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Seasonal and interannual variability of size-fractionated phytoplankton biomass and community structure at station Kerfix, off the Kerguelen Islands, Antarctica

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Abstract. Time series of phytoplankton biomass and taxonomic composition have been obtained for the 3 years 1992, 1993 and 1994 in the northern part of the Southern Ocean (station Kerfix, 50°40'S, 68°25'E). Autotrophic biomass was low throughout the year (<0.2 mg m^{-3}), except during a short period in summer when a maximum of 1.2 mg chlorophyll (Chl) *a* m^{-3} was reached. During winter, the integrated biomass was low (<10 mg m^{-2}) and associated with deeply mixed water, whereas the high summer biomass (>20 mg m^{-2}) was associated with increased water column stability. During summer blooms, the >10 μm size fraction contributed 60% to total integrated biomass. Large autotrophic dinoflagellates, mainly *Prorocentrum* spp., were associated with the summer phytoplankton maxima and accounted for >80% of the total autotroph carbon biomass. In November and December, the presence of the large heterotrophic dinoflagellates *Protoperidinium* spp. and *Gyrodinium* spp. contributed a high proportion of total carbon biomass. During winter, the <10 μm size fraction contributed 80% of total Chl *a* biomass with domination of the picoplankton size fraction. The natural assemblage included mainly naked flagellates such as species of the Prasinophyceae, Cryptophyceae and Prymnesiophyceae. During spring, picocyanobacteria occurred in sub-surface water with a maximum abundance in September of 10^6 cells l^{-1}.

Introduction

For several years, the Southern Ocean was recognized to be largely low productive and with a low biomass with, however, some sites of enhanced productivity located along the marginal ice zones or coastal and frontal regions. For a long time, the Antarctic food web was considered to consist of large-size diatoms, krill and mammals (Hart, 1934; Guillard and Kilham, 1977). In contrast, recent investigations have shown that nano- and pico-size flagellates are important components of the phytoplankton community (Weber and El Sayed, 1987; Hewes *et al.*, 1990). These newer data changed the perception of the Antarctic food web which was expanded to include the 'microbial loop'. In Antarctic waters, the nanoplankton (size range 2–20 μm) include diatoms, flagellates and protozoa (Gieskes and Elbrächter, 1986; Brandini and Kutner, 1987; Becquevort *et al.*, 1992; Menon *et al.*, 1995). The picoplankton (<2 μm) are dominated by flagellates, typically prasinophytes and prymnesiophytes. Occasionally, picocyanobacteria have been reported (Marchant *et al.*, 1987; Lételier and Karl, 1989; Walker and Marchant, 1989; Andreoli *et al.*, 1993; Wright *et al.*, 1996).

The species composition, abundance and distribution of the microphytoplankton (size fraction >20 μm) are well documented (Hasle, 1969; Steyaert 1973;

Kopczynska *et al.*, 1986). Detailed information on the abundance, distribution and relative importance of the different size fractions is presented by various authors (von Bröckel, 1981; Sasaki, 1984; Kosaki *et al.*, 1985; Hosaka and Nemoto, 1986; Weber and El Sayed, 1987; Hewes *et al.*, 1990; Jacques and Panouse, 1991; Fiala and Delille, 1992; Carrada *et al.*, 1994; Xiuren *et al.*, 1996; Detmer and Bathmann, 1997; Fiala *et al.*, 1998).

Most shipboard studies have focused on regional variability. Thus, the seasonal variability in phytoplankton biomass and productivity distribution in the Southern Ocean is poorly documented (Horne *et al.*, 1969; Whitaker, 1982; Satoh *et al.*, 1986; Domanov and Lipski, 1990; Rivkin, 1991; Helbling *et al.*, 1995; Villafañe *et al.*, 1995; Delille *et al.*, 1996; Moline and Prézelin, 1996).

From 1990 to 1994, the research programme Kerfix (a part of the French contribution to JGOFS) established a time series station in the Indian sector of the Southern Ocean, southwest off the Kerguelen Islands. The primary objective was to monitor the seasonal and interannual variability of the carbon flux, and to understand the processes controlling the primary production (Jeandel *et al.*, 1998). Here, we present seasonal and interannual changes in the biomass, abundance, species composition and distribution of the total and size-fractionated phytoplankton.

Method

Sampling

The Kerfix station is located 60 miles southwest off the Kerguelen Islands (50°40'S, 68°25'E; Figure 1) in the north of the POOZ (Permanently Open Ocean Zone). It was investigated from January 1992 to March 1995. Samples were collected monthly aboard the coastal oceanographic ship 'La Curieuse' using 8 l Niskin bottles equipped with reversing thermometers. Biological samples were collected at 12 depths in the upper 300 m. Water samples were prefiltered through a 200 µm mesh screen to remove larger detrital material and large biota.

