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Annual and interannual variability in phytoplankton at a permanent station off Kerguelen Islands, Southern Ocean

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Abstract From November 1992 to February 1995 a quantitative and qualitative phytoplankton study was conducted at a permanent station (Kerfix) southwest off the Kerguelen Islands, in the vicinity of the Polar Front (50°40'S–68°25'E). Phytoplankton populations are low in this area both during summers and winters. They consist, in order of decreasing cell abundance, of pico- and nanoflagellates (1.5–20 µm), coccolithophorids (< 10 µm), diatoms (5–80 µm) and dinoflagellates (6–60 µm). Flagellates form the dominant group throughout the year and attain the highest summer average of 3.0×10^5 cells l⁻¹. Next in abundance year-round are coccolithophorids with the dominant *Emiliana huxleyi* (highest summer 1992 average 1.9×10^5 cells l⁻¹), diatoms (summer 1992 average 1.0×10^5 cells l⁻¹) and dinoflagellates (average 3.8×10^4 cells l⁻¹). Winter mean numbers of flagellates and picoplankton do not exceed 8.4×10^4 cells l⁻¹; those of the three remaining algal groups together attain 2×10^4 cells l⁻¹. Summer peaks of diatoms and dinoflagellates are mainly due to the larger size species (> 20 µm). The latter group contributes most to the total cell carbon biomass throughout the year. Dominant diatoms during summer seasons include: *Fragilariopsis kerguelensis*, *Thalassionema nitzschioides*, *Chaetoceros dichchaeta*, *C. atlanticus*, *Pseudonitzschia heimii*, and *P. barkleyi/lineola*. This diatom dominance structure changes from summer to summer with only *F. kerguelensis* and *T. nitzschioides* retaining their first and second positions. Any one of the

co-dominant species might be absent during some summer period. The variable diatom community structure may be due to southward meandering of the Polar Front bringing “warmer” species from the north, and to the mixing of the water masses in this area. The entire community structure characterized both during summer and winters by the dominance of flagellates can be related to deep mixing (ca. 40–200 m) of the water column as the probable controlling factor.

Introduction

Early studies of phytoplankton in the Southern Ocean were carried out over large oceanic areas during the austral spring/summer period (Hart 1942; Cassie 1963; Kozlova 1964; Hasle 1968, 1969). They showed the biogeographic distribution of mainly the larger size diatoms thought at first to form the base of the Antarctic food web (El-Sayed 1971). More recent phytoplankton investigations have been carried out in specific areas of differing primary productivity, such as in the rich coastal zone (Steyaert 1973b; Ligowski 1983; Fryxell et al. 1989; Kopczyńska et al. 1995), the marginal ice zone (Smith and Nelson 1986; Smith 1987; Kopczyńska 1991; Ligowski and Kopczyńska 1991; Becquevort et al. 1992), the frontal zones (Lutjeharms et al. 1985; Kopczyńska 1988; Laubscher et al. 1993; Bathmann et al. 1997; Socal et al. 1997), or in the impoverished open ocean zone (Steyaert 1973a; Jacques et al. 1979). Some of these works give comparisons of phytoplankton biomass and/or species distributions in a few zones of variable productivity (Kopczyńska et al. 1986; Jacques and Panouse 1991; Tréguer and Jacques 1992; Fiala et al. in press (b)). These mesoscale studies show great variations both in size of phytoplankton development and in species occurrence, and they often include besides the larger diatoms, the distribution and composition of the nano- and pico- size algae such as flagellates (< 20 µm) which often

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form summer blooms (Kopczyńska 1980, 1992; Estrada and Delgado 1990; Villafaña et al. 1995) and account for a high proportion of phytoplankton biomass and primary productivity (Hewes et al. 1985; Weber and El-Sayed 1987). The understanding of their dynamics and contribution to the plankton is necessary in order to elucidate the intricacies of the Antarctic food webs, such as the “microbial loop”.

Comparatively very few studies have been carried out year-round at permanently chosen stations (Whitaker 1982; Domanov and Lipski 1990; Clarke and Leakey 1996; Delille et al. 1996); for logistic reasons such investigations can only be done in the vicinity of Antarctic scientific bases. Some of such annual studies at a fixed station in Admiralty Bay at King George Island, West Antarctica (Kopczyńska 1980, 1981, 1992, 1996) showed seasonal and interannual phytoplankton variability both in terms of algal abundance and species composition.

From 1990 to 1994, the research programme Kerfix (a part of French contribution to Joint Global Ocean Flux Studies JGOFS) established a time-series station in the Indian sector of the Southern Ocean, southwest off Kerguelen Islands, in order to monitor the ocean/atmosphere gas exchanges and to understand the temporal variability of the carbon fluxes and associated elements (Fiala et al. in press (a); Jeandel et al. in press; Park et al. in press; Pondaven et al. in press). The objective of the present study carried out in the period November 1992/February 1995 was to gain quantitative information about major phytoplankton groups, species composition and their seasonal and interannual variability. In particular, we tried to find answers to such questions as whether or not the community structure of phytoplankton is stable during the summer seasons of increased growth, and whether there are any differences among the years in the timing of development of the dominant species.

