



## Spring development of phytoplankton biomass and composition in major water masses of the Atlantic sector of the Southern Ocean

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**Abstract**—The distribution and composition of phytoplankton stocks in relation to water masses were studied during the SO-JGOFS cruise of R.V. *Polarstern* in the Atlantic sector of the Southern Ocean in October/November 1992. The cruise comprised one west-to-east transect along the ice edge from 49°W to 6°W and several meridional transects along 6°W that extended from the closed pack ice of the Weddell Sea, across the southern Antarctic Circumpolar Current (ACC) and into the Polar Frontal Zone. Chlorophyll (chl *a* concentrations, temperature and salinity were recorded continuously in surface water during the transects. Vertical distribution and species composition of microplankton were assessed microscopically in discrete water samples collected at stations. Contrary to expectations, no significant enhancement of phytoplankton biomass was found in the vicinity of the retreating ice cover. Melt-water-influenced zones were indicated by low salinity but also by abundance of characteristic sea-ice species such as *Nitzschia closterium* and *N. prolongatoides*, but chlorophyll concentrations averaged only 0.3 mg chl *a* m<sup>-3</sup> and barely increased during the spring. Values were even lower and remained constant in the southern ACC (ca 0.2 mg chl *a* m<sup>-3</sup>). In contrast, large phytoplankton blooms developed during the 6 weeks of investigation in the region of the Polar Front (PFR), from 0.7 to > 4 mg chl *a* m<sup>-3</sup>. Three distinct blooms extended below 70 m depth, each dominated by a different diatom species (*Fragilariopsis kerguelensis*, *Corethron inerme* and *C. criophilum*). We speculate that the large phytoplankton stocks below 40 m depth are a result of subduction of surface layers as sinking and *in situ* growth can be ruled out. The factors leading to the accumulation of high phytoplankton stocks in the PFR (up to 270 mg chl *a* m<sup>-2</sup>), but not in the melt-water zones or in the front between ACC and Weddell Gyre, are not clear, but higher iron concentrations in the former region seem to have played a role. © 1997 Elsevier Science Ltd. All rights reserved

### INTRODUCTION

Phytoplankton blooms play an important role in biogeochemical cycling because they generally result in substantial transport of biogenic elements from the surface layer to the ocean interior and sediments. Over much of the Southern Ocean, phytoplankton biomass distribution is known to be uniformly low throughout the year despite high nutrient concentrations (Smetacek *et al.*, 1990). The reasons underlying this paucity of biomass are still under debate. However, phytoplankton blooms have been reported from a variety of disparate environments: coastal waters (Holm-Hansen and Mitchell, 1991), the marginal sea-ice zone (Smith and Nelson, 1986; Sullivan *et al.*, 1988), and along fronts between water masses (Laubscher *et al.*, 1993; Turner and Owens, 1995). High biomass values occur under such widely differing conditions, suggesting that more than one factor is involved in

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promoting biomass build-up. The conditions necessary for bloom development in the Southern Ocean are the presence of a shallow mixed layer (Sverdrup, 1953), availability of trace metals, particularly iron (Martin *et al.*, 1990) and low grazing pressure relative to algal growth rates (Smetacek and Passow, 1990; Sakshaug *et al.*, 1991). In regions such as the Antarctic Peninsula and the southern Ross Sea where all three conditions are met, large phytoplankton blooms have been reported frequently (von Bodungen *et al.*, 1986; Smith and Nelson, 1986; Holm-Hansen and Mitchell, 1991). These regions also are well investigated, but much less is known about conditions prevailing in the land-remote, hence iron-poor regions of the open ocean where frequent storms result in deep mixed layers.

A major aim of the R.V. *Polarstern* cruise ANT X/6 to the land-remote, eastern Atlantic sector of the Southern Ocean was to study the ecology and biogeochemistry of the marginal ice zone (MIZ), the open Antarctic Circumpolar Current (ACC) and the region of the Polar Front during spring. The interdisciplinary cruise was organized as part of the Joint Global Ocean Flux Study (JGOFS). In this paper, phytoplankton biomass distribution and species composition in the different water masses covered by the cruise are presented. The study is based on continuous recordings of chlorophyll fluorescence, temperature and salinity in water from 8 m depth combined with water column profiles obtained from discrete water bottle samples.

## MATERIAL AND METHODS

The R.V. *Polarstern* cruise was carried out in austral spring (3 October–26 November 1992) and comprised one latitudinal transect along the ice edge and five meridional transects extending from the northern rim of the ice-covered Weddell Gyre into the Polar Frontal region (PFR) along 6°W.

The latitudinal transect was carried out from 3 to 10 October. It followed the 57°S parallel from 49°W to 20°W and crossed the arc of the South Sandwich Islands (at about 28°W). Because of heavy ice cover, the transect was shifted north to the 56°S parallel from 20°W to 15°W. From 15°W, *Polarstern* cut obliquely south to 57°45'S; 6°W through closed, heavy ice cover (Fig. 1). All other transects dealt with here were carried out along the 6°W meridian, each time extending from well within closed ice pack to the PFR. Transects 2 and 3 were carried out from 12 to 22 October. Stations south of 53°S were occupied on the northward-bound Transect 2 and stations between 48°S and 50.5°S on the southward-bound Transect 3. Stormy weather interrupted station work on Transect 2 and again on Transect 3, resulting in the station gap between 50°30'S and 53°S. Stations were worked only along northward-bound Transect 5 which was carried out between 24 and 30 October. Transect 6 was completed between 31 October and 2 November. The northward-bound Transect 11, slowed by intensive station work, was carried out between 10 and 21 November (Bathmann *et al.*, 1994).

Continuous recordings of *in vivo* chlorophyll *a* fluorescence were made with a Turner-Design flow-through fluorometer supplied with sea water by a membrane pump. The water intake was located in the ship's bow at 8 m depth. Data (10 min means) from the flow-through fluorometer were stored on a data logger (LICOR LI 1000) and plotted against the ship's position derived from the GPS-navigation system. The fluorometer readings were converted into chlorophyll *a* (chl *a*) concentrations based on measurements (see below) of extracted pigment from triplicate 1-l sub-samples taken every 4 h during the first 2 days,