Analysis

For the total chlorophyll (Chl) *a* analysis, 1 l of seawater was filtered through a Whatman GF/F glass fibre filter at a vacuum differential of <20 cmHg. Fractionation was carried out by parallel filtering of subsamples of water (0.5 l) through Nuclepore polycarbonate membranes of 10 and 2 µm pore size. The pigment filter samples were either ground manually in pure acetone (GF/F filters) or by dipping them in 90% acetone (Nuclepore membranes) followed by an extraction period of ~12 h at 5°C. The fluorescence of the acetone extract was measured on a Perkin Elmer MPF 66 spectrofluorometer at six excitation and emission wavelengths (Neveux and Panouse, 1987). Each coupled wavelength corresponds to the fluorescence excitation and emission of each pigment analysed: Chl *a*, *b* and *c*, and phaeophytins *a*, *b* and *c*.

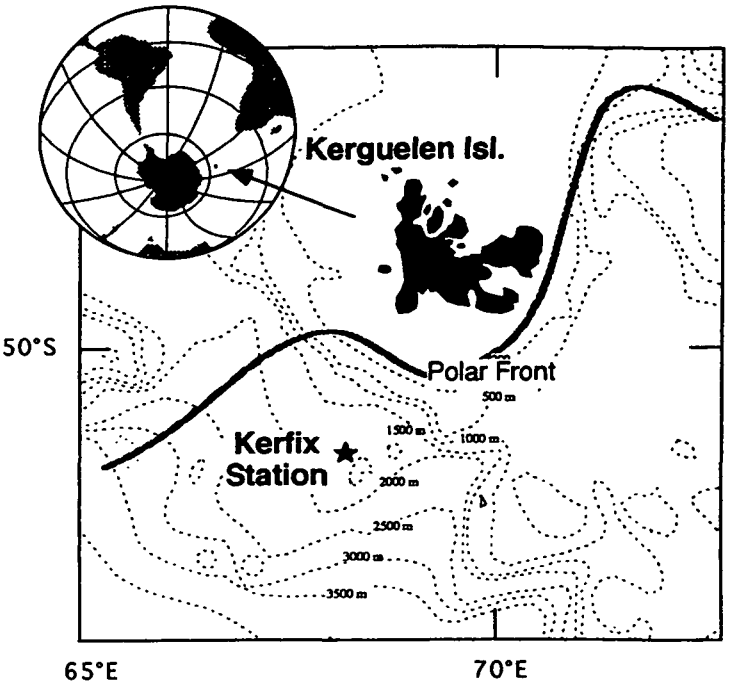

Fig. 1. Location of the time series station Kerfix (50°40'S–68°25'E), 60 miles southwest off the Kerguelen Islands. The mean position of the Polar Front (PF) is indicated according to Park *et al.* (1998).

Flow cytometric measurements

Cell numbers were determined from the Nuclepore filtrates which were fixed with glutaraldehyde (Merck, final concentration ~1%) and stored in liquid nitrogen as described by Vaulot *et al.* (1989). A Bruker ACR-1000 flow cytometer was used for analysis. We measured forward light scatter (FLS) as an indicator of size, fluorescence from phycoerythrin (580 ± 40 nm) and fluorescence from Chl *a* (680 ± 20 nm) after excitation by 480 nm light from a mercury arc lamp (Steen, 1986). Instrument calibration was checked frequently by analysing 0.94- and 1.96-μm-diameter fluorescent standard beads (Polysciences, Inc.).

Microscope cell counting

Water samples for taxonomic analysis and enumeration of phytoplankton were collected monthly at three depths: surface, Chl maximum and 100 m. Aliquots of 100 ml were preserved with formalin (final concentration 0.4%). Cells were enumerated in an Olympus inverted microscope according to procedures described by Utermöhl (1958). Cell volumes were estimated using appropriate geometric shapes (Smayda, 1978). Cell carbon biomass was calculated from cell

volume and cell abundance using the following equations: for diatoms, log C = 0.76 (log V) – 0.352; for other phytoplankton, log C = 0.94 (log V) – 0.60 (Eppley *et al.*, 1970) with V representing total cell volume (μm^3) and C cell carbon (pg).

Owing to the sample preservation and lens resolution, the microscope cell counting technique largely underestimates the picophytoplankton.

Results

Seasonal and interannual variability in autotrophic biomass

A clear seasonal trend was recorded in the Chl *a* distribution (Figure 2). During winter, the mean Chl *a* concentration was <0.2 mg m^{-3}, after which it increased from September to October and reached >0.8 mg m^{-3} in November–December in the upper 100 m. During summer, the vertical biomass distribution was closely related to the thickness (50–75 m) of the upper mixed layer (UML) (Figure 2). The highest Chl *a* values were found in the upper 100 m and a maximum was reached in the sub-surface waters. In winter, when the depth of the UML was ~200 m, the Chl *a* biomass was low and homogeneously distributed throughout the water column.

Over the 3 years of observation, the temperature and salinity showed interannual variability (Park *et al.*, 1998), whereas the distribution of the autotrophic biomass repeated itself. The highest Chl *a* concentrations were always observed in the upper 100 m, during November and December, with values around 1 mg Chl *a* m^{-3} (1.15 mg m^{-3} in 1992, 0.92 mg m^{-3} in 1993, 1.03 mg m^{-3} in 1994).

