

Wintertime abundance of picoplankton in the Atlantic sector of the Southern Ocean

by

Daniel F. Doolittle^{1,2}, William K. W. Li³ and A. Michelle Wood^{4*}

¹ Rosentstiel School of Marine and Atmospheric Sciences, University of Miami, Miami, Florida 33149, USA

² Kachemak Bay National Estuarine Research Reserve, Homer, Alaska, 99603, USA

³ Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada B2Y 4A2

⁴ Center for Ecology and Evolutionary Biology, Dept. of Biology, University of Oregon, Eugene, Oregon. 97405, USA

* Corresponding author, e-mail: miche@uoregon.edu,

With 6 figures and 1 table

Abstract: Data on the distribution of picophytoplankton from the Southern Ocean are relatively scant and primarily collected during the austral spring and summer. During the ICEFISH (International Collaborative Expedition to collect and study Fish Indigenous to Sub-Antarctic Habitats) expedition conducted in the austral winter, 2004, we examined the abundance of picophytoplankton in surface waters along a 366 km W–E transect at ~55°S latitude between the South Sandwich Islands and Bouvetoya Island, a 2780 km S–N transect from Bouvetoya Island to Tristan da Cunha Island, and a 2050 km W–E transect extending east from Tristan da Cunha toward Capetown, South Africa. The cruise track traversed a region of the Antarctic Circumpolar Current (ACC) that included four major frontal features: the Southern Antarctic Circumpolar Current Front (SACCF), the Antarctic Polar Front (APF), the Subantarctic Front (SAF), and the Subtropical Front (STF). In waters less than 1 °C, and south of the SACCF, picoeukaryotes represented more than 99% of the picophytoplankton in the community. Phycoerythrin-containing picoplankton <2 µm in equivalent spherical diameter (ESD) were observed along our S–N transect once water temperatures exceeded 1.3 °C, placing their southernmost limit of distribution close to the Antarctic Polar Front. Substantial populations of these organisms, which had a flow cytometric signature comparable to those of PE-containing marine *Synechococcus* and other PE-containing picocyanobacteria, were seen in all samples collected in water >4 °C and north of the APF. Thus, both PE-containing picoplankton <2 µm in equivalent spherical diameter (ESD) and picoeukaryotes appear to be part of the phytoplankton community in Antarctic polar waters year-round. In contrast, *Prochlorococcus* did not appear in water <10 °C or south of the southern expression of the STF, as expected from other reports. A strong linear relationship exists between log phytoplankton abundance and temperature, which is only observed when all functional groups are pooled. Picoplankton distributions show marked changes at frontal boundaries and support the hypothesis that water mass related phenomena, and not just temperature alone, determine phytoplankton community structure in the Southern Ocean.

Key words: picophytoplankton, picocyanobacteria, *Synechococcus*, *Prochlorococcus*, picobiliphytes, picoeukaryotes, microbial loop, Antarctic Circumpolar Current, polar biology

Introduction

Picophytoplankton, or those cells between 0.2 and 2.0 μm in diameter, are recognised as important members of marine ecosystems throughout the globe. In most oligotrophic waters, they represent the dominant phytoplankton biomass and they can be very abundant in coastal and more eutrophic waters (Li 2007). In the Antarctic, picoplankton may also constitute a notable portion of both the phytoplankton standing stock and primary production (Ning et al. 1996, Froneman et al. 2004). Picoplankton may be a critical element of the food web of the Southern Ocean, representing a seasonally stable biomass that is important for maintaining the food web (Detmer & Bathman 1997). However, this idea is hard to evaluate because scant data on picoplankton abundance have been collected during the austral winter, the period when these small cells would be most necessary to compensate for a lack of production by bloom-forming net plankton species.

The distribution of different picophytoplankton groups at high latitudes was first examined by Murphy & Haugen (1985) who used epifluorescence microscopy to describe the vertical profile of autotrophic picoeukaryotes and phycoerythrin (PE)-containing picoplankton at 50 stations in the North Atlantic. They found that PE-containing picoplankton abundance decreased by nearly two orders of magnitude, whereas eukaryotic picophytoplankton abundance increased fivefold as latitude increased between 36.8°N and 61.5°N. The great decrease in abundance of PE-containing picoplankton was interpreted to reflect a temperature effect and led to a picophytoplankton community dominated by picoeukaryotes. At the most northern stations in their study, picoeukaryotes were >96% of the cells in the <3 μm fraction. Later, and more recent work, has confirmed the ubiquity and importance of picoeukaryotic prasinophytes and other phytoflagellates in the central Arctic Ocean and its pan-Arctic shelves (Booth & Horner 1997, Booth & Smith 1997, Sherr et al. 2003, Hill et al. 2005, Not et al. 2005, Lovejoy et al. 2007). Compilation of data on picophytoplankton abundance from diverse waters around the world indicates that picoeukaryotes range from 10^2 to 10^4 cells ml^{-1} at sub-zero temperatures (Li 2008).

Prochlorococcus, which were not yet discovered at the time of the Murphy & Haugen study, are thought to be absent from polar waters (Partensky et al. 1999). Fouilland et al. (1999) found that *Prochlorococcus* did not occur south of the subtropical frontal zone (STFZ) in the Indian Ocean, and that the abundance of PE-containing picoplankton progressively decreased south of the Subtropical Frontal Zone (STFZ), effectively disappearing at about 52°S. In contrast to the results of Murphy & Haugen (1985) for the North Atlantic, concentrations of picoeukaryotes decreased with increasing latitude in the Indian Ocean study (Fouilland et al. 1999). These authors attributed the distribution of *Prochlorococcus* they observed to isolation by the frontal barrier of the STFZ and the distribution of picoeukaryotes and PE-containing cells to temperature effects (Fouilland et al. 1999).

Decreasing concentrations of PE-containing picoplankton with increasing latitude in the Southern Ocean have been observed in the Drake Passage (Letelier & Karl 1989), the Pacific sector of the Southern Ocean (Detmer & Bathman 1997), and the Crozet Basin, where they were not observed south of the STFZ (Fiala et al. 2003). These distribution patterns are generally attributed to a temperature effect, although Letelier & Karl (1989) expressed skepticism about the mechanistic role of temperature and suggested that other variables should be considered as the determining factors. Supporting this idea are a number of observations that suggest cold temperatures alone do not exclude picocyanobacteria from a water mass. For example, chroococcoid picocyanobacteria can occur in coastal waters of the Antarctic during winter (Walker & Marchant 1989), sometimes showing peaks in abundance at higher latitude (~35–40°S) fronts in the South Atlantic (Zubkov et al. 2000), can predominate over picoeukaryotes in subantarctic water during the austral summer (Mikaelyan 1987), and can occur at low levels in the Pacific Sector of the Southern Ocean when water temperatures are below 0 °C (Marchant et al. 1987).