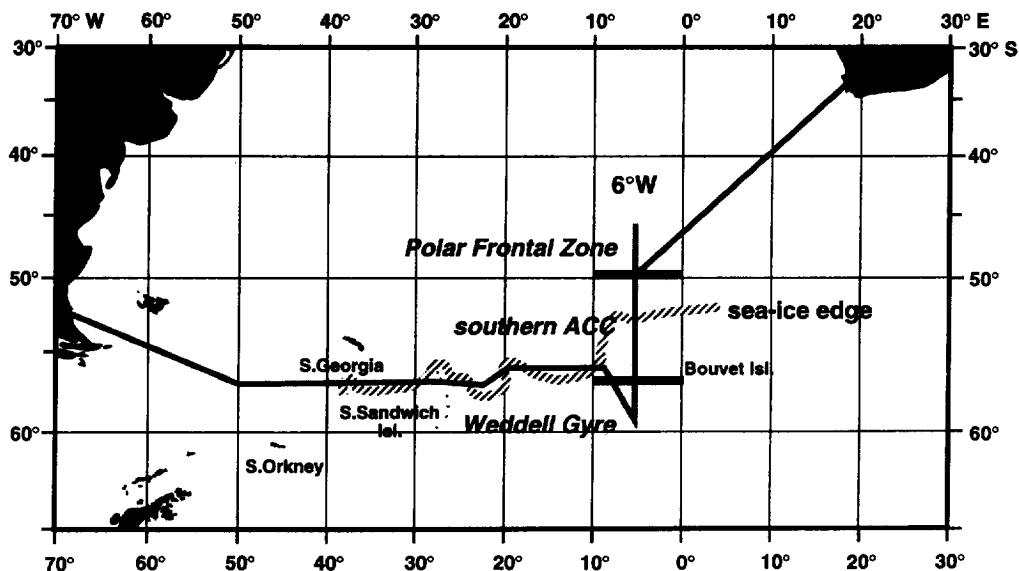


Fig. 1. Cruise track of R.V. *Polarstern* during ANT X/6 showing the position of the latitudinal Transect 1 and meridional Transects 2–11 along 6°W relative to the water masses covered: Polar Frontal Zone, Antarctic Circumpolar Current (ACC) and Weddell Gyre. The horizontal bars indicate the approximate location of the boundaries between the water masses. The location of the ice edge in early October (during Transects 1 and 2) is denoted by the hatched line.

thereafter at every station. Temperature and salinity were recorded simultaneously (10 min means) with a thermo-salinograph with precisions of 0.05°C and 0.1 salinity, respectively. The instrument was calibrated regularly.

Chlorophyll *a*, particulate organic carbon (POC) and phytoplankton species composition were determined on water samples collected with 24 Niskin bottles (12-l) mounted on a rosette equipped with a Neil-Brown CTD from up to 12 discrete depths. Chlorophyll *a* and phaeopigments were determined after filtration of 1–2 l of sea water on to GF/F filters. The filters were placed in 90% (v/v) acetone/water and homogenized in a cell mill for 5 min. Fluorometric measurements were performed before and after acidification with two drops of 1 N HCl (Strickland and Parsons, 1972; Evans *et al.*, 1987). Filters were measured within a few days on board.

Samples for particulate organic carbon (POC) were taken from the same bottles as chlorophyll samples and 2–3 l were filtered on pre-combusted GF/F filters. POC was determined by means of a Carlo Erba (CHN 1500) autoanalyser some months later in the home laboratory. Filters were stored in the interim at –20°C.

Qualitative and quantitative phytoplankton composition was determined from Transects 1, 5 and 11 on formalin-preserved samples (0.6% final concentration) under an inverted microscope according to the method described by Utermöhl (1958).

The data presented here were obtained from samples taken from the first cast (sometimes the only one) at each station. Data on various properties of particulate matter from the same cruise presented by other authors in this volume were taken from subsequent casts, sometimes separated by over 7 h.

## RESULTS

*The west-east transect (Transect 1)*

The position of Transect 1 was based on the location of the ice edge ascertained from the weekly ice charts supplied by NOAA and photographs taken by the Soviet Meteor satellite. The 57°S parallel was selected as it provided a section from open water into ice pack west of the South Sandwich Islands. Temperature and salinity distribution indicate that Transect 1 initially crossed open water of the Antarctic Circumpolar Current (ACC) to about 47°W (indicated by the temperature peak) and then cut across eddies in the Weddell-Scotia-Confluence (WSC) (fluctuating temperature and salinity) and entered a strip of loose pack-ice at about 38°W. Satellite images showed that this plume of ice had been advected northward. Surface chl *a* concentrations were fairly high ( $> 0.5 \text{ mg chl } a \text{ m}^{-3}$ ) and reached a peak of well over  $1 \text{ mg chl } a \text{ m}^{-3}$  in the WSC and declined to values below  $0.3 \text{ mg chl } a \text{ m}^{-3}$  east of 33°W [Fig. 2(a, b)]. The patch of high chlorophyll unfortunately was not covered by a station, and hence does not appear in Fig. 2(b).

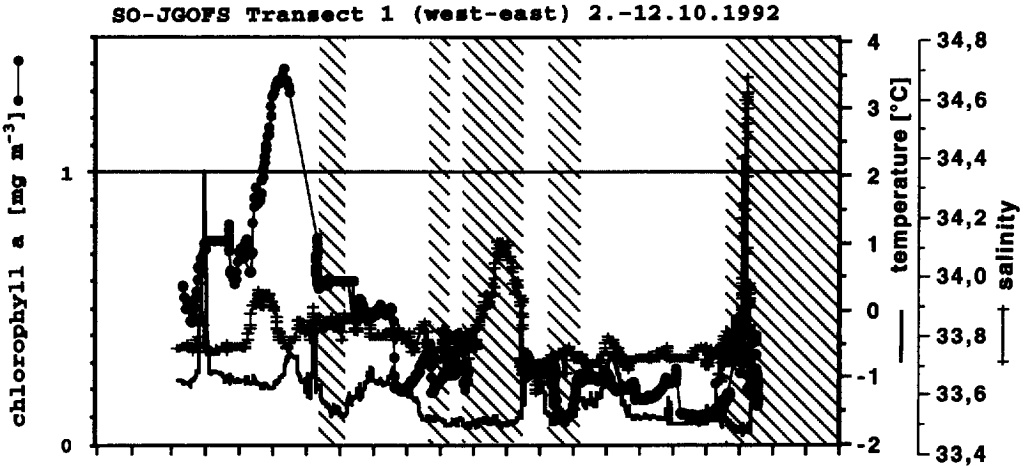
East of the South Sandwich Islands the transect crossed a tongue of high-salinity water of Weddell Sea origin covered by loose pack ice. Northward advection of Weddell water in this region is well known. Farther to the East, open water was again encountered till 22°W where satellite images showed that closed ice cover extended northward to about 56°S. The stretch of Transect 1 between 18°W and 8°W along 56°S was accordingly conducted in open water adjacent to the ice pack. The low temperature and salinity values (the latter are the lowest of the transect) indicate that this stretch was strongly influenced by ice-melt water. At 8°W, the ship was directed south into closed pack ice. The very high salinity values here are probably an artefact caused by blockage of the intake by ice pieces. The higher chlorophyll values on the other hand are due to ice algae released from ice crushed by the ship in the vicinity of the intake; sea-ice floes encountered in the outer margin of the pack were invariably coloured brown by intense algal growth. Apart from these latter higher values, chlorophyll concentrations along the entire stretch east of the South Sandwich Islands ranged between 0.1 and  $0.3 \text{ mg chl } a \text{ m}^{-3}$  [Fig. 2(a, b)] in striking contrast to the much higher values in the WSC.