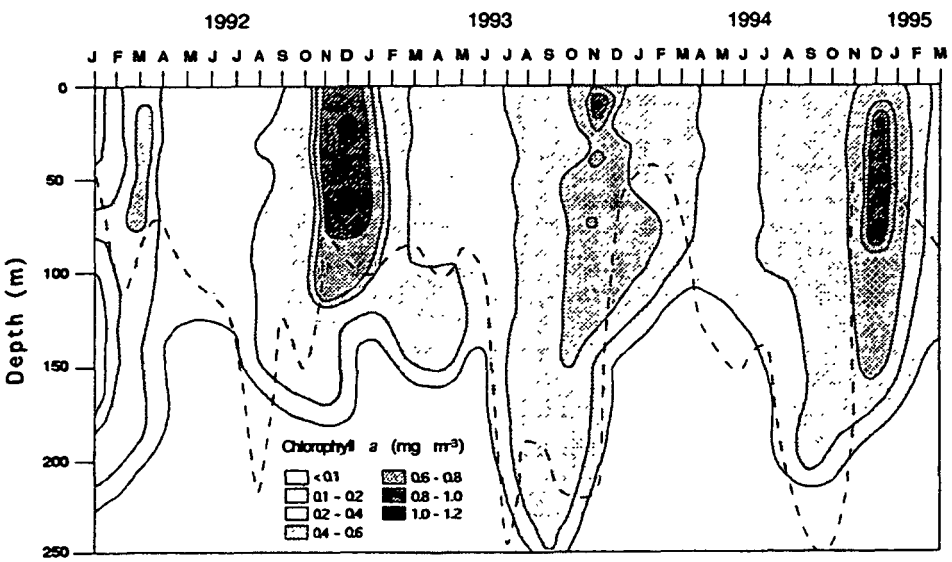

Fig. 2. Seasonal change at station Kerfix in depth distribution of chlorophyll *a* (mg m^{-3}) in the upper 100 m layer from 1992 to early 1995. The dotted line shows the upper mixed layer depth.

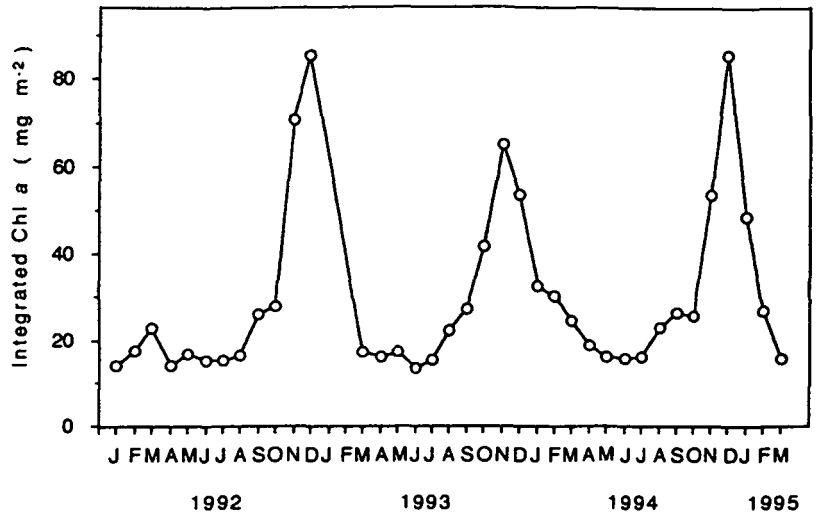

Fig. 3. Total integrated Chl *a* (mg m^{-2}) in the upper 100 m layer from 1992 to early 1995.

Integrated Chl *a* in the upper 100 m showed low values between 15 and 20 mg m^{-2} during winter, and a sharp increase to >80 mg m^{-2} in November–December (Figure 3). The maximum integrated Chl *a* ranged from 65 mg m^{-2} in 1993 to 85 mg m^{-2} in 1992 and 1994.

Seasonal size-fractionated chlorophyll a distribution

The >10 μm size fraction was predominant during summer and its integrated biomass in the upper 100 m reached a maximum value of 50.8 mg Chl *a* m^{-2} in December 1994 (Figure 4). In winter, it was low, between 3 and 5 mg m^{-2}. The seasonal variation of the picoplankton showed the same pattern as the >10 μm size fraction: low biomass during winter (between 5 and 10 mg Chl *a* m^{-2}) and high biomass during summer (22 mg Chl *a* m^{-2}). In contrast, the biomass of the 2–10 μm fraction did not show any seasonal pattern. It was low throughout the year (5–10 mg m^{-2}). During winter, Chl stock of the <10 μm size fraction always showed the highest values with the dominance of the picophytoplankton.

When expressed as percentages of the integrated Chl *a* biomass, the <2, 2–10 and >10 μm fractions contributed on average 38, 30 and 32%, respectively. The picoplankton and the >10 μm size fraction showed opposite seasonal patterns (Figure 5). During winter, the picoplanktonic fraction was predominant and contributed up to 50% of total autotrophic biomass, whereas the >10 μm size fraction contributed only 20%. In summer, during the phytoplankton bloom, the largest size fraction was the major contributor (60%) while the <2 μm size fraction contributed only around 30%. The contribution of the 2–10 μm size fraction ranged on average from 10 to 35% of Chl *a* biomass (Figure 5).

