 400 x magnification and blue light epifluorescent excitation (filter set 487909 with 450-490 nm exciter filter, 510 nm chromatic beam splitter and 520 nm barrier filter) was used to discriminate autotrophic cells due to chlorophyll autofluorescence.

Identification of cryptic species was aided by electron microscopy. One-litre samples were fixed with 1% glutaraldehyde and stored at 4 °C until processed after the BROKE-West survey. Each sample was concentrated over a 47-mm-diameter 0.8-μm polycarbonate membrane (Poretics) at a vacuum of <5 KPa and the concentrate resuspended into the sea water remaining above the filter by gentle agitation. For scanning electron microscopy (SEM) cells were settled onto a polylysine-coated glass coverslip, dehydrated with a graded series of acetone, critical point dried, sputter coated with gold and examined using a JEOL JSM 840 SEM. For transmission microscopy (TEM), approximately 40-μl aliquots of concentrate were placed on polylysine treated formvar-coated