Phytoplankton composition along Transect 1 was recorded from stations east of the chlorophyll peak [859–867, Fig. 2(b)]. Hence, the composition of the peak is not known. Consistent with chlorophyll values, biomass levels dropped steadily from west to east. Throughout, diatoms contributed a half to a third of the total biomass with nanoflagellates comprising another third. The typical ice alga *Nitzschia (Cylindrotheca) closterium* was most abundant in the east at stations close to the pack ice. Apart from this species, no consistent trend in composition could be ascertained. *Fragilariopsis kerguelensis* was prominent at stations 859 in the west and 867 in the east. *Corethron criophilum* was most prominent at 860 and again at 867. These species are mentioned here because of their dominance in blooms of the Polar Frontal region (PFR) discussed later. The bulk of the low biomass was provided by various genera.

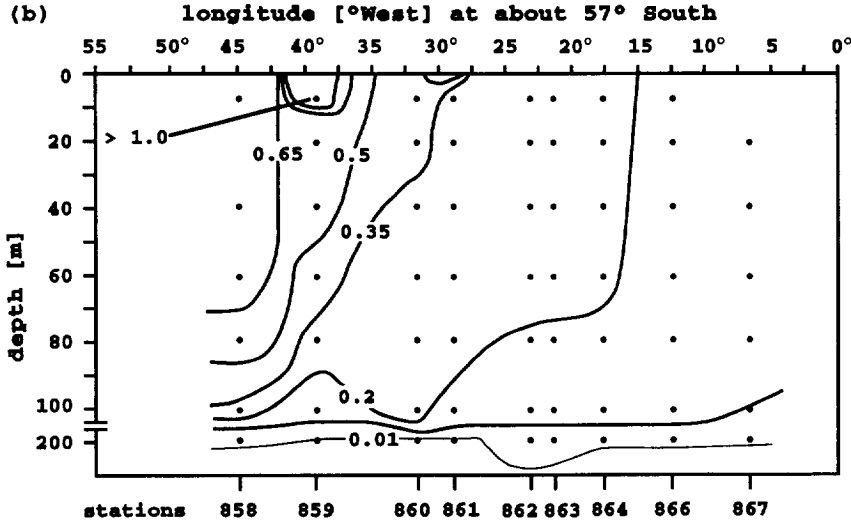
*Meridional transects along 6°W (Transects 2–11)*

*Temperature and salinity.* The hydrography of the investigation area has been described in greater detail by Veth *et al.* (1997). Surface recordings of temperature and salinity carried out along the 6°W meridian between 11 October and 21 November exhibit the same basic

(a)



(b)



integrated chlorophyll to 100 m water depth  
(mg chl. a m<sup>-2</sup>)

67	43	34	26	22	21	22	14	17
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Fig. 2. Chlorophyll *a* concentrations measured during Transect 1 (49°W to 6°W) conducted parallel (along 57°S and east of 20°W along 56°S) to the ice edge till 8°W. Thereafter, the ship steamed south through closed pack ice till 57°S; 6°W. (a) Continuous surface (8 m depth) recordings of chlorophyll, temperature and salinity (10 min means). Shaded areas indicate zones where the ship was more or less surrounded by ice. (b) Depth distribution of chlorophyll from stations along the transect (dots represent sampling depths).

pattern on all transects. The three transects (2, 6 and 11) extended from the northern edge of the Weddell Gyre (freezing-point temperature, > 34.0 salinity), and covered the entire southern branch of the Antarctic Circumpolar Current (temperatures between -1.5 and 2.0°C, and salinities around 33.85) and the southern part of the Polar Frontal Zone (temperatures above 2°C and salinities around 33.80) (Figs 3-5). Transects 3 and 5 did not