In the southern Ocean frontal features are particularly good candidates for factors other than temperature that may determine the distribution and abundance of different phytoplankton taxa. Numerous studies have shown that fronts define the limits of larger phytoplankton (e.g., Kop-

cynska & Fiala 2003, Laubscher et al. 1993) and several authors show a correlation between the southern limits of *Prochlorococcus* (Fouilland et al. 1999, Furuya et al. 1986) or PE-containing picoplankton (Detmer & Bathman 1997) and the STFZ.

The 2004 ICEFISH cruise (International Collaborative Expedition to collect and study Fish Indigenous to Sub-Antarctic Habitats, www.icefish.neu.edu) was a unique opportunity to examine the wintertime distribution of picophytoplankton across a large latitudinal gradient of the Atlantic sector of the Southern Ocean during the austral winter. Here we report the abundance of major picophytoplankton groups observed in polar, subantarctic, and subtropical waters during the austral winter, along portions of the cruise track that encountered a wide range of water temperatures and traversed across at least four major frontal features.

Material and Methods

During the ICEFISH expedition aboard the R/V Nathaniel Palmer (Cruise NBP-0404, 17 May–17 July, 2004), we examined the abundance of picophytoplankton in surface waters along a 366 km W–E transect at $\sim 55^{\circ}\text{S}$ latitude between the South Sandwich Islands and Bouvetoya Island, along a 2,780 km S–N transect from Bouvetoya Island to Tristan da Cunha Island, and along a 2,050 km W–E transect at ~ 37 to 35°S latitude between Tristan da Cunha Island and Capetown, South Africa (Fig. 1).

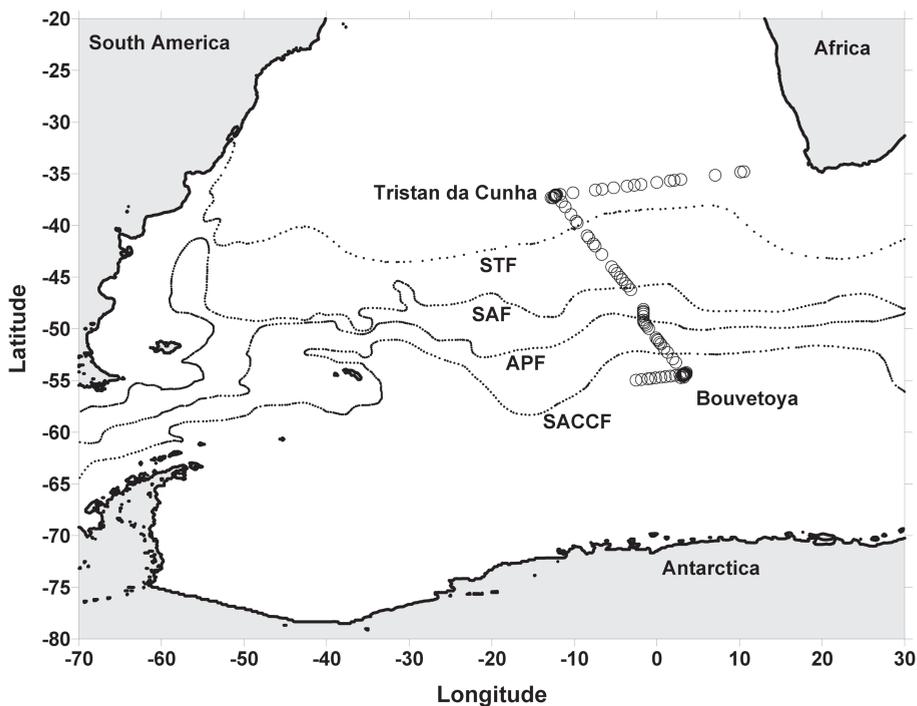


Fig. 1. Sampling locations shown as open circles in the southern Atlantic Ocean and Atlantic sector of the Southern Ocean. Climatological position of major frontal features are shown with dotted lines: Southern Antarctic Circumpolar Current Front (SACCF), Antarctic Polar Front (APF), Subantarctic Front (SAF), and the Subtropical Front (STF), based on Orsi et al. (2001, 1995).

All water samples were collected while underway using the ship's flow-through seawater system, which has an intake at ~5.6 m water depth. Duplicate flow cytometry samples were preserved in 1.0% buffered paraformaldehyde, held at 4 °C for ten to fifteen minutes, and then flash frozen in liquid nitrogen. Samples were stored in liquid nitrogen or in a freezer at -80 °C until they were analyzed at Bedford Institute for Oceanography; the samples were always shipped on dry ice while in transit. Temperature and salinity of the water at sampling point were recorded from the vessel's underway data collection system (RV/DAS) when samples were taken. Also used in this analysis are the continuous underway temperature records consisting of more than 32,000 one minute time averages (for processing information, cf. Knap et al. 1996).

Cell concentrations of picophytoplankton, nanophytoplankton, and bacterioplankton (i.e., non-autofluorescent picoplankton) were analysed by flow cytometry (FACSort, Becton Dickinson) following standard protocols (Marie et al. 1999) in routine use (Li & Dickie 2001). Phytoplankton were detected by natural autofluorescence using blue laser excitation (488 nm) and long-pass red emission (>650 nm). Cells smaller than 2 µm equivalent spherical diameter were classified as picoplankton and those larger as nanoplankton. In turn, picophytoplankton were partitioned into three groups: PE-containing cells (detected in the orange waveband, 585 ± 21 nm), *Prochlorococcus* cyanobacteria, and picoeukaryotes. Bacterioplankton were stained with SYBR® Green 1 (Molecular Probes, Oregon), a nucleic-acid binding fluorochrome, and detected in the green waveband (530 ± 15 nm). Measurements of fluorescence and light scatter were collected using logarithmic amplification and recorded in relative units in a 4-decade range spanned by 256 channels. Fluidic flow rate was calibrated by regression of the aspirated volume versus duration of analysis. Data were extracted from listmode format using WinMDI Version 2.8 (copyright Joseph Trotter, <http://facs.scripps.edu/>).