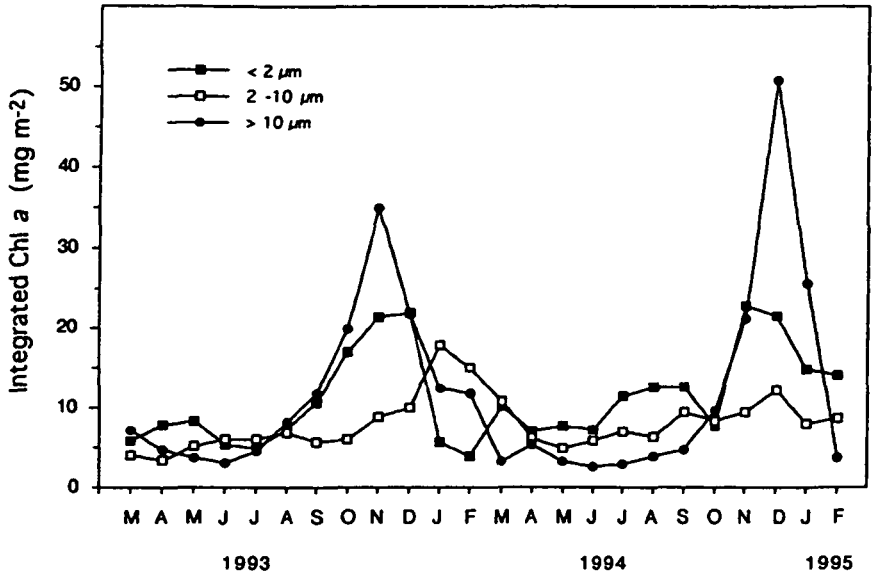

Fig. 4. Distribution of integrated Chl *a* (0 –100 m) in the <2, 2–10 and >10 µm size fractions from March 1993 to February 1995.

Temporal changes in carbon biomass of the main taxonomic groups

From December 1992 to February 1995, integrated phytoplankton carbon biomass in the upper 100 m ranged from 38.8 to 852.1 mg C m^{-2} (mean 225.3 mg C m^{-2}). Throughout the year, dinoflagellates were the dominant group and contributed on average 51.2% of total integrated carbon biomass (Figure 6). It was low during winter and increased sharply in summer, contributing >80% of the total biomass. This increase was mainly due to the larger (size > 60 µm) heterotrophic dinoflagellates *Protoperidinium* spp. and *Gyrodinium* spp.

The carbon biomass of other groups was <70 mg C m^{-2} (Figure 6). The mean contribution to the total biomass was 11, 10 and 7% for diatoms, coccolithophorids and flagellates + monads, respectively. Coccolithophorids and diatoms exhibited a seasonal trend with a higher biomass during the summer phytoplankton bloom. Throughout the year, the flagellate + monad biomass fluctuated between 7 and 37 mg C m^{-2} without any distinct maximum.

The seasonal change in the autotrophic carbon biomass was mirrored by that of Chl *a*. Summer blooms were dominated by the larger sized (>10 µm) dinoflagellates and diatoms. Autotrophic dinoflagellates were the most important carbon contributors during the Chl peaks in December 1992 and November 1993, accounting for 48 and 75% of the total autotrophic biomass, respectively. In contrast, in December 1994, diatoms contributed 44% of total biomass, followed by dinoflagellates (32%) and coccolithophorids (15%).

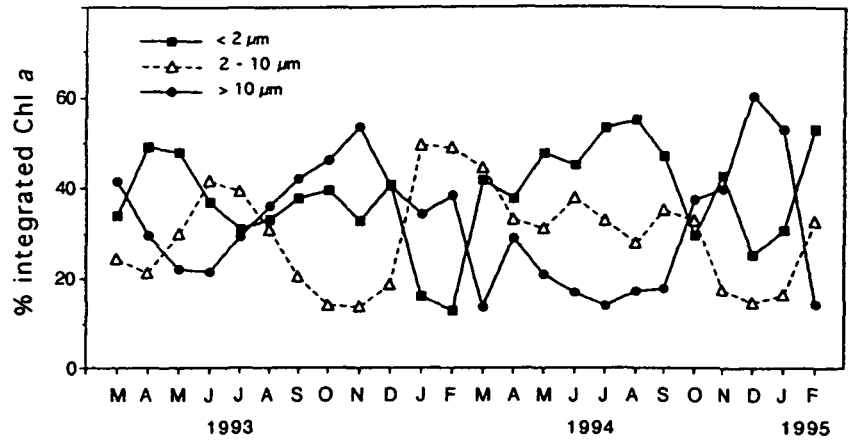

Fig. 5. Per cent contribution of the <2, 2–10 and >10 µm size fractions to total integrated chlorophyll *a* in the upper 100 m.