Materials and methods

Quantitative and qualitative phytoplankton studies were conducted at a permanent station Kerfix (50°40'S, 68°25'E) located in the vicinity of the Polar Front in the open ocean zone of the Indian sector of the Southern Ocean (Fig. 1). Water samples for taxonomic analysis and counting were collected monthly from three depths (surface, chlorophyll maximum depth of 20 and 75 m, 100 m) during a 25-month period between November 1992 and February 1995. No samples were taken in January and February 1993 and in September 1994. Samples were obtained using Niskin bottles on board the French coastal oceanographic vessel “La Curieuse”. Aliquots of 100 ml were preserved with formalin at a final concentration of 0.4%. Algal cells were counted with the Olympus inverted microscope according to the procedures described by Utermöhl (1958). The data reported in Figs. 2–5 and Table 2 show average counts from three sampling depths. Due to samples preservation and optical resolution, the inverted microscope cell counting technique largely underestimates the picoplankton (<2 µm) size species.

Cell carbon biomass was estimated from cell volumes and cell abundances. Cell volumes were calculated by comparing cell shapes to appropriate geometric figures (Smayda 1978). The following cell

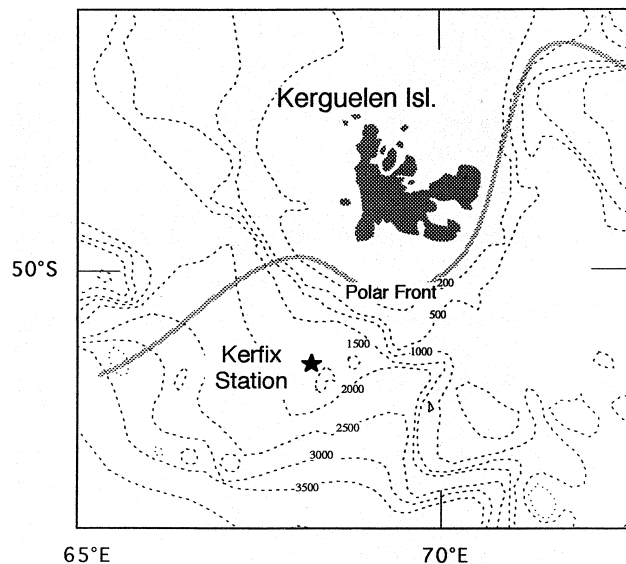


Fig. 1 Location of Kerfix station. The mean position of the Polar Front is indicated according to Park et al. (in press). Isobaths are in meters.

volume to carbon relationships were used for diatoms (Eppley et al. 1970): $\log C = 0.76(\log V) - 0.352$, and for other phytoplankton, $\log C = 0.94(\log V) - 0.60$, with V representing total cell volume (μm^3) and C cell carbon (pg).

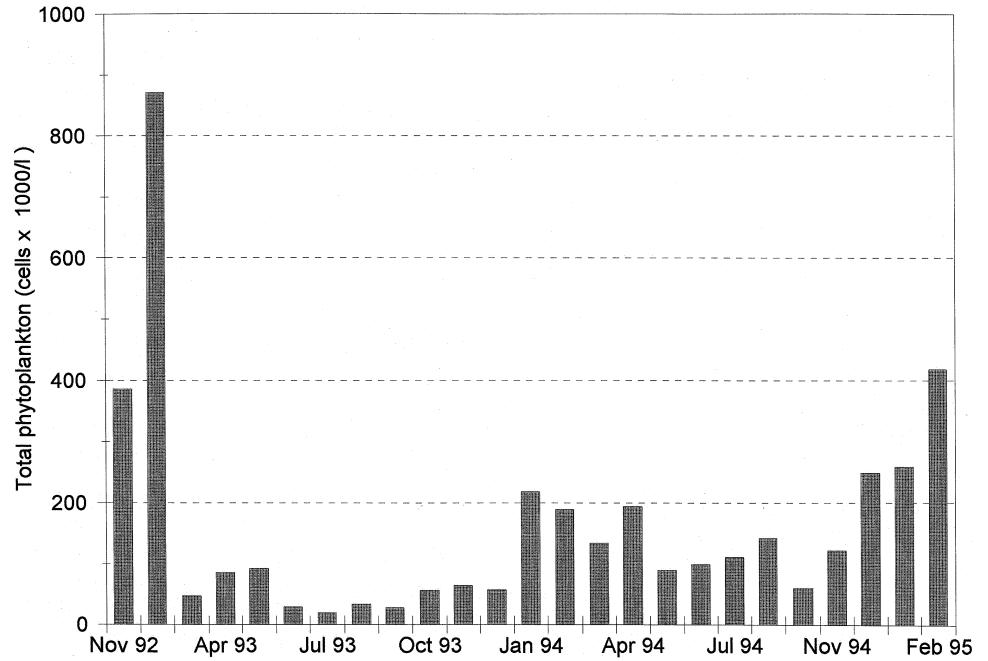
Results

Seasonal characteristics of surface water at Kerfix

Table 1 shows the physical-chemical data recorded during our study. Salinity, temperature, upper mixed layer depth (UML) and nutrient data are from C. Jeandel, D. Ruiz-Pino, P. Pondaven, C. Fravallo, Y.H. Park, E. Charriaud (unpublished work). During spring and summer, surface water was relatively warm (2.4–4.1°C) and well mixed, with salinity values ranging between 33.81 and 33.91 psu. A seasonal thermocline had developed below the mixed layer down to 200 m. An evolution from a summer stratified system with a marked thermocline to a deep homogeneous water column in winter was observed. The upper mixed layer depth varied from a minimum of 40 m in summer to a maximum of 250 m in winter with a great interannual variability. In winter, the water temperature was homogeneous in the upper 500 m water column with values <2°C (Park et al. in press).