Results

A total of 111 locations were sampled in this study, spanning the latitudes of 55.0°S to 34.8°S and water temperatures that ranged from -0.8 to 17.0 °C. Overall, because of the pattern of our cruise track (Fig. 1), there is a general trend of decreasing latitude, and increasing temperature and salinity as the cruise progressed. The underway temperature record for the cruise is shown in Fig. 2 and data on temperature and phytoplankton abundance are plotted against latitude in Figs. 3 and 4; phytoplankton abundance is plotted against temperature in Figs. 5 and 6. As is apparent, all groups had their lowest abundance in cold water, reached peak abundance in the warm (~14–15 °C) water sampled at about 35°S, but then began to decrease in abundance when water temperatures exceeded 16 °C.

The underway temperature record plotted against elapsed cruise time shows the relatively small range of temperature variation observed along the southern west-to-east transect, located at approximately 54.5°S (Fig. 2). Water temperatures ranged from -0.90 to -0.37 °C, with an average of -0.68 °C. The temperature record for the S–N transect shows at least six strong temperature gradients where temperature increased rapidly over a small increment of latitude (Labelled A–F in Fig. 2). These occurred at approximately 52, 49, 45, 43, 42, and 38°S, respectively, and represented changes of between 1.2 and 1.5 degrees temperature in less than 0.3 degrees latitude (B, C, D, E, F) At A, the temperature gradient is not so steep, representing about one degree temperature change in one degree of latitude. Another region, of even smaller gradient, but overall large magnitude of change, can be noted in the temperature record between 37 and 36°S where the temperature increases from ~15 °C to >17 °C. The locations and properties of the fronts we observed are compared to previously reported locations of major frontal features in the Antarctic Circumpolar Current in Table 1. Based on the historical data, we have identified Front A as the Southern Antarctic Circumpolar Front (SACCF), Front B as the Polar Front (PF), Front C as the Subantarctic Front (SAF), Front E as the Southern Subtropical Front and Front F as the Northern

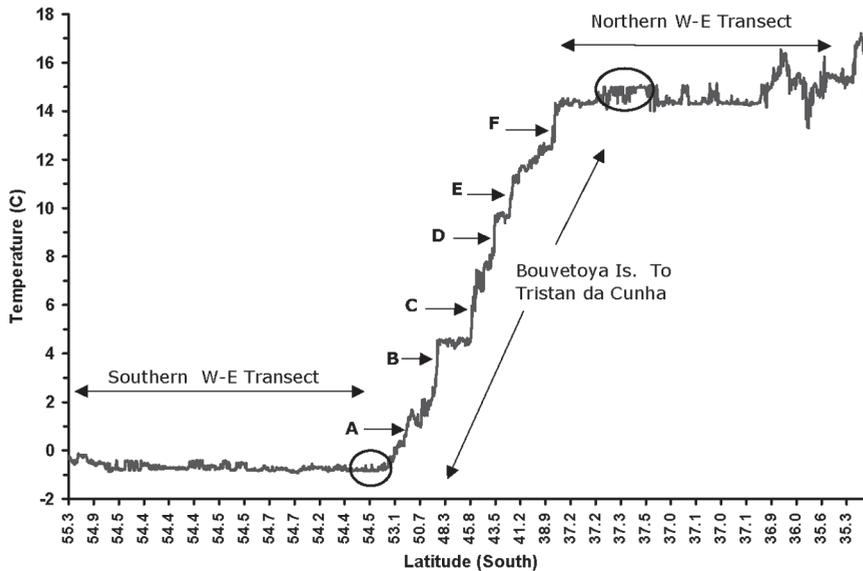


Fig. 2. Surface temperature record from the underway sampling system plotted as a linear function of elapsed cruise time and labelled according to latitude. Three segments of the cruise are noted, west-to-east transects near Bouvetoya Island, south-to-north transects from Bouvetoya Island, to Tristan da Cunha, and a subtropical west-to-east transect between Tristan da Cunha and Capetown. Data collected while the ship was sampling around each island region is enclosed in a circle. Fronts, or regions or rapid temperature change, are noted with letters as discussed in the text.

Subtropical Front. In Figure 1, a single location for the Subtropical Front is shown, following the data of Orsi et al. (1995) as made available through the Global Change Master Directory of NASA/Goddard (<http://gcmd.nasa.gov>; Keywords Ocean_Circulation_Fronts) and the Australian National Oceanographic Data Center (Orsi & Ryan 2001).

Picoeukaryotes were found at all sampling locations and were essentially the only picophytoplankton group in the coldest, southernmost sampling locations (Fig. 3A, Fig. 4). *Prochlorococcus* was only observed in waters exceeding 10 °C, whereas, as discussed below, PE-containing picoplankton were absent from the coldest stations, but began to occur consistently once temperatures exceeded 0 °C and regularly reached concentrations greater than 10³ ml⁻¹ in water as cold as 2.7 °C (Figs. 3A, 4B).

Total picophytoplankton abundance ranged from a minimum of 1.1 x 10³ cells ml⁻¹, composed entirely of picoeukaryotes, at our southernmost station to a maximum of 2.3 x 10⁵ cells ml⁻¹, in subtropical water near the end of the sampling (Fig. 3C). At the subtropical sampling location where maximum picophytoplankton abundance was observed, as well as one other location where total picophytoplankton abundance exceeded 2.0 x 10⁵ cells ml⁻¹, water temperature was >14 °C, and the community was dominated by *Prochlorococcus*, which exceeded 73% of the total picophytoplankton abundance. Even though *Prochlorococcus* dominated these warmer waters, this is also the region where picoeukaryote concentrations were the highest (Fig. 4A).

Picoeukaryotes were present in lowest abundance at our southernmost stations, where water temperatures were coldest and where picoeukaryotes were the only form of pigmented picoplankton found in the samples (Figs 3A, 4A). Picoeukaryotic phytoplankton abundance ranged from 1–2.5 x 10³ at temperatures below 0.0 °C to 1.7 x 10⁴ ml⁻¹ just east of Tristan da Cunha.