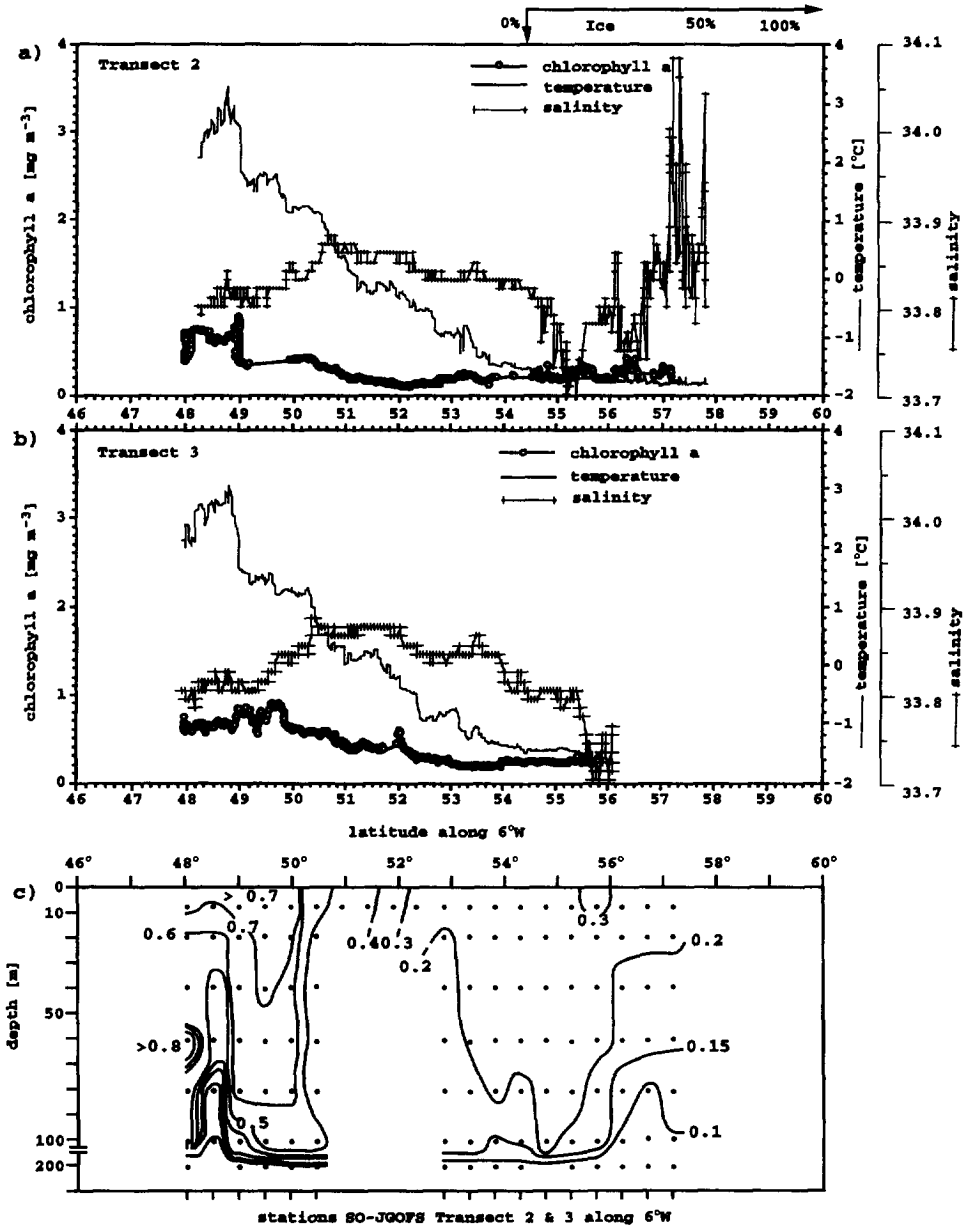


Fig. 3. Chlorophyll *a* concentrations measured during Transects 2 and 3 along 6°W (57°30'S to 49°30'S) (a) and (b) at the ocean surface (8 m) continuously as 10-min averages and (c) with depth at various stations (dots represent sampling depths) along Transects 2 and 3. Stations south of 53°S were taken on Transect 2 and north of 50° 30'S on Transect 3.

cross into Weddell water; the temperature increased steadily, with several step-wise features, across the ACC and into the PFr. Seasonal warming, by about 1°C, was most pronounced in the PFr but did not alter the zonal trend.

The location and structure of the boundary between the major water masses vary

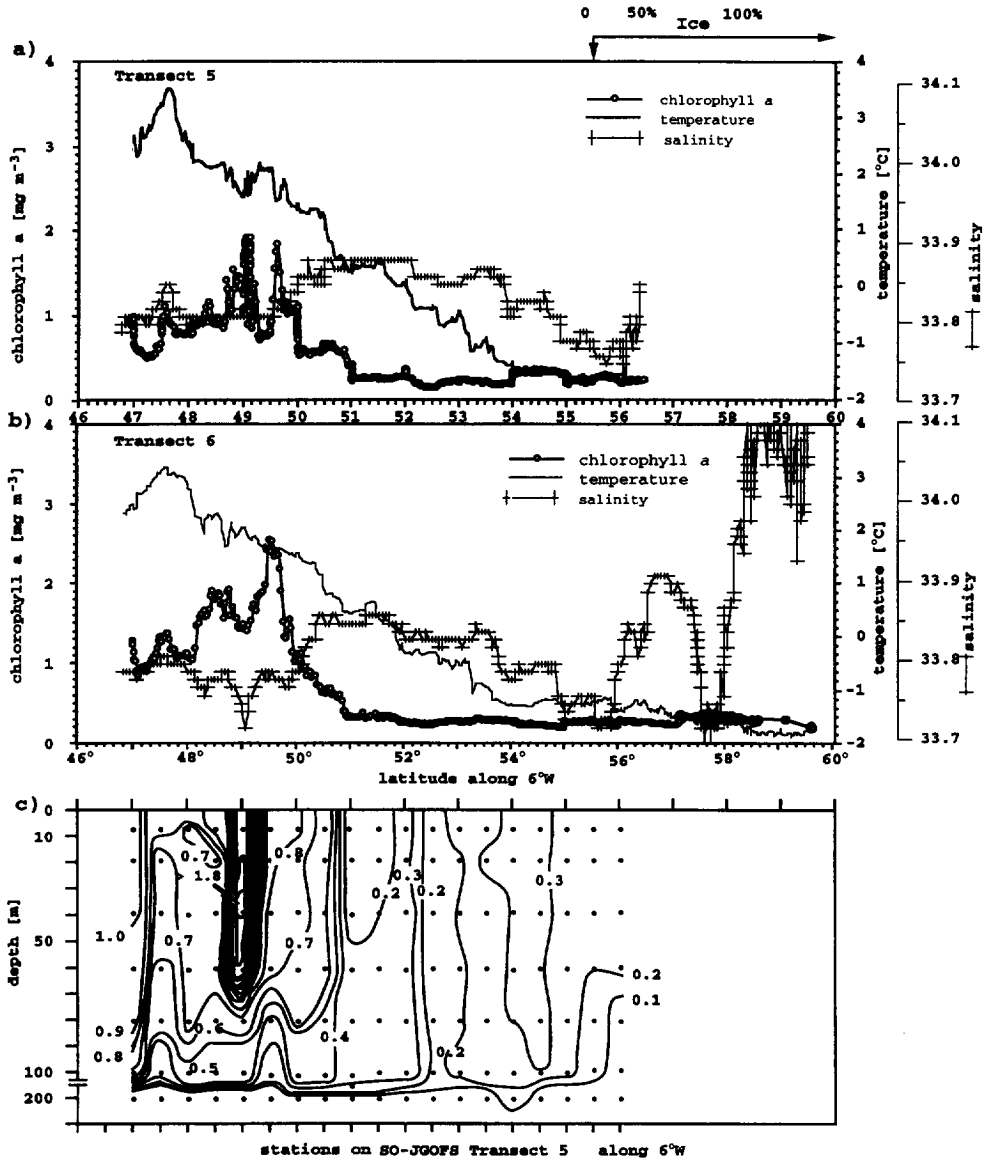


Fig. 4. Chlorophyll *a* concentrations measured during Transects 5 and 6 at 6°W (59°30'S to 46°40'S) (a) and (b) at the ocean surface (8 m) continuously as 10-min averages and (c) with depth at various stations (dots representing sampling depths) along Transect 5.

somewhat between the transects. The most striking variation is exhibited by the surface salinity south of 54°S from Transects 2, 6 and 11, which can be attributed to the combination of mesoscale frontal dynamics (meandering and mixing) and input of melt water from the retreating ice edge. It is interesting to note that the lowest salinities recorded along these transects (<37.5) were encountered in the zone of about 50% ice cover, which moved south in the period between the transects. This zone was located between 55° and

