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Phytoplankton community structure in a high-nutrient, low-chlorophyll region of the eastern Pacific Subantarctic region during winter-mixed and summer-stratified conditions

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ABSTRACT

Phytoplankton community structure was analysed in the Subantarctic sector of the eastern South Pacific, a high-nutrient, low-chlorophyll (HNLC) region, during a period of deep vertical mixing (austral winter Aug–Oct, 2005) when Antarctic Intermediate Water (AAIW) gets formed, and during a period of water-column stratification characterised by shallow mixed layers (austral summer Feb–Mar, 2006). We examined both the entire phytoplankton assemblage through the use of diagnostic pigments and also the picophytoplankton fraction (<3 μm) through the use of class-specific molecular probes and flow cytometry. Both the pigment and molecular data reveal a dominance of prymnesiophytes during both the winter-mixed and summer-stratified periods. Chrysophytes and their diagnostic pigments were also present throughout most of the study region. Flow cytometric analysis revealed that the contribution of photosynthetic picoeukaryotes (PPEs) to total picophytoplankton (PPEs + picocyanobacteria) abundances increases systematically with increasing latitude and decreasing temperature, highlighting the importance of PPEs in the Southern Ocean.

1. Introduction

The boundary between the Southern Ocean and the South Pacific comprises a series of complex frontal zones separating water masses with distinct physical and chemical properties and thereby provides a diverse range of pelagic niches. It is also the place where circumpolar Sub-Antarctic Mode Waters, and particularly Antarctic Intermediate Water, get formed. Although iron (Fe) is considered by many authors to be the limiting nutrient for phytoplankton growth in the Southern Ocean; light can also be considered as an important factor governing the growth of marine phytoplankton, especially during the winter when surface irradiances are low and strong winds lead to mixed layers exceeding 400 m (Sunda and Huntsman, 1997; Boyd, 2002; Platt et al., 2003). Such turbulent environments can be rich in nutrients, including Fe, but provide insufficient light for rapid algal growth (Mitchell and Holm-Hansen, 1991).

As a consequence of their high surface-area-to-volume ratio, small cells can out-compete larger cells under nutrient limitation (Raven, 1998). Moreover, the efficiency with which phytoplankton cells harvest light increases with decreasing cell size (Morel and Bricaud, 1981). One would therefore anticipate that smaller cells would be able to out-compete larger cells under the light- and nutrient-limiting conditions characteristic of the Southern Ocean in winter and summer, respectively (Sunda and Huntsman, 1997).

Picophytoplankton have been formerly defined as cells <2 μm (Sieburth et al., 1978; Li and Dickie, 2001), but more recently studies have included cells <3 μm in diameter (see Vaulot et al., 2008 for a review) since field studies have often used 3-μm filters to separate small plankton from larger ones (e.g., Moon-van der Staay et al., 2001). The photosynthetic eukaryotic component of this size fraction (PPEs) contribute significantly to the total carbon fixation in oceans (Li, 1994; Jardillier et al., 2010; Cuvelier et al., 2010) and include representatives from all known algal lineages. In polar and sub-polar ecosystems they are believed to play a significant role, replacing their cyanobacterial counterparts, which dominate numerically at lower latitudes as the major picophytoplankton group (Wright et al., 2009). Thus, in the Southern Ocean, picocyanobacteria tend to decline in abundance from north to south (Letelier and Karl, 1989; Marchant et al.,

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1987; Detmer and Bathmann, 1997) leading to a dominance of PPEs in Antarctic waters (Gall et al., 2001). Temperature has been implicated as a factor governing the decrease in abundance of picocyanobacteria with increasing latitude (Marchant et al., 1987; Detmer and Bathmann, 1997). Moreover, small eukaryotes including *Phaeocystis* sp. and prasinophytes appear to favour the coldest waters (Lovejoy et al., 2007; Wright et al., 2009). As a result, it has been proposed that the potential temperature sensitivity of these organisms might make such communities particularly sensitive to global warming (Wright et al., 2009).

However, the taxonomic composition of these small eukaryotes is still poorly known, especially in polar seas, a prerequisite if such organisms might be used as bioindicators of global change. Furthermore, sparse sampling of the Southern Ocean provinces in the winter has left a gap in our understanding of the composition and significance of PPEs in HNLC regions during the period of dynamic vertical mixing (Doolittle et al., 2008), when light, not trace elements, are believed to be the ultimate factor limiting phytoplankton growth (Boyd, 2002). Here, we characterise the taxonomic composition of phytoplankton communities across the Subantarctic region of the Pacific Ocean (Fig. 1). Remote from continental sources of Fe, this region has some of the lowest Fe concentrations of the Southern Ocean (de Baar et al., 1999). Water samples for pigment, flow cytometry and dot-blot hybridisation analysis were taken during two seasons of contrasting physical and chemical conditions: during the austral winter, when mixed layer depths exceeded 400 m and surface macronutrient concentrations were high, and during the austral summer, when the surface mixed layers were often within the top 60 m of the water column and the concentrations of silicate were greatly diminished.