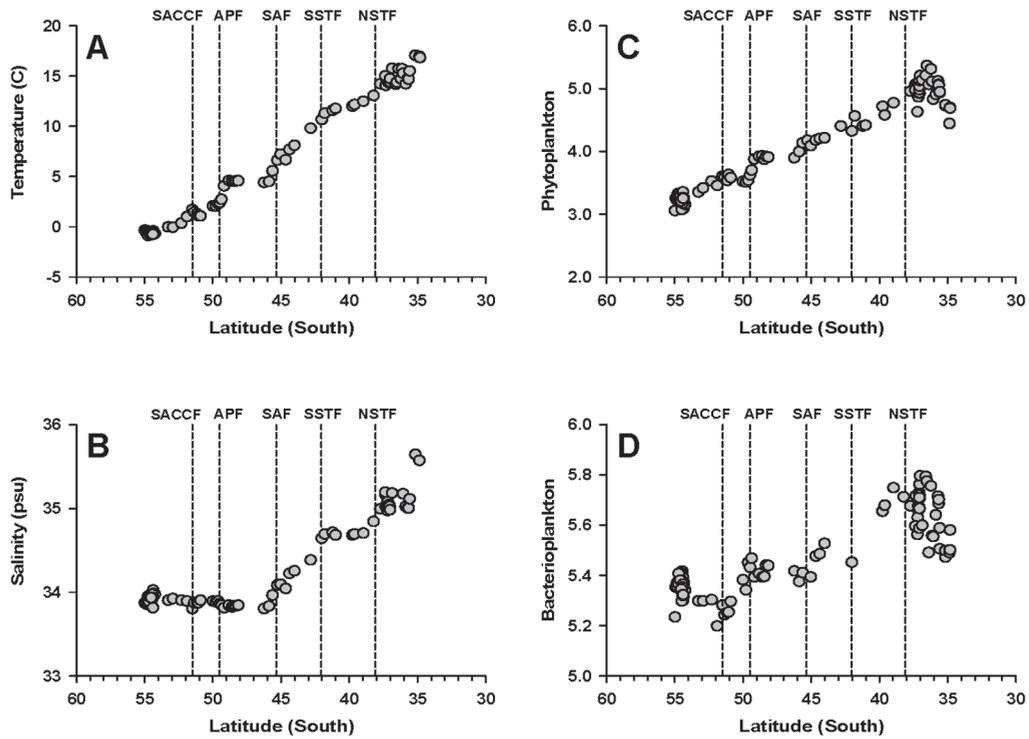


Fig. 3. Latitudinal distribution of temperature (A), salinity (B), phytoplankton (C) and bacterioplankton (D). Cell concentrations are in log cells per millilitre. Positions of frontal zones noted in the text are shown with vertical dotted lines. Abbreviations as in Fig. 1 except NTSF and STSF represent the northern and southern tropical fronts, respectively (see text and Table 1).

Of the nearly 111 locations sampled, 41 occurred where water temperature was <1 °C. In general, PE-containing picoplankton were absent from these very cold waters, but trace levels (<10 ml⁻¹) of PE-containing picophytoplankton were observed in four of the 41 samples and slightly higher concentrations (26 ml⁻¹ and 175 ml⁻¹, respectively) in two more. At trace levels, too few of these cells were counted to constitute a recognisably distinct cytometric cluster; thus, cell concentrations were based on the number of particles that met cytometric criteria (light scatter and orange fluorescence) established from nearby samples with unambiguous PE signatures. PE-containing picoplankton did not appear consistently in samples until the water temperature exceeded 1.26 °C, at which point abundance went up incrementally with increasing temperature, consistently exceeding 10² ml⁻¹ at temperatures >2.0 °C, 10³ ml⁻¹ at temperatures >4 °C, and 10⁴ ml⁻¹ at temperatures >9 °C. Maximum abundance of PE-containing picoplankton (5.9×10^4 ml⁻¹) was observed in the same subtropical waters as maximum picoeukaryote abundance (Fig. 4). As noted earlier, these stations were dominated by *Prochlorococcus*.

Prochlorococcus were not observed in water cooler than 10.65 °C or south of 42°S, but they were the dominant picophytoplankton in all samples collected in water warmer than 14 °C. All samples containing detectable *Prochlorococcus* populations were collected north of 38°S. *Prochlorococcus* reached highest abundance ($>10^5$ ml⁻¹) at stations along the northern W–E transect between 10.1 and 1.1°E, where water temperatures ranged from 14.3 to 15.7 °C and salinity from 35.0 to

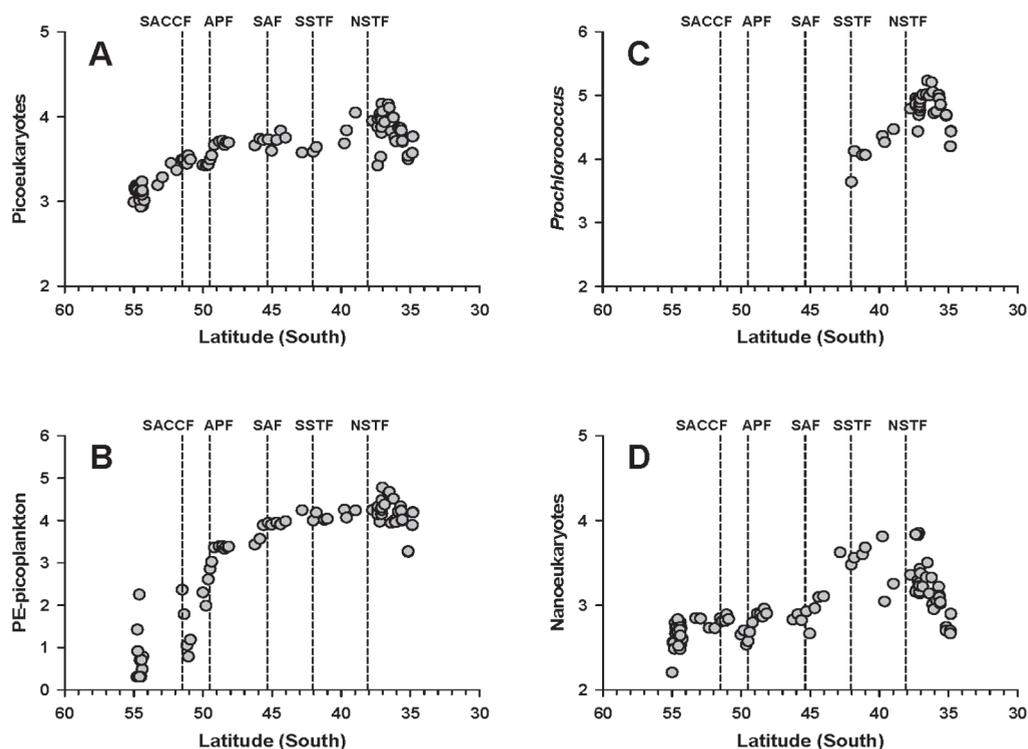


Fig. 4. Latitudinal distribution of picoeukaryotic phytoplankton (A), phycoerythrin-containing picophytoplankton (B), *Prochlorococcus* (C), and nano-eukaryotic phytoplankton (D). Cell concentration units are log cells per millilitre. The sum of these four groups is shown in Fig. 2C as phytoplankton. Abbreviations as in Fig. 3.