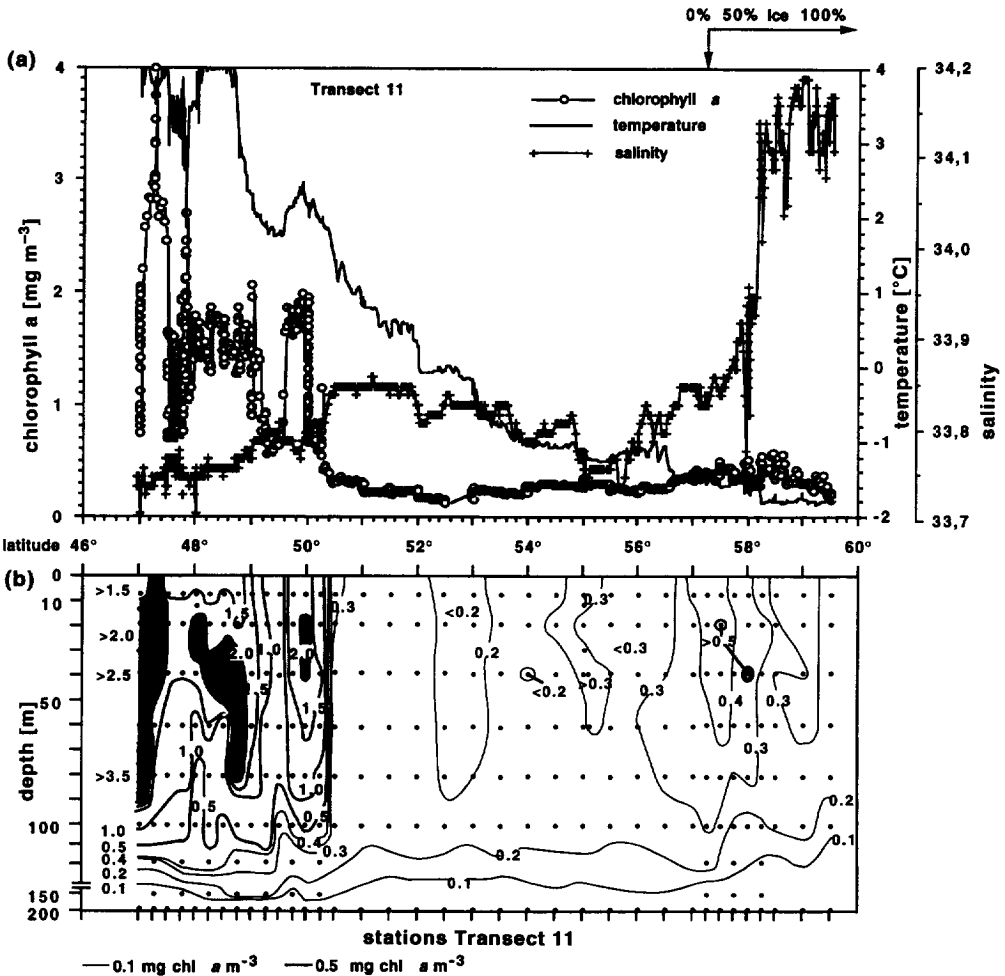


Fig. 5. Chlorophyll *a* concentrations measured during Transect 11 along 6°W (59°30'S to 47°S) (a) at the ocean surface (8 m) continuously as 10-min averages and (b) with depth at various stations (dots represent sampling depths) along the transect.

56°S on Transect 2 and between 57 and 58°S on Transect 5. The salinity of the 50% ice-covered zone of Transect 11 is much higher, probably due to a significant change in the location of mesoscale water masses. However, one also should remember that admixture of the same amount of melt water to ACC and Weddell Gyre water will result in very different end-salinities. The data clearly show that a variety of mesoscale features was present along the MIZ that retreated from the southern edge of the ACC well into Weddell water during the cruise.

*Chlorophyll a distribution.* A comparison of surface chlorophyll concentrations from all five transects (Figs 3–5) shows two large-scale features: (a) persistently low values throughout the entire stretch south of 50°S comprising the open water of the southern



ACC and the marginal ice zone (MIZ); chlorophyll concentrations increased slightly in the MIZ (from 0.25 to 0.4 mg chl  $a\ m^{-3}$ ) and remained constant in the ACC (at ca 0.25 mg chl  $a\ m^{-3}$ ) in the course of the investigation; (b) much higher values in the region north of 50°S that increased about three-fold in the period (from 0.8 to 2.5 mg chl  $a\ m^{-3}$ ). This is remarkable because, contrary to expectation, only a minor build-up of phytoplankton biomass occurred in the MIZ throughout the period, despite extensive melting and retreat of the ice cover.

The depth distributions of chlorophyll show that the surface concentrations extend to depths below 70 m. Indeed, a remarkable feature of the isopleth diagrams is the absence of a shallower surface layer along any of the transects. Even the sharp boundaries between chlorophyll-rich PFr and chlorophyll-poor ACC waters extend down to 100 m. Within the PFr, chlorophyll concentrations exhibit a large degree of latitudinal variation with pronounced peaks and troughs. These features increase in prominence in the course of the spring. Three distinct peaks or blooms can be ascertained on Transect 11, with integrated chlorophyll stocks in the upper 200 m as high as 277 mg chl  $a\ m^{-2}$ , 223 mg chl  $a\ m^{-2}$  and 177 mg chl  $a\ m^{-2}$  at 47°S, 48°45'S and 50°S, respectively [Fig. 5(b)]. Maximum stocks on Transects 3 and 5 are 77 and 146 mg chl  $a\ m^{-2}$ , respectively, indicating about a doubling every 3 weeks. The highest concentrations recorded on the Transects 2, 6 and 11 were 0.9, 2.9 and 4.1 mg chl  $a\ m^{-3}$ , respectively, and were found by the continuous surface measurements. Because of the patchy horizontal distribution, these peaks were missed by the discrete stations. It should be noted that, in the blooms covered by discrete stations, the highest values invariably occurred well below the surface.

*Particulate organic carbon.* The zonal distribution pattern of chlorophyll is mirrored by that of particulate organic carbon [POC; Fig. 6(a, b)]. Spatial coverage was much poorer than in the case of chlorophyll; hence, the three blooms encountered on Transect 11 do not appear in the POC data. Nevertheless, a two- to three-fold increase in the 3 weeks between Transects 5 and 11 can be ascertained. The maximum value recorded ( $>0.6\ g\ C\ m^{-3}$ ) was found at 47°30'S at 40 m depth in the PFr. South of the PFr, POC remained low ( $<0.1\ g\ C\ m^{-3}$ ) throughout. The carbon-to-chlorophyll ratio exhibited considerable scatter with a tendency to decrease with increasing chlorophyll concentrations. Thus, at values  $<1.0\ mg\ chl\ m^{-3}$ , the average ratio was 242 (SD = 120,  $n = 360$ ) and  $>1.0\ mg\ chl\ m^{-3}$ , the average ratio was 123 (SD = 53,  $n = 39$ ).