The Kerfix site is characteristic of an HNLC area (High Nutrient Low Chlorophyll). The inorganic nutrients distribution exhibited a seasonal pattern that was correlated with physical and biological dynamics. During winter when strong mixing occurred, nitrate and silicate concentrations reached 27 and 19 mM m^{-3} , respectively. Autotrophic biomass was low throughout the year (<0.2 $\text{mg chl } a \text{ m}^{-3}$) except during the summer when a maximum of 1.2 $\text{mg chl } a \text{ m}^{-3}$ was reached in the upper 100 m (Fiala et al. in press (a)). After the summer bloom,

Fig. 2 Monthly variations of the mean water column cell densities (cells × 10³ l⁻¹) Kerfix station, November 1992 to February 1995



nutrient concentrations decreased to values around 24 mM for nitrate and between 6 and 13 mM for silicate.

Seasonal variations in abundance and species composition

In the period November 1992/February 1995 phytoplankton populations were low (Table 2, Figs. 2, 3) with

the total numbers in individual samples ranging between 10³ and 1.7 × 10⁶ cells l⁻¹. In 2 successive years they were composed, in order of decreasing numerical abundance, of naked pico- and nanoflagellates, coccolithophorids, diatoms and dinoflagellates. Coccolithophorids, diatoms and dinoflagellates showed distinct seasonal patterns in cell abundance, with summer maxima and winter minima (Table 2, Fig. 3). The pattern was less pronounced in the case of the combined

Fig. 3 Monthly variations of the mean water column cell numbers (cells × 10³ l⁻¹) of major phytoplankton groups. Total dinoflagellates include *Prorocentrum* spp., Kerfix station, November 1992 to February 1995

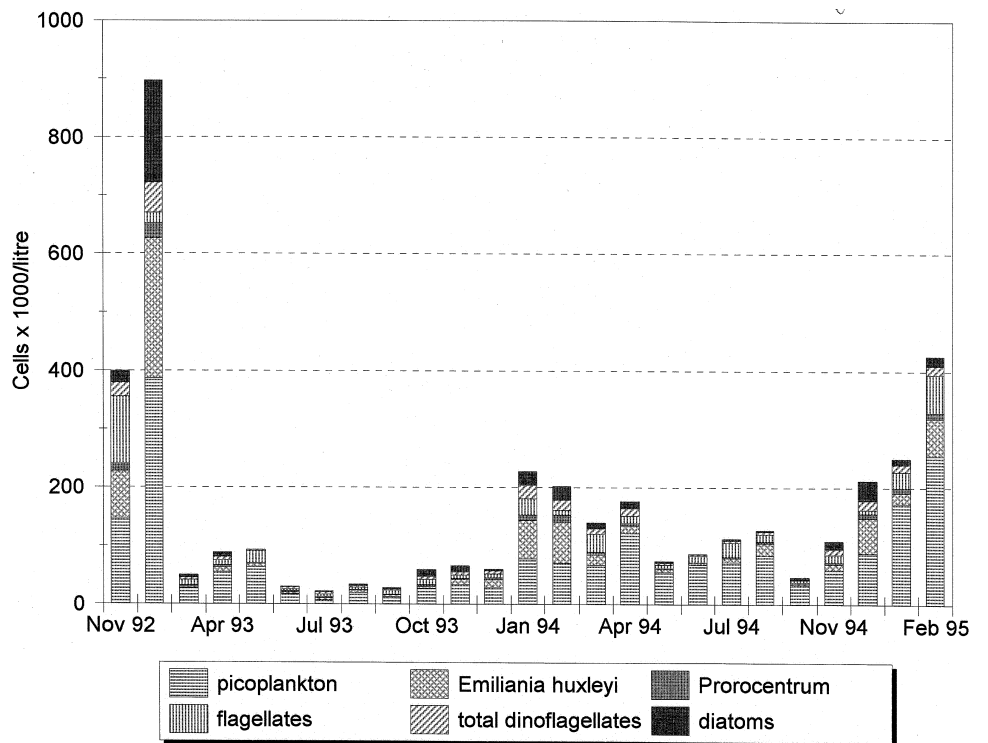


Fig. 4 Monthly distributions of mean water column total phytoplankton cell carbon values ($\mu\text{g C l}^{-1}$)