35.18 psu. These were neither the warmest nor most saline waters sampled, but they were the most centrally located stations on the transect between Tristan da Cunha and Capetown.

Bacterioplankton, like picoeukaryotes, were found at all stations and in increasing numbers as water temperatures increased and latitude decreased (Fig. 3D). Like all other sampled groups, bacterioplankton concentration reached maximum levels $\sim 8 \times 10^5 \text{ ml}^{-1}$ in 14–15°C water just east of Tristan da Cunha and decreased substantially in the warmer water ($>16^\circ\text{C}$) that was sampled further east along the transect towards Cape Town (Figs. 3,4).

Discussion

In both the North Atlantic (Murphy & Haugen 1985) and South Atlantic (Fig. 4), there is a general trend of decreasing abundance of PE-containing picophytoplankton as latitude increases and temperature decreases, and a very strong dominance of the picoplankton by picoeukaryotes in the coldest water sampled. However, our results differ from those of Murphy & Haugen (1985) in two important ways. First, we found stable, relatively high, concentrations of PE-containing picophytoplankton at $\sim 4^\circ\text{C}$, a much lower temperature than appears to support substantial populations of PE-containing cells in the North Atlantic (Murphy & Haugen 1985), or elsewhere in

Table 1. Position of major frontal features in the Antarctic Circumpolar Current in the vicinity of the Greenwich Meridian, with comparison to the location of the fronts identified in Figure 2.

| Front (Label in Fig. 2) | Temperature Range (°C) | Temperature Change (°C) | Approximate Latitudes (Degrees South) | Citation |
|--|---------------------------|----------------------------|--|----------|
| Southern Antarctic Circumpolar Current Front (SACCF) | | | | |
| (Front A) | 0.33–1.68 | 1.38 | 52.3–52.5 51.5 | 5 6 |
| Antarctic Polar Front (APF) | 3.7–6.6 3.5–7.0 | 2.9 3.5 | 49.7 49.5 | 1 2 |
| | NR | 1.8 | 50.2 | 3 |
| | NR | 1.6 | 49–50 | 4 |
| (Front B) | 1.35–4.38 | 2.93 | 48.8–50.0 49.0–50.0 | 5 6 |
| Subantarctic Front (SAF) | 7.3–10.5 6.5–9 | 3.2 2.5 | 45–45.5 44.5–45.2 | 1 2 |
| | NR | 3.9 | 45.2–47.3 | 3 |
| | NR | 3.5 | 45, 46 | 4 |
| | | | 46 | 5 |
| (Front C) | 4.54–7.27 | 2.73 | 45.0–45.7 | 6 |
| Subtropical Convergence (STF) | 14.5–19 15–20 | 4.5 5 | 39.3–39.7 38–39 | 1 2 |
| | NR | 4.8 south | 38–40 | 3 |
| | NR | 2.9 north | 35–36 | 3 |
| | NR | 7.3 | 40.3–43 | 4 |
| | | | 40.1 | 5 |
| (Front E) (SSTF) | 9.77–11.25 | 1.48 | 41.9–42.2 | 6 |
| (Front F) (NSTF) | 12.71–14.07 | 1.36 | 37.9–38.3 | 6 |

Refs: ¹Eyraud et al. 1999; ²Laubscher et al. 1993; ³Lutjeharms et al. 1984;
⁴Belkin et al. 1996; ⁵Orsi et al. 1995 (at longitude of intersection with portion of
ICEFISH cruisetrack sampled for this study); ⁶This Study, (see text and Fig. 2)

the Southern Ocean (Fouilland et al 1999, but see Marchant et al. 1987 and Mikaelyan 1987). Second, whereas picoeukaryotes completely dominate the picoplankton in the coldest waters we sampled, their abundance increases with temperature as latitude decreases, but Murphy & Haugen (1985) described a pattern of increasing picoeukaryotic abundance as latitude increased. It should be noted that, whereas Murphy & Haugen sampled between 63 and 35°N, a similar latitudinal range to ours (but in the opposite hemisphere), the temperature range included in their work was much warmer, with many samples collected at stations where surface temperatures exceeded 20 °C and essentially none where water temperatures were less than 4 °C. Thus, the apparent difference in the relationship between picoeukaryote abundance and temperature may reflect that fact that we sampled more sites with extremely low temperatures (< 0 °C) and they sampled more sites with very high temperatures (> 20 °C). From the combined data sets, it appears that both very high and very low water temperatures may be associated with decreased overall abundance of picoplankton (Fig. 5).

This study is based on flow cytometric characterization of the cells using standard protocols (Marie et al. 1999, Li & Dickie 2001). We stress that the conclusions we make about the structure of the pico- and nanoplankton community are based on cells that have been assigned to major groups based on the properties of their fluorescence and forward angle light scatter (FALS). However, for both *Prochlorococcus* and small eukaryotes these parameters represent fairly good

characters for identification to these broad taxonomic levels (Marie et al. 1999, Li & Wood 1985, Partensky 1999, Wood et al. 1985),

Phycocyanin-containing picoplankton are generally assumed to be cyanobacteria, and therefore prokaryotic. However, recent evidence reports the existence of small eukaryotic algae with a phycobiliprotein-containing organelle. These algae are described as slightly oblong cells 2 x 6 µm in size (Not et al. 2007). They were recovered in filtrates after size fractionation of marine plankton through 3 µm membranes (Not et al. 2007) and are somewhat larger than picoplankton as traditionally defined (Sieburth et al. 1978). Standard flow cytometric protocols (Marie et al. 1999) would not assign them to the picoeukaryotes group because they emit orange fluorescence, even if they showed FALS properties associated with 2 µm cells. Instead, they would be accounted among the PE-containing cells. Because these small PE-containing eukaryotes are somewhat larger than picocyanobacteria, they would present a distinctive light scatter signature amongst the orange-fluorescing cells and be described as 'PE-containing nanoplankton' in this study (See Methods). Hydrodynamic considerations and evidence indicate that non-spherical cells tend to align in the direction of their longest dimension before they enter the sensing zone of a flow cytometer, thus presenting the larger dimension to the path of the light beam, and producing FALS based on that dimension (Kachel et al. 1990). Determination of the actual flow cytometric signature of these small PE-containing eukaryotes, termed 'picobiliphytes' by Not et al. (2007), will be an important step toward identifying their global abundance. In our samples from the Southern Ocean, we did not detect cytometric clusters of orange-fluorescing cells that were larger than 2.0 µm equivalent spherical diameter. The presence of picobiliphytes in the Southern Ocean remains to be established.