#### *Phytoplankton species composition*

The diatom species *Fragilariopsis kerguelensis* and *Corethron criophilum* occurred throughout the region but attained high biomasses only in the PFr. The chlorophyll peak centred on 49°S in Transect 5 was dominated by *Fragilariopsis kerguelensis*, with *Corethron criophilum* more prominent at 47°S. *Corethron inerme* was absent on this transect. On Transect 11, the three distinct peaks were each dominated by a single species, from south to north: *Fragilariopsis kerguelensis*, *Corethron inerme* and *C. criophilum*, respectively [Fig. 7(a-c)]. On both transects, the *F. kerguelensis* peak was of a similar magnitude and located on the southern rim of the PFr. The *C. criophilum* peak was further to the north, and maximum concentrations on Transect 11 were three-fold higher than those recorded on Transect 5. The distribution of other common diatom species such as *Thalassionema nitzschioides*, *Chaetoceros dictyota*, *C. bulbosum*, but also coccolithophorids, was restricted

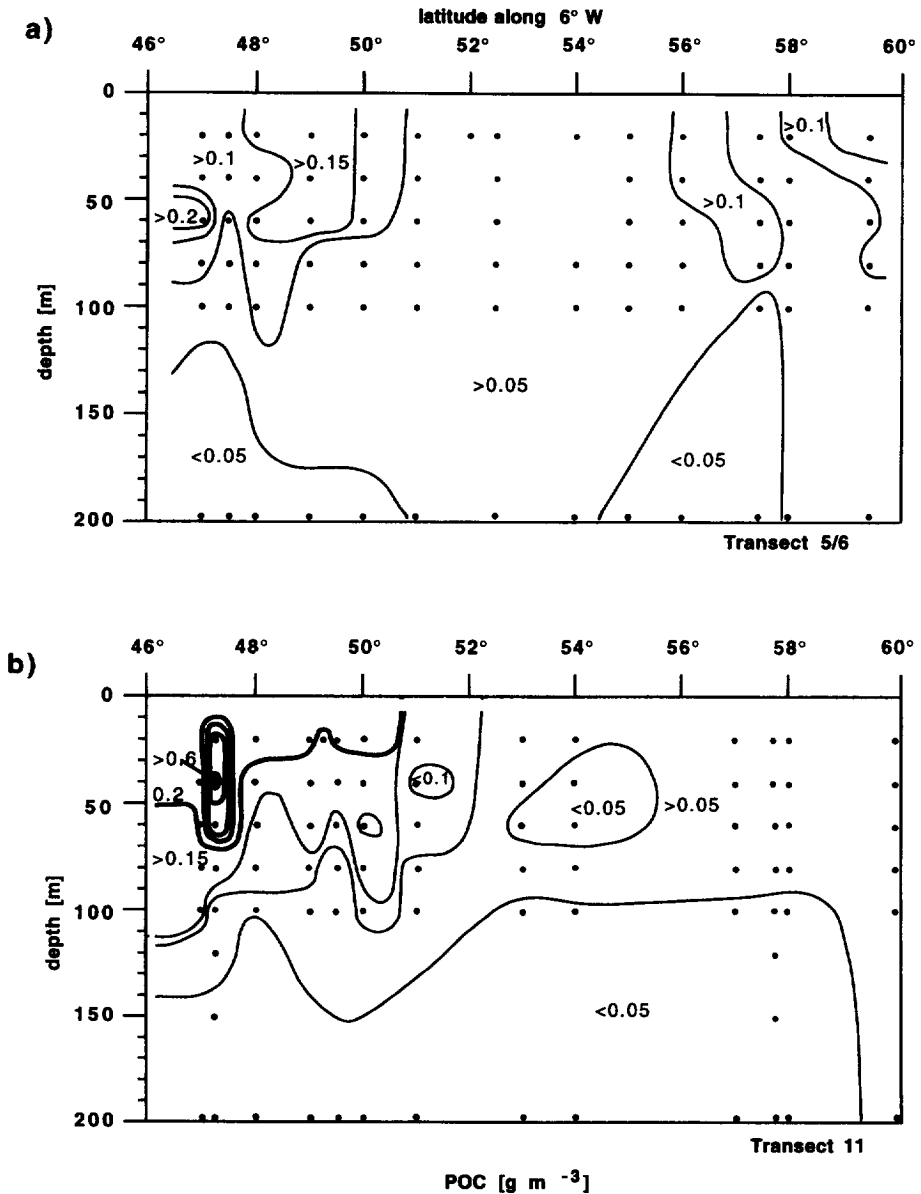


Fig. 6. Concentrations of particulate organic carbon (POC,  $\text{gm}^{-3}$ ) measured with depth at various stations along 6°W (59.5°S to 46.66°S) during (a) Transects 5/6 and (b) Transect 11 (dots represent sampling depths).

to the PFr. These species declined drastically south of the PFr and were absent by about 52°S. The distribution of coccolithophorids [Fig. 7(d)] is representative for these species.

The typical ice algae *Nitzschia* (*Cylindrotheca*) *closterium*, *N. prolongatoides* and other species of the genus *Fragilariopsis* were most abundant in the MIZ. On Transect 5, *N. closterium* exhibited two centres of abundance at 54°S and 56°S, which coincided with lower salinities and hence signalled melt-water input. The centre of abundance shifted

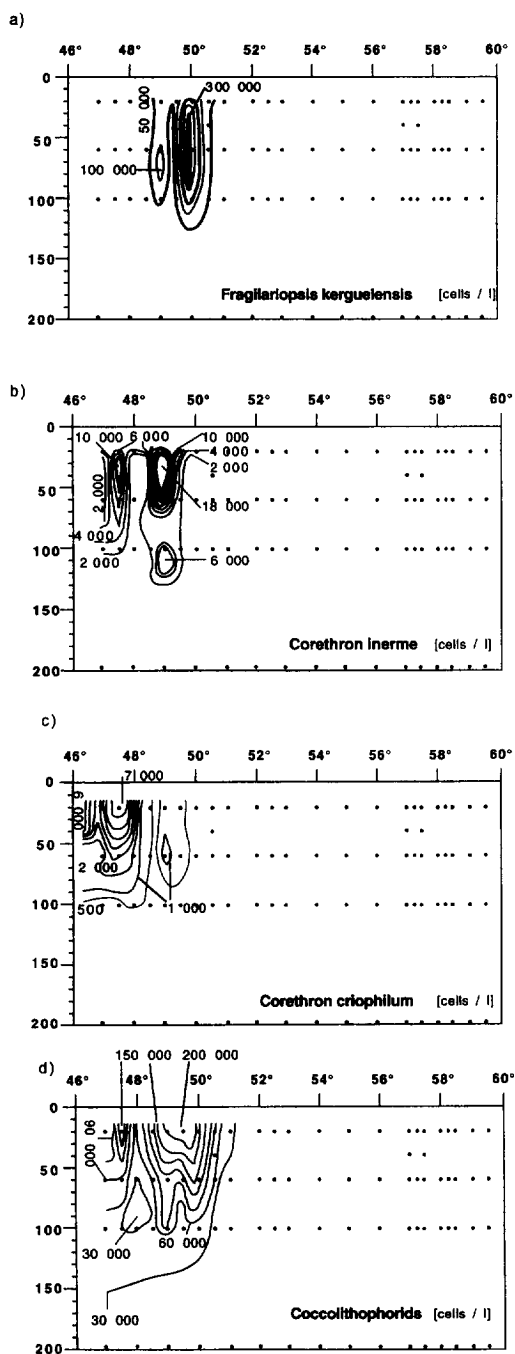


Fig. 7. Distribution and abundance of the phytoplankton species (a) *Fragilariopsis kerguelensis*, (b) *Corethron inerme*, (c) *C. criophilum* and (d) Coccolithophorids along Transect 11 in the upper 200 m water column (dots represent sampling depths).

south to 57–58°S during Transect 11 (Veth *et al.*, 1997), indicating that this species originated from melting ice and did not proliferate in the water column. The autotrophic ciliate *Mesodinium rubrum* was fairly abundant in the MIZ and was also present in lower numbers in the southern ACC. Another interesting feature of the MIZ was the high percentage of empty to total diatom frustules on Transect 5. Whereas this percentage was below 30% north of 54°S, values as high as 60% were recorded in the water column at 55°S. Whether this high mortality had occurred within the ice or was due to heavy grazing in the water column could not be ascertained.