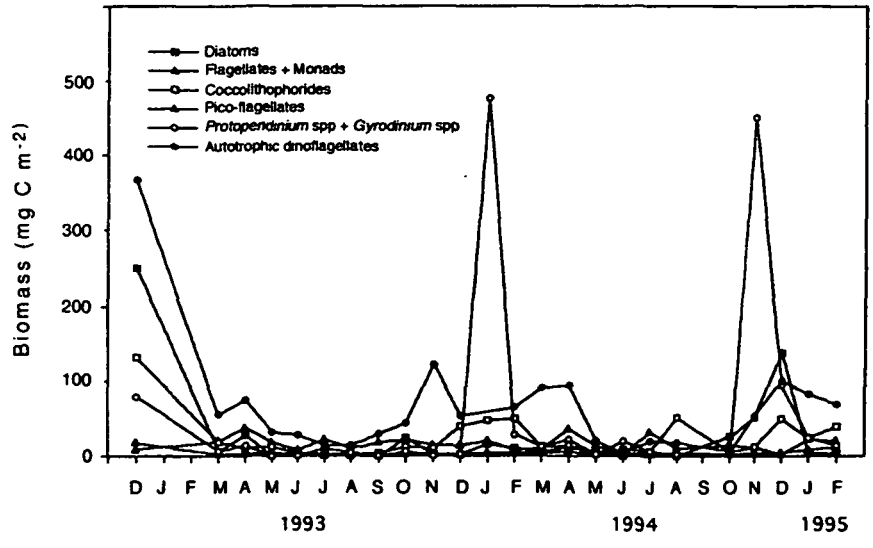

Fig. 6. Seasonal changes in integrated cell carbon (mg C m^{-2}) between 0 and 100 m of the main plankton groups.

Abundance of size-fractionated phytoplankton cells

Cell abundance measured by flow cytometry showed the same seasonal pattern as Chl *a* biomass (Figure 7). During winter, the autotrophic cell concentrations in the upper 100 m were on average 2×10^6 cells l^{-1}. During summer, abundance of phytoplankton cells increased; thus, the maximum number was measured in December (>4×10^6 cells l^{-1}). Throughout the year, the autotrophic picoplankton

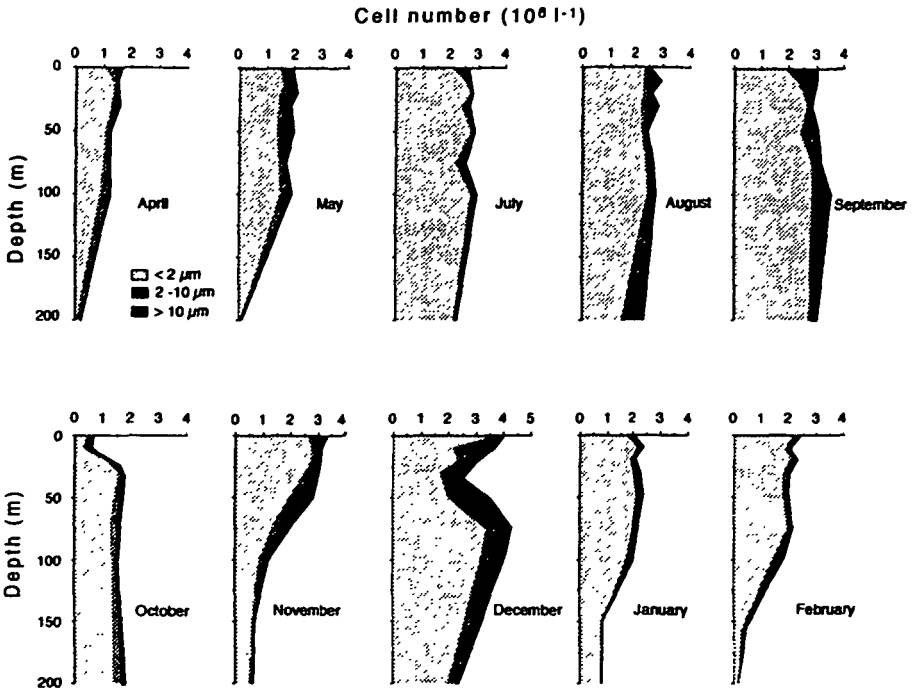

Fig. 7. Abundance of different phytoplankton size fractions as investigated by flow cytometry from April 1994 to February 1995.

were predominant, contributing an average of 72% to the total cell count. The mean contribution of the 2–10 and >10 µm size fractions was 18 and 10%, respectively. The density of the >10 µm size fraction was low during winter. A marked increase occurred from August, approaching a mean value of 0.9×10^6 cells l^{-1} in December. The mean abundance of picoplankton was ~10^6 cells l^{-1} during winter and >3×10^6 cells l^{-1} in December.

Chroococcoid cyanobacteria were detected by flow cytometry from September to December (Figure 8); in sub-surface water the numbers ranged from 10^5 to 0.6×10^6 cells l^{-1}. Their vertical distribution was homogeneous in the upper 150 m, except in September when a marked maximum of 10^6 cells l^{-1} was observed between 60 and 100 m. No cyanobacterial cells were found during the rest of the year.