Picophytoplankton community complexity appears to increase at each frontal boundary we crossed, moving from the polar regions north. South of the SACCF, the picophytoplankton community consisted of picoeukaryotes. They occurred in substantial abundance ($>10^3$ cells ml⁻¹) at all 40 stations south of the SACCF where water temperatures were less than 0 °C. Whereas nanoeukaryotes and heterotrophic bacteria were also observed in these samples, photosynthetic cyanobacteria were essentially absent. Picoeukaryotes completely dominated the picophytoplankton, representing >99% of the community in all but one sample. However, north of the front we identified as the SACCF (Front A, Fig. 2), water temperatures increased to ~2 °C and PE-containing picoplankton were observed at very low levels ($\sim 10^2$ ml⁻¹) in nearly all samples. From this point northward, this functional group was always present in the community and their abundance increases abruptly, and by an order of magnitude, at the APF (Fig. 4B). It increases again by nearly an order of magnitude at the SAF, and again at the NSTF (Fig. 4B). *Prochlorococcus*, which were completely absent south of the SSTF, appear abruptly as members of the community at the SSTF, and further north (Fig. 4C). We do not interpret these changes in abundance as frontal blooms because, once the abundance of a functional group increases as we cross a front, it remains high in the zone between fronts (Fig. 4).

This pattern of change in community structure and picoplankton abundance occurring abruptly at fronts strongly supports the idea that temperature alone is not the causal mechanism defining picophytoplankton abundance in the Southern Ocean (cf. Letelier & Karl 1989). Instead, community structure appears to be determined by an interplay between water mass coherence, the maintenance of particular phytoplankton assemblages within a water mass, and the physiological temperature limits of different phytoplankton groups. This phenomenon is easier to observe in the regions we studied because the distance between fronts is greater than in the Drake Passage. In this setting, diffusion of a few cells across frontal boundaries from a region of favourable conditions to a less favourable region cannot explain patterns of distribution that persist throughout our entire inter-frontal sampling area. Following this logic, it is important to note that we observed substantial populations of PE-containing picoplankton in all the samples collected between the APF and SSTCF, a distance of roughly 300 km. This indicates that these cells are regular members of the wintertime plankton community in this portion of the ACC.

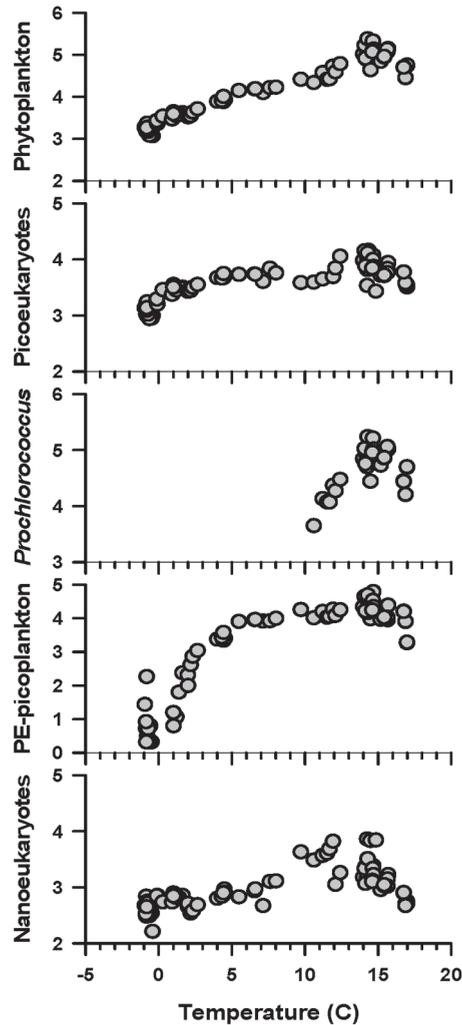


Fig. 5. Distribution of different phytoplankton groups with temperature. Cell concentration units are log cells per millilitre.

In spite of their small size, picoplankton can be a direct source of organic carbon for higher trophic levels (protists and invertebrates), contributing to the carbon pool that fuels the flux of particles sinking to the deep ocean (Barber 2007). Food web modelling indicates that all primary producers, including picoplankton, can contribute to biogenic carbon export from the surface layer of the ocean at rates proportional to their production rates (Richardson & Jackson 2007). Our data suggest that picoeukaryotes and PE-containing picoplankton should also be incorporated into models of food web dynamics for this area. Further, it is possible that each water mass defined by the frontal boundaries we observe supports a particular food web network. With different food web dynamics operating in each inter-frontal water mass, a strong possibility exists that biotic factors (such as top down control or interspecies interactions) are more important than temperature *per se* in shaping the changes in abundance of different picoplankton groups at frontal boundaries.

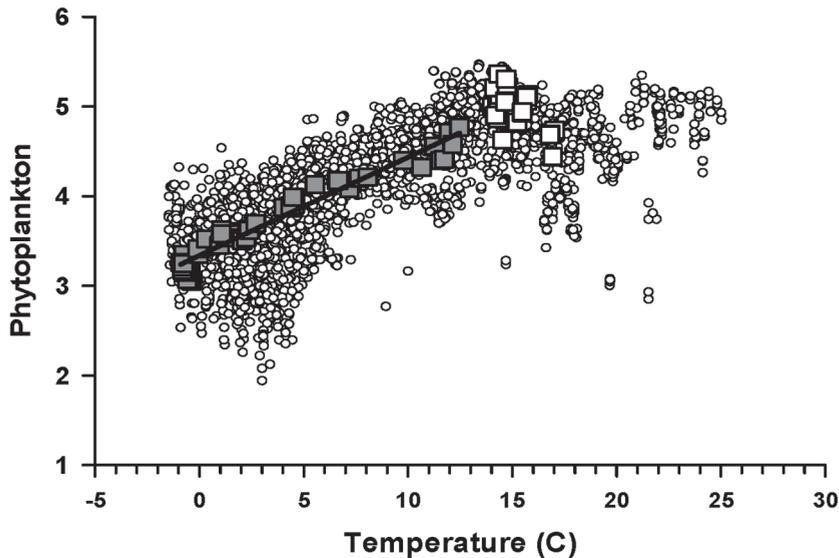


Fig. 6. Relationship between phytoplankton abundance and temperature. ICEFISH stations, shown as squares, are overlain on a global database of phytoplankton in the upper ocean (c.f. Li 2008). ICEFISH stations south of North Subtropical Front (NSTF), as defined in the text and Table 1, are shown in solid symbols; those north of NSTF shown with open symbols. The regression equation for ICEFISH stations south of NSTF is: $\log N = 3.34 + (0.11 * T)$, $R^2 = 0.96$.