## DISCUSSION

It has been suggested that seasonal retreat of the sea-ice cover around the Weddell Sea leads to the development of phytoplankton blooms in the marginal ice zone (MIZ). This conclusion is based on nutrient deficits between winter and summer in the northeastern Weddell Sea (Jennings *et al.*, 1984) and observations from the northwestern Weddell Sea (Smith and Nelson, 1990). During our 6-week investigation, however, phytoplankton biomass accumulation in the MIZ was only moderate to negligible, despite extensive melting and retreat of the sea ice. Melt-water-influenced water masses of different provenance were assessed during Transects 1, 2 and 6 and also Transects 7–10 (data not shown here), but chlorophyll concentrations were monotonously low throughout. Further, although accumulations of diatoms typically found in sea ice (Scharek, 1991) were found in the MIZ, presumably released by melting, their input did not significantly enhance biomass.

Blooms are reported to be induced by melt-water stabilization of shallow mixed layers (Smith and Nelson, 1986; Sullivan *et al.*, 1988). Veth *et al.* (1997) suggest that frequent, wind-induced, vertical mixing prevented accumulation of biomass to bloom proportions in this zone. In striking contrast to the situation in the MIZ, large phytoplankton blooms developed in the PFr but also in the apparent absence of a shallow mixed layer. This discrepancy probably was not due to latitudinal differences in solar radiation. Fairly high chlorophyll concentrations were found at the beginning of the cruise on Transect 1 at the same latitude as the MIZ (57°S) but to the West of 40°W in the Weddell–Scotia Confluence (WSC). Bianchi *et al.* (1992) also reported chlorophyll concentrations as high as 3.5 mg chl m<sup>-3</sup> in October in the region of the WSC. However, it is possible that these early blooms were facilitated by shallow mixed-layer depths often reported from the Antarctic Peninsula region and the WSC (von Bodungen *et al.*, 1986; Bianchi *et al.*, 1992). On the other hand, the distinct melt-water-influenced zones found along the MIZ east of the South Sandwich Island (Transect 1) and along the 6°W transects also should have resulted in at least temporary stratification of the surface layer long enough for phytoplankton biomass to increase. However, no such signal was found.

A more likely explanation for the phytoplankton blooms in the PFr and in the WSC and their absence in the land-remote MIZ is the presence of higher iron concentrations in the former regions (de Baar *et al.*, 1995). The higher biomass values were due to the accumulation of diatoms, as the smaller algae comprising the microbial food web, i.e. nano- and picoplankton, remained fairly constant throughout the investigated area (Jochem *et al.*, 1995; Detmer and Bathmann, 1997; Peeken, 1997). Diatom growth is known to be stimulated by the presence of higher iron concentrations (Scharek *et al.*, 1997), but the fact that their biomass accumulates in contrast to that of smaller algae suggests that

they also have lower mortality rates. Primary production in the MIZ during this cruise was, on average, about  $300 \text{ mg C m}^{-2} \text{ day}^{-1}$ , and P/B ratios were generally lower than in the PFr (Jochem *et al.*, 1995). Grazing pressure by nano- and microprotozoa in the MIZ, estimated by Becquevort (1997) and Klaas (1997), together accounted for 80% of the primary production. Protozoan grazing therefore could have constrained phytoplankton biomass accumulation, particularly of the small-celled species. Heavy grazing pressure also is indicated by the high POC/chl *a* ratios (*ca* 250) prevalent at chlorophyll concentrations  $< 1 \text{ mg chl m}^{-3}$ . As the C/chl *a* ratio of phytoplankton is  $< 50$ , the high POC/chl ratios suggest that phytoplankton biomass contributed less than 20% to the particulate carbon pool. The remaining 80% will have comprised not only detritus but also heterotrophic biomass. It appears that comparatively low growth rates of the entire population, as a result of deep mixing and that of large diatoms by iron deficiency, combined with the high grazing pressure exerted by protozooplankton, were the underlying causes constraining bloom development in the MIZ. However, differences in mesoscale hydrography between the Polar and Weddell/ACC fronts might well have played a more decisive role.

The consistently low biomass in the southern ACC conformed with our expectations. Low chlorophyll stocks ( $< 20 \text{ mg m}^{-2}$ ) were recorded at the beginning and end of the investigation in this region. The same factors that are likely to have constrained biomass build-up in the MIZ also would have applied here. Mixed layer depths were deeper than in the other two regions (Veth *et al.*, 1997) and in addition, heavy grazing pressure by salps was suggested (Dubischar and Bathmann, 1997). The average bacterial carbon demand amounted to about a half of primary production, double the value found for the MIZ and PFr (Lochte *et al.*, 1997). It is not surprising, therefore, that biomass levels remained low during the investigation period.

The maximum standing stock of chl *a* in the PFr increased four-fold in the month between Transects 2 and 11, from  $77$  to  $277 \text{ mg m}^{-2}$ . Bloom development in this region was patchy, with lower values ( $80 \text{ mg m}^{-2}$  during Transect 11) between bloom peaks. The patchiness, but also the species composition, could be related to the position of characteristic water masses within the PFr (Veth *et al.*, 1997), which was consistent between Transects 5 and 11. de Baar *et al.* (1995) and Veth *et al.* (1997) have argued that latitudinal displacement in the position of blooms between transects will have been due to meandering of the Polar Front; indeed, noticeable differences in the location of chlorophyll peaks within the PFr were observed within a time span of days. Nevertheless, the increase in total biomass between Transects 2/3, 5 and 11 can be attributed to temporal development of the populations within the PFr. This implies that the conditions recorded during each transect will have prevailed along a broad stretch of the PFr equivalent to a band of at least 500 km west-east extension, which is roughly the distance that a given water mass will have drifted in 1 month at easterly surface current speeds of about  $0.2 \text{ m s}^{-1}$  (Burkov, 1993). Laubscher *et al.* (1993) also reported chlorophyll concentrations similar to our values in December in the PFr at about  $28^\circ\text{W}$ . Tréguer and Jacques (1992) suggest that the Polar Frontal Zone is one of the most productive oceanic Antarctic ecosystems.