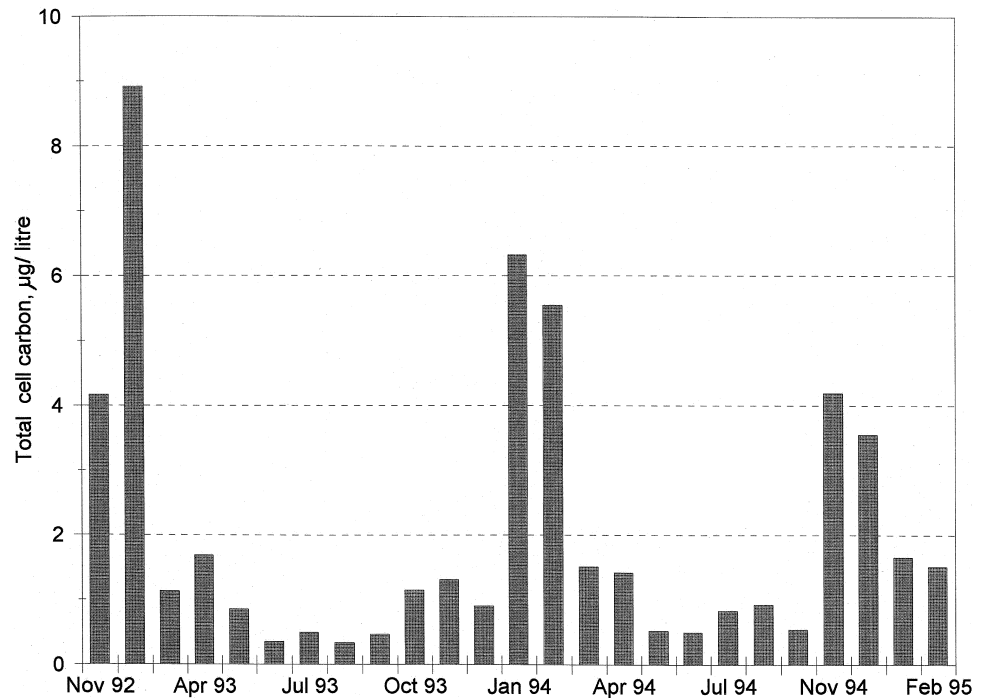
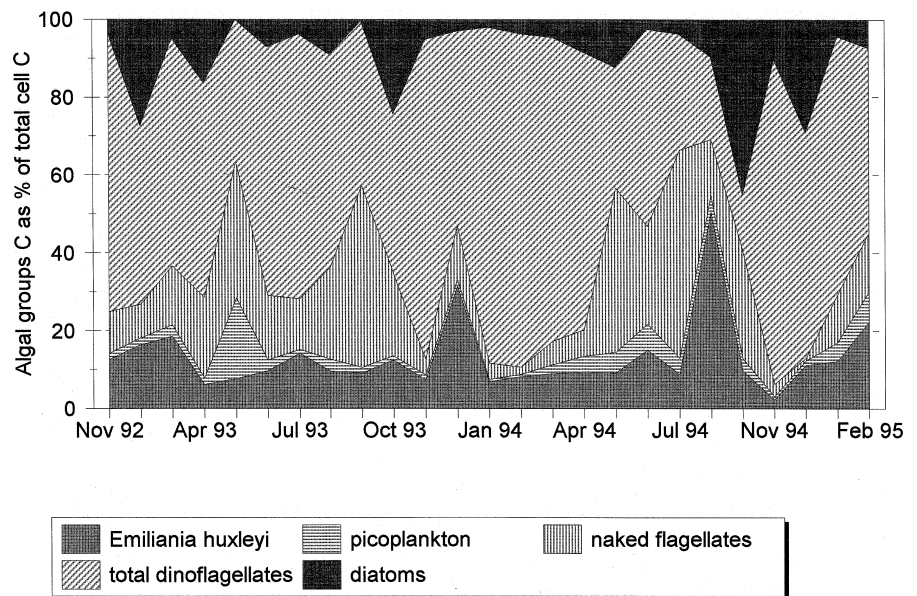


Fig. 5 Relative contribution of major algal groups carbon to total cell carbon values ($\mu\text{g C l}^{-1}$)



group of pico- and nanoflagellates whose winter 1994 quantities were similar to, or exceeded, those in the summer of 1993/1994. Generally, the average numbers of total phytoplankton ($6.4 \times 10^5 \text{ cells l}^{-1}$) in the summer of 1992 were 5 times greater than in the summer of 1993/1994 and 2.5 times higher than in the season 1994/1995; this was mainly due to the presence of naked flagellates and coccolithophorids. However, algal quantities in the two later summer seasons were only about twice as great as those in the preceding respective winters of 1993 and 1994 (Table 2).

Flagellates and picoplankton

Flagellates and picoplankton generally made up the highest percentage of the counts, usually exceeding 50%. The maximum quantity ($9 \times 10^5 \text{ cells l}^{-1}$) in December 1992 exceeded sevenfold the maximum count in the summer of 1993/1994 and almost twice the highest count in the summer of 1994/1995 (Table 2, Fig. 3).

Formalin-preserved flagellates and picoplankton are difficult to identify accurately; however, the naked flagellates appeared to include mainly biflagellates such as

Table 1 Mean values (\pm SD) of temperature, salinity and nutrient concentrations in the upper 100-m water column from November 1992 to February 1995 at Kerfix station, (UML upper mixed layer thickness, m, n.d. no data)