In surface waters of the world's oceans, at any particular temperature, the abundance of phytoplankton is variable and spans a range of about one to two orders of magnitude (Li 2008). The wintertime abundance of phytoplankton in the Atlantic sector of the Southern Ocean lies entirely within this range of variability (Fig. 6). From 55°S to 38°S, the apparent linear increase in log phytoplankton abundance with decreasing latitude or increasing temperature arises from underlying distributions of picoeukaryotes, PE-containing cells, *Prochlorococcus* and nanoeukaryotes, which are themselves not similarly distributed over the latitudinal or temperature range. In other words, the community is structured in such a way that the sum of its components gives rise to a striking pattern that is closely aligned with temperature (Fig. 5), but which is not reflected in the individual functional groups. This ecological community assembly over a temperature range, which spans over space (55–38°S) is remarkably similar to the community assembly of phytoplankton over time through the annual temperature cycle in the North Atlantic Ocean (Li et al. 2006). In both cases, a strong linear dependence of log phytoplankton abundance on temperature is evident only when component groups are summed. However, in the North Atlantic, the ecological community assembles within a physical context that is largely undifferentiated by the presence of an extensive frontal system, reflecting replacement of one group by another during a form of seasonal succession, rather than the spatially defined mode of assembly reported here.

The Southern Ocean serves as a particularly striking example of temperature-related change in phytoplankton community assembly, which may be a process of wide generality at the large scale. Indeed, there is niche partitioning even amongst *Prochlorococcus* ecotypes that is largely related to temperature change at the basin-scale in the North and South Atlantic Ocean (Johnson et al. 2006). In this study, there is also a suggestion that water mass-related phenomena also influences community organisation across trophic levels, either placing limits on the response of the phytoplankton community to temperature-based assembly rules or providing a mechanism

that enhances stability in response to changes in temperature. Regardless, our new data indicate that picophytoplankton are a significant component of the ecological community in the Southern Ocean and South Atlantic in winter.

Dedication and Acknowledgements

This paper is dedicated to Greta Fryxell, who has been my friend since I (AMW) was an undergraduate studying the “hexagonal aereolae” of *Coscinodiscus* in Matagorda Bay, Texas. Greta is a peerless role model for those seeking an honourable path through life or the best a scientific career has to offer. This study was chosen for your book, Greta, because, like our *Thalassiosira tumida* paper, it represents the wonder that can be achieved when a few people combine their resources to do something no one planned for when they went to the Antarctic.

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References

- BARBER, R. T. (2007): Picoplankton do some heavy lifting. – *Science* **315**: 777–778.
- BELKIN, I. M. & A. L. GORDON (1996): Southern Ocean fronts from the Greenwich meridian to Tasmania. – *J. Geophys. Res.* **101**: 3675–3696.
- BOOTH, B. C. & R. A. HORNER (1997): Microalgae on the Arctic Ocean Section 1994: species abundance and biomass. – *Deep-Sea Res. II* **44**: 1607–1622.
- BOOTH, B. C. & W. O. SMITH, JR. (1997): Autotrophic flagellates and diatoms in the Northeast Water Polyna, Greenland: summer 1993. – *J. Mar. Sys.* **10**: 241–261.
- DETMER, A. E. & U. V. BATHMANN (1997): Distribution patterns of autotrophic pico- and nanoplankton and their relative contributions to algal biomass during spring in the Atlantic sector of the Southern Ocean. 1997. – *Deep-Sea Res. II* **44**: 299–320.
- EYNAUD, F., J. GIRAUDEAU, J.-J. PICHON, & C. J. PUDSEY (1999): Sea-surface distribution of coccolithophorids, diatoms, silicoflagellates, and dinoflagellates in the South Atlantic Ocean during the austral summer 1995. – *Deep-Sea Res.* **46**: 451–82.
- FOUILLAND, E., C. DESCOLAS-GROS, C. COURTIES, & V. PONS (1999): Autotrophic carbon assimilation and biomass from size-fractionated phytoplankton in the surface waters across the subtropical frontal zone (Indian Ocean). – *Polar Biol.* **21**: 90–96.
- FIALA, M., B. DELILLE, C. DUBREUIL, E. KOPSYNSKA, K. LEBLANC, J. MORVAN, B. QUÉGUINER, S. BLAIN, C. CAILLIAU, P. CONAN, R. CORVAISIER, M. DENIS, M. FRANKIGNOULLE, L. ORIOL & S. ROY (2003): Mesoscale surface distribution of biogeochemical characteristics in the Crozet Basin frontal zones (South Indian Ocean). – *Mar. Ecol. Prog. Ser.* **249**: 14.
- FRONEMAN, P. W., E. A. PAKHOMOV & M. G. BALARIN (2004): Size-fractionated phytoplankton biomass, production and biogenic carbon fixation in the eastern Atlantic sector of the Southern Ocean in late austral summer 1997–1998. – *Deep-Sea Res. II* **51**: 2715–2729.
- FURUYA, K., H. HASUMOTO, T. NAKAI & T. NEMOTO (1986): Phytoplankton in the Subtropical Convergence during the austral summer: community structure and growth activity. – *Deep-Sea Res.* **33**: 621–30.