Phytoplankton community composition and seasonal variations

Variation in cell numbers of the major phytoplankton groups in surface waters is generally well representative of the fluctuations at the depth of the Chl maximum, or at 100 m (Figure 9). Phytoplankton populations were composed, in order of decreasing abundance, of naked flagellates and picoplankton (1.5–20 µm), coccolithophorids (<10 µm), diatoms (5–80 µm) and dinoflagellates (5–60 µm)

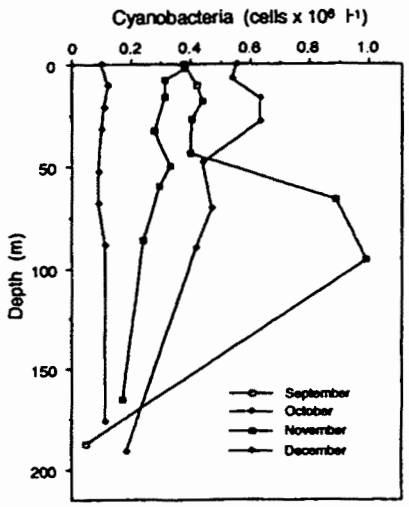

Fig. 8. Vertical distribution of cyanobacterial abundance as investigated by flow cytometry from September to December 1994.

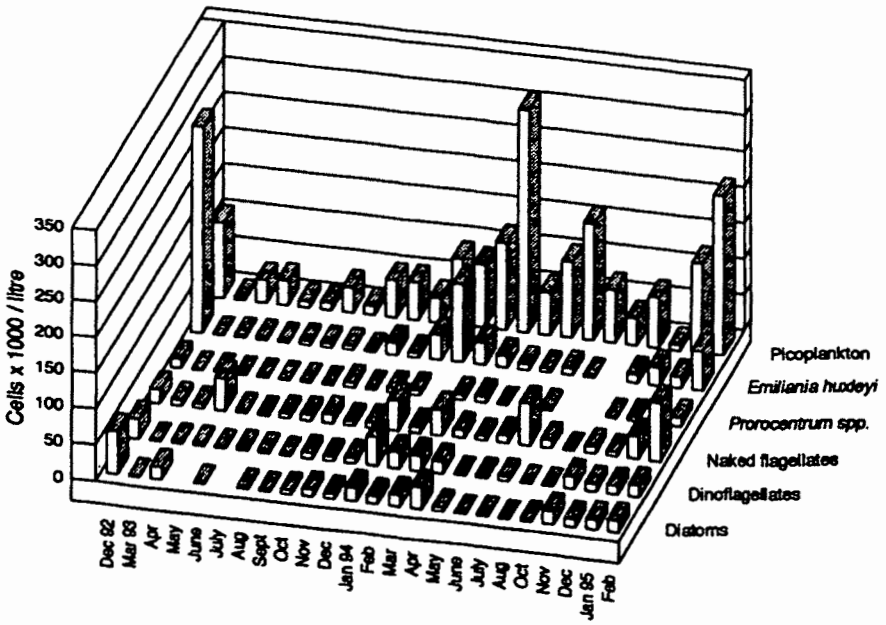

Fig. 9. Seasonal variations in cell numbers ($\times 10^3$ l^{-1}) of the major phytoplankton groups in surface water from December 1992 to February 1995. *Prorocentrum* spp. are also included within total dinoflagellates.

(Kopczynska *et al.*, submitted). In contrast to naked flagellates and picoplankton, dinoflagellates, diatoms and coccolithophorids exhibited distinct seasonal patterns with maxima during summer and minima in winter.

Formalin-preserved flagellates and picoplankton are difficult to identify accurately; however, naked flagellates of size 2–20 μm appeared to represent mainly biflagellates such as several species of Prasinophyceae (*Pyramimonas* spp.), Cryptophyceae (e.g. *Hillea fusiformis*) and Prymnesiophyceae (*Chrysochromulina* sp., *C.alifera* Parke et Manton). The latter genus is known for mixotrophy. The picoplankton were represented by both mono- and biflagellates. Species resembling *Imantonia rotunda* Reynolds (Prymnesiophyceae), *Micromonas* sp., *Micromonas pusilla* (Butcher) Monton et Parke (Prasinophyceae) and *Hillea* sp. (Cryptophyceae) were found in most samples. Dinoflagellate numbers during the summer peaks in surface water were generally $<40 \times 10^3$ l^{-1}. This group consisted mainly of small *Prorocentrum* species (6–24 μm) which were present year round. Most frequently found, particularly during the summer, were *P.micans* Ehrenberg, *P.dentatum* Stein, *P.triestinum* Schiller and *P.minimum* (Pavillard) Schiller. *Gymnodinium* spp. were the next in abundance and often included *G.minor* Lebour, *G.modestum* Balech, *G.guttula* Balech, *G.flavum* Kofoid et Swezy and *G.soyai* Hada. The heterotrophic genus *Protoperidinium* spp. (18–60 μm) and *Gyrodinium* spp. (8–24 μm) were particularly noticeable during summer (December 1994, January 1995 and February 1995). Diatom summer peaks (maximum 60 $\times 10^3$ cells l^{-1} at the surface, December 1992) were chiefly made up by *Fragilariopsis kerguelensis* (O'Meara) Hustedt (= *Nitzschia kerguelensis*), length 30–48 μm, *Thalassionema nitzschioides* (Grun.) Hust. and *Chaetoceros* spp. (12–16 μm), e.g. *C.atlanticus* Cl., *C.bulbosus* (Eh.) Heiden and *C.dichaeta* Eh. and *Pseudonitzschia* spp. (= *Nitzschia*, *Pseudonitschia* group) (34–90 μm), i.e. *P.heimii* Mangin and *P.lineola* Cl. Diatom community structure changed from summer to summer with only *F.kerguelensis* and *T.nitzschioides* retaining their first and second positions. Any of the other co-dominant species could be absent during some summer season. Next in abundance, particularly in January and February 1994, were *F.pseudonana* Hasle, *F.cylindrus* (Grun.) Krieger, *Nitzschia closterium* (Eh.) W. Sm., *N.heimii* Manguin, *N.lineola* Cl. and *N.barkleyi* Hustedt. Small *Thalassiosira* species, e.g. *T.gracilis* (Karsten) Hustedt, and *Coscinodiscus* spp. showed month to month fluctuations; however, they were often absent from both summer and winter collections. Infrequently found were the large species *Corethron criophilum* Castr., *Eucampia balaustium* Castracane and *Proboscia alata* (Brightwell) Sundstrom. In some winters (May–September), diatoms were found only in surface waters or were entirely absent. Coccolithophorids were apparently represented by only *Emiliania huxleyi* (Lohmann) Hay & Mohler which was present year round. A summer maximum of nearly 300×10^3 cells l^{-1} at the surface and 100 m depth was recorded in December 1992.