Date	Temperature (°C)	Salinity (psu)	UML (m)	NO ₃ (mM m ⁻³)	SiO ₂ (mM m ⁻³)
1/11/92	2.73 \pm 0.02	33.843 \pm 0.005	80	24.3 \pm 0.5	15.7 \pm 0.6
17/12/92	2.92 \pm 0.15	33.850 \pm 0.008	90	24.0 \pm 0.7	10.7 \pm 2.3
12/03/93	4.10 \pm 0.02	33.843 \pm 0.001	80	25.0 \pm 1.0	n.d.
6/04/93	3.98 \pm 0.01	33.828 \pm 0.010	100	24.2 \pm 0.5	n.d.
15/05/93	3.85 \pm 0.01	33.809 \pm 0.003	90	25.1 \pm 0.1	7.2 \pm 0.6
10/06/93	3.08 \pm 0.04	33.825 \pm 0.003	100	25.3 \pm 0.1	13.4 \pm 0.3
16/07/93	2.25 \pm 0.01	33.863 \pm 0.004	240	27.3 \pm 0.2	10.7 \pm 0.5
17/08/93	1.95 \pm 0.00	33.883 \pm 0.008	190	27.3 \pm 0.2	13.2 \pm 0.2
16/09/93	1.68 \pm 0.07	33.912 \pm 0.003	80	27.6 \pm 0.2	14.1 \pm 1.0
27/10/93	1.79 \pm 0.01	33.918 \pm 0.002	90	26.8 \pm 0.3	19.5 \pm 0.8
28/11/93	1.99 \pm 0.01	33.929 \pm 0.001	220	26.4 \pm 0.4	15.5 \pm 0.8
27/12/93	2.84 \pm 0.06	33.903 \pm 0.007	60	25.1 \pm 0.7	13.5 \pm 1.2
18/01/94	3.23 \pm 0.01	33.908 \pm 0.007	50	n.d.	10.5 \pm 0.7
6/02/94	3.68 \pm 0.03	33.903 \pm 0.009	40	n.d.	n.d.
14/03/94	n.d.	n.d.	60	24.2 \pm 1.5	n.d.
17/04/94	3.42 \pm 0.01	33.892 \pm 0.005	120	24.2 \pm 0.2	10.8 \pm 0.5
12/05/94	2.99 \pm 0.00	33.877 \pm 0.009	140	24.9 \pm 0.2	12.1 \pm 0.3
12/06/94	2.46 \pm 0.00	33.877 \pm 0.007	150	n.d.	13.1 \pm 0.8
9/07/94	2.43 \pm 0.00	33.867 \pm 0.008	140	24.1 \pm 0.2	15.2 \pm 0.5
29/08/94	1.65 \pm 0.01	33.927 \pm 0.011	180	26.4 \pm 0.9	18.2 \pm 0.4
17/10/94	1.63 \pm 0.01	33.916 \pm 0.009	250	25.9 \pm 0.2	19.8 \pm 0.9
7/11/94	1.81 \pm 0.07	33.900 \pm 0.006	50	27.1 \pm 0.5	19.8 \pm 0.4
8/12/94	n.d.	33.895 \pm 0.005	40	23.9 \pm 0.8	n.d.
8/01/95	3.15 \pm 0.02	33.900 \pm 0.004	42	23.6 \pm 0.3	7.9 \pm 0.1
27/02/95	3.65 \pm 0.07	33.844 \pm 0.003	50	24.4 \pm 0.3	5.8 \pm 0.6

Table 2 Mean water column cell densities and ranges (cells $\times 10^3$ l⁻¹) of major phytoplankton groups during the summer and winter seasons (November 1992 to February 1995), Kerfix station

Season	Flagellates 1.5–20 μ m	Coccolithophorids < 10 μ m	Diatoms 5–80 μ m	Dinoflagellates 5–60 μ m	Total phytoplankton
Summer 1992 (Nov–Dec)	307.2	194.74	104.13	38.24	644.3
Winter 1993 (Mar–Oct)	125–918	66–296	6–357	19–96	267–1719
Summer 1993–1994 (Nov–Feb)	37	4.6	5.2	3.6	50.4
Winter 1994 (Mar–Oct)	9–112	1.12–15	0.5–21	0.8–9	10.7–121
Summer 1994–1995 (Nov–Feb)	65	39	16	13	133
Winter 1994 (Mar–Oct)	13–134	2–109	0.5–63	2–41	27–246
Summer 1994–1995 (Nov–Feb)	84	9	5	6	104
Winter 1994 (Mar–Oct)	25–321	2–31	0.7–36	0.6–25	33–397
Summer 1994–1995 (Nov–Feb)	176	38	23	14	251
Winter 1994 (Mar–Oct)	14–492	3.8–116	6–125	5.7–29	62–621

several species of Prasinophyceae (*Pyramimonas* spp.), Cryptophyceae (e.g. *Hillea fusiformis*) and Prymnesiophyceae (*Chrysochromulina* sp., *C. alifera* Parke et Manton). The last genus is known for mixotrophy (Parke et al. 1955, 1956). Prymnesiophyceae were generally most numerous during all seasons.

Picoplankton (<2 μ m) contained 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.

Coccolithophoridae

The group contributed 8–57% to the total cell densities. *Emiliania huxleyi* (Lohmann) Hay et Mohler was the only conspicuous species present year-round. Summer maxima of mean water column densities (Fig. 3) ranged

between 6.4×10^4 cells l⁻¹ (January, February 1994) and 3×10^5 cells l⁻¹ (December 1992).