- HILL, V., G. COTA & D. STOCKWELL (2005): Spring and summer phytoplankton communities in the Chukchi and eastern Beaufort Seas. – *Deep-Sea Res. II* **52**: 3369–3385.
- JOHNSON, Z. I., E. R. ZINSER, A. COE, N. P. MCNULTY, E. MALCOLM, S. WOODWARD & S. W. CHISHOLM (2006): Niche partitioning among *Prochlorococcus* ecotypes along ocean-scale environmental gradients. – *Science* **311**: 1737–1740.
- KACHEL, V., H. FELLNER-FELDEGG & E. MENKE (1990): Hydrodynamic properties of flow cytometry instruments. – In: M. R. MELAMED, T. LINDMO & M. L. MENDELSON (eds.): *Flow Cytometry and Sorting*: 27–44. 2nd Ed., Wiley-Liss, N.Y.
- KNAP, A., A. MICHAELS, A. CLOSE, H. DUCKLOW & A. DICKSON (1996): Protocols for the Joint Global Ocean Flux Study (JGOFS) Core Measurements.
- JGOFS Report Nr. 19: vi+170 pp. Reprint of the IOC Manuals and Guides No. 29, UNESCO 1994.
- KOPCZYNSKA, E. E. & M. FIALA (2003): Surface phytoplankton composition and carbon biomass distribution in the Crozet Basin during austral summer of 1999: variability across frontal zones. – *Polar Biol.* **27**: 17–28.
- LAUBSCHER, R. K., R. PERISSINOTTO & C. D. MCQUAID (1993): Phytoplankton production and biomass at frontal zones in the Atlantic Sector of the Southern Ocean. – *Polar Biol.* **13**: 471–81.
- LETELIER, R. M. & D. M. KARL (1989): Phycoerythrin-containing cyanobacteria in surface waters of the Drake Passage during February 1987. – *Ant. J.* **24**: 185–188.
- LI, W. K. W. (2008): Plankton populations and communities. – In: WITMAN, J. & K. ROY (eds.): *Marine Macroecology*: in press. University of Chicago Press, Chicago.
- LI, W. K. W. & P. M. DICKIE (2001): Monitoring phytoplankton, bacterioplankton, and virioplankton in a coastal inlet (Bedford Basin) by flow cytometry. – *Cytometry* **44**: 236–246.
- LI, W. K. W. & A. M. WOOD (1988): Vertical distribution of ultraphytoplankton in the North Atlantic: Analysis by flow cytometry and epifluorescence microscopy. – *Deep-Sea Res.* **35**: 1615–38.
- LI, W. K. W., W. G. HARRISON & E. J. H. HEAD (2006): Coherent assembly of phytoplankton communities in diverse temperate ocean ecosystems. – *Proc. Roy. Soc. B* **273**: 1953–1960.
- LOVEJOY, C., W. F. VINCENT, S. BONILLA, S. ROY, M.-J. MARTINEAU, R. TERRADO, M. POTVIN, R. MASSANA & C. PEDRÓS-ALIÓ (2007): Distribution, phylogeny, and growth of cold-adapted picoprasinophytes in Arctic seas. – *J. Phycol.* **43**: 78–89.
- LUTJEHARMS, J. R. E. & H. R. VALENTINE (1984): Southern Ocean thermal fronts south of Africa. – *Deep-Sea Res.* **31**: 1461–1475.
- MARCHANT, H. J., A. T. DAVIDSON & S. W. WRIGHT (1987): The distribution and abundance of chorococoid cyanobacteria in the Southern Ocean. *Proc. NIPR Symp.* – *Polar Biol.* **1**: 1–9.
- MARIE, D. M., PARTENSKY, F., D. VAULOT & C. BRUSSAARD (1999): Enumeration of phytoplankton, bacteria, and viruses in marine samples. – *Current Protocols in Cytometry* 11.11.1–11.11.15, Wiley & Sons, New York.
- MIKAELIAN, A. S. (1987): Picophytoplankton of subantarctic waters of the Pacific Ocean. – *Ocean.* **27**: 615–620.
- MURPHY, L. S. & E. M. HAUGEN (1985): The distribution and abundance of phototrophic ultraplankton in the North Atlantic. – *Limnol. Oceanogr.* **30**: 47–58.
- NING, X., L. ZILIN, G. ZHU & J. SHI (1996): Size-fractionated biomass and productivity of phytoplankton and particulate organic carbon in the Southern Ocean. – *Polar Biol.* **16**: 1–11.
- NOT, F., R. MASSANA, M. LATASA, D. MARIE, C. COLSON, W. EIKREM, C. PEDRÓS-ALIÓ, D. VAULOT & N. SIMON (2005): Late summer community composition and abundance of photosynthetic picoeukaryotes in Norwegian and Barents Seas. – *Limnol. Oceanogr.* **50**: 1677–1686.
- NOT, F., K. VALENTIN, K. ROMARI, C. LOVEJOY, R. MASSANA, K. TÖBE, D. VAULOT, & L. K. MEDLIN (2007): Picobiliphytes: A marine picoplanktonic algal group with unknown affinities to other eukaryotes. – *Science* **315**: 253–255.
- ORSI, A. H., T. WHITWORTH, & W. D. NOWLIN (1995): On the meridional extent and fronts of the Antarctic Circumpolar Current. – *Deep-Sea Res. I*, **42**: 641–673.
- ORSI, A. & U. RYAN (2001, updated 2006): Locations of the various fronts in the Southern Ocean, Australian Antarctic Data Centre – CAASM Metadata (/aacd/metadata/) (Direct link to metadata is http://aacdmaps.aad.gov.au/aacd/metadata/metadata_redirect.cfm?md=AMD/AU/southern_ocean_fronts)
- PARTENSKY, F., W. R. HESS & D. VAULOT (1999): *Prochlorococcus*, a marine photosynthetic prokaryote of global significance. – *Microbiol. Mol. Biol. Rev.* **63**: 106–27.
- RICHARDSON, T. A. & G. A. JACKSON (2007): Small phytoplankton and carbon export from the surface ocean. – *Science* **315**: 838–840.

- SHERR, E. B., B. F. SHERR, P. A. WHEELER & K. THOMPSON (2003): Temporal and spatial variation in stocks of autotrophic and heterotrophic microbes in the upper water column of the central Arctic Ocean. – *Deep-Sea Res. I* **50**: 557–571.
- SIEBURTH, J. MC-N., V. SMETACEK & J. LENZ (1978): Pelagic ecosystem structure and the relationship to plankton size fractions. – *Limnol. Oceanogr.* **23**: 1256–63.
- WALKER, T. D. & H. J. MARCHANT (1989): The seasonal occurrence of chroococcoid cyanobacteria at an Antarctic Coastal site. – *Polar Biol.* **9**: 193–196.
- WOOD, A. M., P. K. HORAN, K. MUIRHEAD, D. A. PHINNEY, C. M. YENTSCH & J. B. WATERBURY (1985): Discrimination between pigment types of marine *Synechococcus* by scanning spectroscopy, epifluorescence microscopy, and flow cytometry. – *Limnol. Oceanogr.* **30**: 1303–15.
- ZUBKOV, M. V., M. A. SLEIGH, P. H. BURKILL & R. J. G. LEAKEY (2000): Picoplankton community structure on the Atlantic Meridional Transect: a comparison between seasons. – *Prog. in Oceanogr.* **45**: 369–386.

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