Although chlorophyll concentrations ranging between  $2$  and  $4 \text{ mg chl m}^{-3}$  will barely qualify for bloom status in other oceans, the total standing stocks attained in the PFr are, indeed, very high when compared with the North Atlantic spring bloom at the same latitude ( $47^\circ\text{N}$ ;  $20^\circ\text{W}$ ). Biomass in the latter region increased from  $50$  to  $160 \text{ mg chl a m}^{-2}$  during 3 weeks (Lochte *et al.*, 1993). The much higher standing stocks found in the PFr ( $177$ – $277 \text{ mg chl a m}^{-2}$ ) were due to the much deeper extension of the blooms ( $> 70 \text{ m}$ ) as compared to

those from other areas. Indeed, based on a survey conducted in coastal waters surrounding Antarctica, Sakshaug and Holm-Hansen (1984) reported that blooms only occurred at mixing depths shallower than 40 m.

The developmental dynamics of the deep PFr blooms cannot be deduced from the current data set, but we can rule out some possible scenarios. Thus, growth below 40 m depth could not have proceeded at the same rate as in the upper 40 m layer to account for the fairly homogeneous depth distribution of the phytoplankton. Further, it is highly unlikely that cells growing in the upper layer had sunk to lower layers. This is shown by the depth distribution of  $^{234}\text{Th}/^{238}\text{U}$  ratios (Rutgers van der Loeff *et al.*, 1997). In the bloom dominated by *Fragilariopsis kerguelensis* recorded in Transect 5, which extended to 70 m depth, the ratio was uniformly 1.0 down to 100 m, indicating that no sinking had occurred. The ratio was 0.90–0.95 in the bloom of the same species in Transect 11, signifying only minor losses and was certainly not enough to explain the presence of maximum concentrations well below the surface. Significant sinking losses (ratios of 0.7–0.9) were observed only in the *Corethron criophilum* bloom at the northern edge of the PFr, which could be explained by mass sinking of empty frustules following a sexual event in the population (Crawford, 1995; Crawford and Hinz, 1997).

Veth *et al.* (1997) have shown that the blooms in the PFr did not occur in vertically homogeneous water masses, which rules out the possibility that deep mixing occurred subsequent to growth in a shallow mixed layer. Rather, the scenario that we favour is subduction of a plankton-rich, shallow surface layer below the adjoining surface layer with similar biomass and species composition. Subduction of surface layers is given much less consideration than vertical mixing in the study of natural phytoplankton populations. A spectacular instance was recorded in the equatorial Pacific during the IRONEX experiment when the surface layer, fertilized with iron and marked with a tracer, was subducted to 30 m depth within a few days (Martin *et al.*, 1994). In the PFr, the plankton in the subducted layer would have maintained viability and remained in suspension despite the poorer light climate. Peters and Thomas (in press) have found that *Fragilariopsis kerguelensis*, kept under total darkness, can maintain viability for several months.

The main results of this cruise—absence of a MIZ bloom and the presence of large phytoplankton stocks extending to 70 m depth in a frontal system—also were recorded by the “STERNA” study in the Bellingshausen Sea (Turner and Owens, 1995). Indeed, Savidge *et al.* (1995) commented that “the absence of a classical stability-induced ice-edge bloom in the Bellingshausen Sea study area” was the most significant observation of the programme. The developmental dynamics of the blooms recorded in this study—about twice the biomass found in the *Polarstern* study—also could not be reconstructed. The physical conditions leading to the development of deep blooms in frontal regions obviously require further study. The presence of high iron concentrations in the PFr, as opposed to the region further south reported by de Baar *et al.* (1995), could explain the regional differences in phytoplankton biomass but not the deep extent of the blooms in the PFr.

Another interesting finding of the *Polarstern* study was the dominance patterns in the blooms in the PFr. Increases in biomass were mainly due to large diatoms rather than the nano- and picoplankton (Jochem *et al.*, 1995; Detmer and Bathmann, 1997), which support the suggestion of Smetacek *et al.* (1990) that the microbial network is ubiquitous but does not accumulate biomass; blooms in the Southern Ocean are due almost entirely to diatoms and *Phaeocystis*. Sommer (1989) has shown that maximal growth rates of Antarctic phytoplankton are not necessarily related to size and that large species can grow as fast as

smaller ones. Selective cropping of smaller cells, though a tempting explanation, hence need not be invoked for the dominance of large diatoms in the blooms. The lower POC:chl *a* ratios at higher biomass levels suggest more rapid growth of the dominant forms, as high mortality within the community would have been reflected in higher POC:chl *a* ratios in the southern ACC and MIZ. Grazing pressure of metazooplankton and protozoa relative to phytoplankton stocks was lower in the PFr than in the southern ACC and MIZ (Dubischar and Bathmann, 1997; Klaas, 1997).

The three blooms in the PFr were each dominated by single species, each likely to be of different biogeochemical significance in the region. Laubscher *et al.* (1993) also reported a dominance of *Fragilariopsis kerguelensis* in blooms observed in early summer in the PFr. Later in the year, *Corethron criophilum* dominated PFr blooms. Crawford (1995) has described the impact of a mass sexual event recorded in the *Corethron criophilum* bloom on vertical flux. Empty gametangial cells sank as a result, but not the living cells; this led to selective removal of silica from the surface layer relative to other biogenic elements. Crawford (1995) speculates that such events are responsible for the monospecific but patchy layers of frustules of this species reported from Southern Ocean sediments. The fate of the *Corethron inerme* bloom is not known. However, frustules of both *Corethron* species are comparatively rare in the sediments, despite their abundance in the water column. In contrast, the heavily silicified frustules of *Fragilariopsis kerguelensis* contribute a major portion of the silica deposits in the sediments underlying the ACC (Burckle and Cirilli, 1987), which accumulate 75% of the biogenic silica deposited in today's ocean (Tréguer *et al.*, 1995). Quéguiner *et al.* (1997) reported the highest Si:C ratios recorded to date in this bloom. Subsequent sinking of the population therefore also will have led to selective silica transport out of the surface layer. What remains to be ascertained is whether the dominance of *F. kerguelensis* frustules in the sediments is a reflection of its dominance status in the water column, such as in the bloom that we found, or whether selective accumulation of the robust frustules of a widely distributed species is a sufficient condition. It also should be pointed out that, despite the heavy armour of this species, hardly any sinking losses occurred during the several weeks of its presence in the water column. Presumably, mass sinking must have occurred later, triggered by some as yet unknown factor.

Interestingly, the diatom *Denticulopsis seminae*, which is superficially similar to *Fragilariopsis kerguelensis*, contributes 30% or more to the diatomaceous oozes of the North Pacific (Sancetta, 1981), which is another major site of silica deposition (Tréguer *et al.*, 1995). Whether these species have more in common than superficial morphology is not known, but this is a tantalizing question because of their importance for the ocean silica cycle. As pointed out by Verity and Smetacek (1996), the intrinsic and environmental factors promoting dominance of such "workhorse" species need to be explored if we are to improve our understanding of biogeochemical processes in the oceans.

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