Diatoms

Whenever present, diatoms composed 0.7–29% of the total cell counts. Summer peak mean numbers (Fig. 3) ranged from 2.3×10^4 cells l⁻¹ (February 1994) to 1.75×10^5 cells l⁻¹ (December 1992). In some summer (November and December 1993, January and February 1995) and winter collections (August, September 1993, May and June 1994) diatoms were only found in surface waters. Summer maxima of the group (Table 3) were mainly composed of the larger species (length 12–90 μ m) such as *Fragilariopsis kerguelensis* (O'Meara) Hust. (= *Nitzschia kerguelensis*), *Thalassionema nitzschioides* (Grun.) Hust., *Chaetoceros* spp., *Chaetoceros atlanticus* Cl., *Chaetoceros bulbosus* (Ehr.) Heiden, *Chaetoceros dictyota* Ehr., and *Pseudonitzschia* spp. (= *Nitzschia* spp.,

Table 3 Summary of the seasonal occurrence of selected species found at Kerfix station from November 1992 to February 1995 (*a* abundant; *m* moderate; *f* few; *r* rare)

Species	Summer 92 (Nov–Dec)	Winter 93 (Mar–Oct)	Summer 93/94 (Nov 93–Feb 94)	Winter 94 (Mar–Oct)	Summer 94/95 (Nov 94–Feb 95)
Diatoms					
<i>Chaetoceros atlanticus</i>					a Dec, Jan
<i>C. bulbosus</i>					m Dec, Jan
<i>C. dichæta</i>	a Dec				
<i>Chaetoceros</i> spp.					a Dec, Jan
<i>Corethron criophilum</i>	r		r		f
<i>Eucampia balaustium</i>		r	r		f
<i>Thalassiosira gracilis</i>			f	f	f
<i>T. lentiginosa</i>	f		f	f	f
<i>Thalassiosira/Coscinodiscus</i>	m	f	f	m	m
<i>Thalassionema nitzschioides</i>	a Nov, Dec	f	m Nov	f	m Nov
<i>Thalassiothrix antarctica</i>	f Dec	r			f Dec
<i>Fragilariopsis curta</i>			f		f
<i>F. cylindrus</i>			m Feb	r	m Nov
<i>F. kerguelensis</i>	a Nov, Dec	f	a Feb	m	a Dec
<i>F. oceanica</i>			m Dec		
<i>F. pseudonana</i>		f	f	f	m Dec, Jan, Feb
<i>Nitzschia closterium</i>			f	r	f
<i>N. longissima</i>	f	r			r
<i>Pseudonitzschia heimii</i>			a Jan, Feb		a Dec
<i>P. lineola</i>		f	a Jan, Feb		
<i>Pseudonitzschia</i> spp.			a Jan, Feb		m Dec
Dinoflagellates					
<i>Amphidinium hadai</i>		r		r	
<i>Ceratium pentagonum</i>			r		
<i>Gymnodinium flavum</i>	m	r	f	r	f
<i>G. guttula</i>	f		f		f
<i>G. minor</i>	r	r	r		f
<i>Gymnodinium</i> spp.	m	f	a	m	a
<i>Gyrodinium</i> spp.	m	f	a	m	a
<i>Gonyaulax</i> spp. (<i>kofoidii</i>)	f	r	f		
<i>Oxytoxum criophilum</i>	m				
<i>Prorocentrum antarcticum</i>			f		f
<i>P. micans</i>	m		f		f
<i>P. minimum</i>	f		f		f
<i>Prorocentrum</i> spp.	a	m	a	m	a
<i>Protoperidinium antarcticum</i>	r		f		r
<i>P. cruciferum</i>			f		f
<i>Protoperidinium</i> spp.	m		f		m
Coccolithophoridae					
<i>Emiliana huxleyi</i>	a	f	a	m	a

Pseudonitzschia group), i.e. *Pseudonitzschia heimii* Mangin and *Pseudonitzschia lineola* Cl. (Hasle).

F. kerguelensis was always the most numerous diatom; however, each summer season, dominant diatom groups were formed of somewhat different species (Table 3). Thus in December of 1992, the most abundant were *F. kerguelensis* (max. 3×10^5 cells l^{-1}); *Thalassionema nitzschioides* (max. 6×10^4 cells l^{-1}) and *Chaetoceros dichæta* (max. 3.7×10^4 cells l^{-1}). In the summer of 1993/1994 when peak numbers were reached in January and February 1994, *F. kerguelensis* (max. 3.6×10^4 cells l^{-1}) was accompanied by *Pseudonitzschia heimii* and *Pseudonitzschia lineola* (1.8 – 2.5×10^4 cells l^{-1}). *Chaetoceros* species were conspicuously absent, while *T. nitzschioides* occurred only more abundantly in November 1993 (10^4 cells l^{-1}). However, the diatom peak in the summer of 1994/1995 in December could mainly be attributed, except for *F.*

kerguelensis, to *Chaetoceros* spp. and especially to *Chaetoceros atlanticus* and to *Pseudonitzschia heimii*. As in November 1993, *Thalassionema nitzschioides* was frequent in November 1994.

In addition to the dominant diatoms, next in abundance, especially in January and February 1994 were: *Fragilariopsis pseudonana* Hasle, *F. cylindrus* (Grun.) Krieger and *Nitzschia closterium* (Ehr.) W. Sm. *Thalassiothrix antarctica* Schimper was numerous in December 1994. Small (usually $< 10 \mu m$) *Thalassiosira* spp., e.g. *Thalassiosira gracilis* (Karsten) Hustedt and *Thalassiosira lentiginosa* (Jan.) G. Fryxell, and also *Coscinodiscus* spp. fluctuated from month to month; however, they were often absent from both summer and winter collections. Infrequently found were the large species of *Corethron criophilum* Castr., *Eucampia balaustium* Castr., and *Proboscia alata* (Brightwell) Sundstrom.