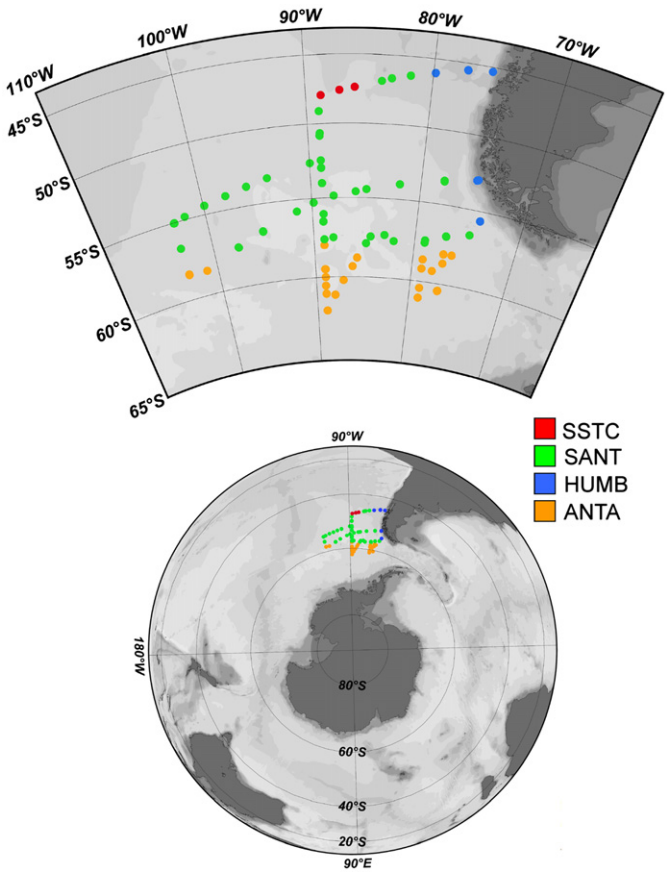

Fig.1. Map of station locations for the AAIW cruises. Symbol colours denote the corresponding biogeochemical province as defined by Longhurst (2007) (Humboldt Current Coastal (HUMB), Subantarctic Water Ring (SANT), Antarctic (ANTA) and Southern Subtropical Convergence (SSTC) Provinces).

2. Materials and methods

2.1. Sampling

Seawater was collected aboard the R/V *Knorr* in the Subantarctic region of the Pacific Ocean during the austral winter (Antarctic Intermediate Water (AAIW) cruise KN182-7: August 23–October 4, 2005) and austral summer (AAIW cruise KN182-11: February 2–March 11, 2006). Water was sampled using a CTD Rosette system comprised of 36 10-L Bullister bottles. During the summer cruise, samples were taken throughout the photic zone. To compare the two seasons, we decided to confine our analyses to a similar depth horizon. Samples for DNA extraction, High Performance Liquid Chromatography (HPLC) pigment, and flow cytometry analysis were collected from multiple depths within the top 30 m of the water column. HPLC and flow cytometry samples were collected at every station, whereas DNA samples were collected at a subset of stations roughly equally spaced across the sampling region and covering Humboldt Current Coastal (HUMB), Subantarctic Water Ring (SANT) and Antarctic (ANTA) Provinces as defined in Longhurst (2007) (Fig. 1). The boundaries for the three provinces are defined based on regional oceanography and climatology of surface chlorophyll fields (Longhurst, 2007). The southern region of the HUMB province sampled in this study is characterised by primarily down-welling winds and high precipitation. In this coastal province, water column stratification is governed by salinity rather than temperature, and tides (rather than winds) are the dominant factor governing the regional hydrodynamics (Longhurst, 2007). The SANT province is that part of the Antarctic Circumpolar Current that lies north of the Polar Front (~50°S). Strong winds and deep winter mixing characterise this region where chlorophyll biomass remains low throughout the year (Longhurst, 2007). The ANTA province is the southern section of the ACC, situated between the Polar Front and the Antarctic Divergence (~60–65°S). This region is complex in terms of silicate limitation, being replete in this macronutrient in the winter and spring, but becoming limited in silicate in the summer due to the rapid uptake of silica by diatom blooms (Longhurst, 2007). Like the SANT province, ice-free waters are prone to deep mixing caused by strong wind events (Longhurst, 2007).

2.2. Physical and chemical properties of the water column

Vertical profiles of temperature, salinity and density were measured using a Conductivity Temperature Depth (CTD) sensor. Density values (ρ) measured every 1 dbar were used to determine the depth of the mixed layer (z_m), which was defined as the depth at which ρ decreased 0.125 (in sigma-t units) from its surface reference depth (10 m in all cases) (de Boyer Montegut et al., 2004).

Macronutrient concentrations (phosphate, silicate, nitrate and nitrite) were measured using an ODF-modified 4-channel Technicon AutoAnalyzer II. Samples were analysed within 2 h of sample collection or were refrigerated for up to 4 h at 4 °C and then analysed. Silicate (SiO_3) was measured using the protocol described in Armstrong et al. (1967). This protocol was also used in the analysis of nitrate and nitrite (NO_2+NO_3), with slight modifications (outlined in Chereskin, 2005). Phosphate (PO_4) was measured using a modification of the method described in Bernhardt and Wilhelms (1967).