Discussion

There is a pronounced seasonal variability in phytoplankton biomass distribution in the northern part of the Southern Ocean. The main feature was low

phytoplankton biomass throughout the year, except for a short summer period. Interannual variability was negligible. From October to January, the autotrophic biomass increased to maxima that never exceeded 1.2 mg Chl *a* m^{-3}. The same seasonal pattern has been observed in the marginal ice zone (MIZ), but the biomass enhancement during summer was larger (Horne *et al.*, 1969; Whitaker, 1982; Satoh *et al.*, 1986; Rivkin, 1991; Helbling *et al.*, 1995; Moline and Prézelin, 1996). Enhanced biomass has also been found to be associated with the Antarctic Polar Front (Laubscher *et al.*, 1993; Bathmann *et al.*, 1997). Biomass enhancement in Antarctic waters may be due to a shallow mixed layer, low grazing pressure and/or availability of trace metals. At Kerfix, the biomass distribution was closely related to the stability of the water column. During the winter, strong winds resulted in very deep mixing (~200 m) (Ruiz-Pino *et al.*, in preparation) and the Chl *a* biomass was low and homogeneous throughout the water column. In summer, the upper mixed layer was only to 50–75 m depth and the biomass at its highest. Increased stability, water temperature and stronger light could be the main factors involved. Yet, the Chl *a* maximum was only moderately large despite these favourable environmental conditions (high nutrient–low Chl features) (Pondaven *et al.*, 1998).

Throughout the year, the pico- and nanophytoplankton were numerically the most abundant, and their contribution to total biomass was on average 38.4 and 29.5%, respectively. Larger cells (>10 μm) contributed 32% of total biomass. It is now recognized that in Antarctic waters, autotrophic nano- and pico-size cells can contribute most of the biomass and primary production (Weber and El Sayed, 1987; Hewes *et al.*, 1990; Rivkin, 1991; Carrada *et al.*, 1994; Magazzù *et al.*, 1996; Xiuren *et al.*, 1996).

At Kerfix, the cell size distribution was highly seasonal. During summer bloom, the >10 μm size species contributed 60% of total autotrophic biomass, while during the winter the <10 μm size fraction contributed 80% of total autotrophic biomass with the dominance of picoplankton. The size distribution of phytoplankton biomass was related to total biomass: the smaller sized phytoplankton were associated with low biomass and microphytoplankton with high biomass. This has been observed elsewhere in open and coastal Antarctic waters, on the basis of size-fractionated biomass and primary production (Jacques and Panouse, 1991; Becquevort *et al.*, 1992; Jochem *et al.*, 1995; Fiala *et al.*, 1998). Detmer and Bathmann (1997) observed that pico- and nanoplankton contributed up to 90% of total autotrophic biomass at a Chl *a* concentration of <0.4 mg m^{-3} and <50% in regions where biomass was >1.8 mg m^{-3}.

High biomass was characterized by a dominance of microphytoplankton. Generally, Antarctic vernal and summer blooms are reported to be dominated by large diatoms that are a major source of carbon (Hasle, 1969; Kopczynska *et al.*, 1995; Fiala *et al.*, 1998). A main feature at station Kerfix is the predominant carbon contribution by large autotrophic dinoflagellates, and to a lesser extent by diatoms during the phytoplankton bloom. However, dinoflagellates may be entirely dominating in some periods (November 1993) or both dinoflagellates and diatoms are predominant, such as in December 1992 and December 1994. Among the dinoflagellates, *Prorocentrum* spp., and to a lesser extent *Gymnodinium* spp.,