Dinoflagellates

These generally contributed 0.8–36.4% to the total phytoplankton. The group (Tables 2, 3, Fig. 3) was dominated by *Prorocentrum* spp. (6–24 µm) present year-round (max. 2.6×10^4 cells l^{-1} in December 1992). Most frequently found, particularly during summer, were *Prorocentrum micans* Ehrenberg, *Prorocentrum dentatum* Stein, *Prorocentrum triestinum* Schiller, and *Prorocentrum minimum* (Pavillard) Schiller. *Gymnodinium* species (5–25 µm) were next in abundance and often included *Gymnodinium flavum* Kofoid et Swezy, *Gymnodinium minor* Lebour, *Gymnodinium modestum* Balech, *Gymnodinium guttula* Balech, and *Gymnodinium soyai* Hada. The heterotrophic species of the genera *Protoperdinium* (18–60 µm) and *Gyrodinium* (8–40 µm) were especially noticeable during the summer months (December 1994, January 1995, February 1995).

Cell carbon distribution

During the entire period of 25 months, the mean water column cell carbon values of total phytoplankton were low and ranged between $0.33 \mu\text{g C l}^{-1}$ (August 1993) and $8.91 \mu\text{g C l}^{-1}$ (December 1992), (Fig. 4). The other highest summer values were noted in January 1994 ($6.33 \mu\text{g C l}^{-1}$) and in November 1994 ($4.19 \mu\text{g C l}^{-1}$).

Most of the carbon biomass, both during summer peaks and in winters, was due to the contribution (Fig. 5) by dinoflagellates (14.1–86.3%; range 0.07 – $5.46 \mu\text{g C l}^{-1}$) with the maximum value occurring in January 1994. Within the dinoflagellates, the species of *Prorocentrum* usually made up 50–89% of the carbon (max. $3.07 \mu\text{g C l}^{-1}$; December 1992). However, much of the summer dinoflagellate carbon (up to 90%) was due to larger heterotrophic species of the genera *Protoperdinium* and *Gyrodinium*.

In the majority of the samples, both diatoms and coccolithophorids each contributed less than 10% to the total carbon. The highest diatom summer values ranged between $0.24 \mu\text{g C l}^{-1}$ (October 1994) and $2.45 \mu\text{g C l}^{-1}$ (December 1992); those of coccolithophorids were 0.1 – $1.45 \mu\text{g C l}^{-1}$, with the maximum in December 1992.

Except for dinoflagellate carbon, winter carbon biomass was largely due (up to 57.5%) to naked flagellates and picoplankton (max. $0.5 \mu\text{g C l}^{-1}$ in July 1994). The highest summer flagellate carbon value was $0.9 \mu\text{g C l}^{-1}$ in December 1992.

Discussion

Phytoplankton abundance and composition

Data from Kerfix station show persistently impoverished phytoplankton populations throughout summer and winter seasons (November 1992/February 1995). It

is interesting to note that the maximum summer numbers, especially those of diatoms, are comparable to the quantities previously reported north of the Polar Front from the Indian (Kozlova 1964, Steyaert 1973a, Koczyńska et al. 1986) and the Pacific sectors (Hasle 1969) of the Southern Ocean. Summer diatom quantities in the present study (average 1.6×10^4 – 1.04×10^5 cells l^{-1}) are also very similar to those observed by Jacques et al. (1979) at the edges of both the Subtropical and Polar Fronts southwest of the Kerguelen Islands, i.e. in an area including the location of our present sampling site. In contrast to these authors, who found the phytoplankton community to be dominated by diatoms and dinoflagellates, our data show the numerical year-round predominance of nano- and picoplanktonic naked flagellates and of coccolithophorids, while diatoms and dinoflagellates are placed as the third and fourth most abundant algal groups. A phytoplankton study in the Indian Ocean between Africa and Antarctica conducted in late summer in March 1980 (Koczyńska et al. 1986) showed that quantities of flagellates and dinoflagellates increased in the vicinity of, and northward of, the Polar Front, and that flagellates outnumbered diatoms in the subantarctic zone. Recently, Fiala et al. (in press (b)) reported a high contribution of the nano- and picoflagellate biomass in the northern areas along the 62°E Indian sector transect in late summer. Also summer studies in the Atlantic sector of the Southern Ocean (Bathmann et al. 1997, Smetacek et al. 1997) reported flagellates and coccolithophorids to be important, besides diatoms and dinoflagellates, which are constituents of the plankton at the Polar Front.

Community structure and environmental factors

The question that arises is how to explain the persistently low phytoplankton abundance at the Kerfix site, as well as the particular community structure characterized by the continuous year-round and year-to-year numerical predominance of flagellates and coccolithophorids over diatoms and dinoflagellates.

It has been suggested that nanoplankton flagellates form a ubiquitous and stable oceanic population (Smetacek et al. 1990) that is usually exceeded by diatoms during summer blooms. It has also been documented for the Antarctic Peninsula area (Koczyńska 1992) that flagellates dominated diatoms at 85 of 102 oceanographic stations located in a well-mixed water column (> 100 m), while diatoms were prevalent at sites (36 of 40) of increased water column stability (UML of 10–50 m). These results provided field evidence that deep vertical mixing creates conditions for the dominance of flagellates (< 20 µm) over diatoms. Nanoflagellates are also the year-round dominant algae in the very unstable waters of Admiralty Bay at King George Island (South Shetlands), which are subject to deep mixing and frequent upwelling (Koczyńska 1980, 1981).