are the main contributors of autotrophic biomass over the year and during summer blooms. Usually, dinoflagellates are not recognized as the major source of carbon in the Southern Ocean. Kopczynska *et al.* (1995) reported a contribution of only 14% to the total cell carbon in Prydz Bay. However, in the Indian sector, Fiala *et al.* (1998) observed a major contribution to carbon biomass by diatoms in the Seasonal Ice Zone shifting towards dinoflagellate dominance in the POOZ. The role of these organisms in the Southern Ocean food web structures is uncertain. Some species are autotrophs, whilst others are heterotrophs (Larsen and Sournia, 1991). The presence of larger heterotrophic dinoflagellates is reported in different Antarctic regions (Dodge and Priddle, 1987; Kopczynska *et al.*, 1995). On the other hand, Becquevort *et al.* (1992) have shown that many nano-sized dinoflagellates in the Weddell Sea also contain many heterotrophic species. In our study, larger heterotrophic dinoflagellates of the genera *Protoperidinium* and *Gyrodinium* displayed a peak abundance of 1.5×10^3 cells l^{-1} in January 1994 and November 1994, which then accounted for 450–480 mg C m^{-2}, contributing 70% of total C biomass. The abundance of heterotrophic flagellates might explain the decreasing relative contribution of pico- and nanoplankton during the summer bloom.

Diatoms contributed significantly to cell carbon, particularly in December 1992 and December 1994. Among the dominant species, *F.kerguelensis* and *T.nitzschioides* were present during all summer seasons, *Chaetoceros* spp. were abundant in the summer of 1992 and 1994–1995, while *Pseudonitzschia* spp. were co-dominant in the summers of 1993–1994 and 1994–1995. These diatoms are known to have somewhat different biogeographical distributions. *Thalassionema nitzschioides* seems to be typical of the subantarctic waters (Hasle, 1969, 1976; Kopczynska *et al.*, 1986). *Pseudonitzschia* spp., although common to the entire Southern Ocean, have been previously reported predominant north of the Polar Front (Hasle, 1969; Steyeart, 1973; Kopczynska *et al.*, 1986). On the other hand, *F.kerguelensis* and *Chaetoceros* spp., especially *C.dichaeta*, are generally found in greater numbers south of the Polar Front. The change in the summer diatom community structure from one year might be due to southward displacements of the Polar Front, bringing 'warmer species' from the north.

Throughout the year, the pico- and nanoplankton fractions (<10 μm) are represented by species belonging to the Chlorophyceae, Prymnesiophyceae, Cryptophyceae and Prasinophyceae. Their contribution was on average 68% of total Chl *a* biomass. During winter, the picoplankton dominated, contributing >50% to the total Chl *a* biomass. A dramatic increase in the picoplankton cell numbers occurred from September to December 1992. During this period, picocyanobacteria appeared in the upper 200 m. A sub-surface peak (10^6 cells l^{-1}) was observed in September. Data for cyanobacterial abundance show that the numbers in the Southern Ocean are >400 times lower than those in tropical and temperate waters (Walker and Marchant, 1989; Andreoli *et al.*, 1993; Wright *et al.*, 1996).

Vertical mixing is an important factor governing phytoplankton growth. At Kerfix, there is a close correlation between water column stability, biomass accumulation and size structure. Larger dinoflagellates and diatoms are associated with increased stratification during summer. In contrast, low biomass and

pico- and nanoplankton dominance are related to deep mixing during winter. This coupling has been reported elsewhere in Antarctic regions (Sakshaug and Holm-Hansen, 1984; Fiala *et al.*, 1998; Semeneh *et al.*, 1998), but in other studies no direct relationship between size structure and water column stability could be established (Jochem *et al.*, 1995; Detmer and Bathmann, 1997). On the other hand, the coupling between the size structure of phytoplankton communities and vertical mixing is a general feature in oligotrophic temperate and tropical oceans (Chisholm, 1992). The dominance of smaller algae in well-mixed areas might be explained by their higher quantum efficiency which induces a good adaptation to deep mixing (Morel and Bricaud, 1981). Grazing could also be a selective factor. In our study, the heterotrophic activity of dinoflagellates would take place only during the very short summer period. On the other hand, the impact of mesozooplankton (copepods) grazing pressure at station Kerfix is negligible (Razouls *et al.* 1998). The grazing activity by protozooplankton, which is recognized to have an impact on the phytoplankton size distribution in Southern Ocean (Becquevort *et al.*, 1992; Froneman and Perissinotto, 1995; Becquevort, 1997; Klass, 1997), was not documented in Kerfix waters.

In summary, results from our 3 year study at the time series station Kerfix permitted us to describe, for the first time in the northern part of the Southern Ocean, the seasonal variability in phytoplankton biomass. Throughout the year, the autotrophic biomass is low, except during the three summer months when blooms occur. A shift occurs in the phytoplankton size structure from large cells dominating the stock in summer to small cells dominating in winter. During 9 months of the year, pico- and nanophytoplankton size cells are the major contributors to the autotrophic biomass, whereas large autotrophic dinoflagellates and diatoms (>10 μm) dominate the summer bloom community. This successional pattern has been repeated during the 3 years of investigation. Our results provide evidence for the dominance of a smaller size community, especially picoplankton, within the Antarctic food web during the largest part of the year. This community becomes accessible to upper trophic levels via heterotrophic grazers.

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