At Kerfix, UML depth varied between ca. 40 m in summer and >200 m in winter. A maximum thickness of 50 m of the mixed layer is considered as a prerequisite for a phytoplankton bloom build-up (Sakshaug and Holm-Hansen 1984; Smetacek and Passow 1990). Thus the generally deep mixing of the water column at our study site and the resulting low light regime might provide one of the likely explanations for the suppression of more prolific algal development in this area, as well as, perhaps, for the community structure in terms of phytoplankton groups.

Surface water temperature might also be important in influencing both algal quantities and composition. The highest numbers were observed in the summer of 1992 and they subsided significantly in the following months both in winters and summers. This situation coincided with the general water temperature decrease at the station from the highest values in 1992 (on average 0.23°C above normal) to a minimum in 1994 (on average 0.23°C below normal), (Park et al. in press). Various authors have suggested that Antarctic diatoms are constrained by low temperatures (Jacques 1983; Fiala and Oriol 1990).

At Kerfix, nitrate concentrations are never depleted and could sustain good-size phytoplankton productivity; however, low silica values, noted in summer, may be limiting for diatoms. This may particularly pertain to some of the dominant diatoms, i.e. *Fragilariopsis kerguelensis* and *Chaetoceros* spp., which appear to require greater silica concentrations for their optimal growth in relation to other diatoms (Jacques 1983). This might be especially true for *F. kerguelensis*, which is one of the most heavily silicified Antarctic species.

Although mesozooplankton grazing, mainly by copepods, is not significant at Kerfix site (S. Razouls, personal communication), the microprotozoans may play an important role. Unfortunately, the nanoflagellates found were not examined using epifluorescence; however, they are likely to include various heterotrophic and mixotrophic forms (Becquevort et al. 1992, Becquevort 1997). The *Chrysochromulina* identified is known for mixotrophy (Parke et al. 1955, 1956). Dinoflagellates in our samples contained heterotrophic species of the genera *Gyrodinium* and *Protoperidinium* able to feed on diatoms >20 µm (Jacobson and Anderson 1986).

Dominant species

The interesting features of our results from the vicinity of the Polar Front are the abundance of coccolithophorids and the variable summer diatom community structure. *Emiliania huxleyi*, the only conspicuous coccolithophorid in the samples, is the most abundantly occurring living species of the group known to form large blooms in the northern hemisphere (Berge 1962). It is cosmopolitan and tolerant of a wide ecological range (Heimdal 1983). It has been reported from the Antarctic (Thomsen et al. 1988; Knox 1994), including the Polar Front region in the Atlantic (Bathmann et al. 1997) and

the Weddell-Scotia Confluence (Jacques and Panouse 1991). It has not previously been observed southwest of the Kerguelen Islands by Jacques et al. (1979) between 43°S and 62°S.

The composition of dominant diatoms showed differences from summer to summer. Of the species observed, *Fragilariopsis kerguelensis* and *Thalassionema nitzschioides* were always present, while *Pseudonitzschia* spp. were only numerous in the summers of 1993/1994 and 1994/1995 and were absent in 1992. However, *Chaetoceros* spp. did not occur in the summer of 1993/1994, and were quite abundant in the summer seasons of 1992 and 1994/1995. In winters diatom numbers were very low and some of the summer dominants were not detectable. These dominant diatoms are known to have somewhat different biogeographical distributions. *Thalassionema nitzschioides* has been reported to have a widespread occurrence in the subantarctic zone between the Polar and Subtropical Fronts (Hasle 1969, 1976). In the study of the Indian Ocean phytoplankton between Africa and Antarctica the species was only found north of the Polar Front (Kopczyńska et al. 1986). Similarly, *Pseudonitzschia* species (= *Nitzschia*, *Pseudonitzschia* group), i.e. *Pseudonitzschia lineola* and *Pseudonitzschia heimii*, although common to the entire Southern Ocean (Hasle 1969, 1976) were previously found to be predominant among diatoms north of, and in the vicinity of, the Polar Front both in the Indian Ocean (Steyaert 1973a, Kopczyńska et al. 1986) and in the subantarctic East Pacific (Hasle 1969). However, *Fragilariopsis kerguelensis*, which is widely distributed in the Southern Ocean, and *Chaetoceros* spp. (*Chaetoceros dictyota* and *Chaetoceros atlanticus*) are generally found in greater abundance in the Antarctic zone south of the Polar Front (Steyaert 1973b, Kopczyńska et al. 1986). At least two studies reported *Chaetoceros dictyota* present only south of the Polar Front (Sournia et al. 1979; Kopczyńska et al. 1986). *Fragilariopsis kerguelensis*, the most abundant diatom in our samples, was also observed to be dominant by Jacques et al. (1979) in their entire study region west of the Kerguelen Islands. The species (together with *Corethron criophilum*) formed blooms in October/November 1992 at the Polar Front in the South Atlantic (Bathmann et al. 1997; Smetacek et al. 1997). The latter authors reported that distribution of other common diatoms such as *Thalassionema nitzschioides*, *Chaetoceros dictyota* and *Chaetoceros bulbosus*, and also coccolithophorids was restricted to the Polar Front. This diatom composition and the presence of coccolithophorids are similar to our results; however, contrary to what we found, in their samples diatoms were the prevalent group.

Considering both the differences in the currently known biogeographical distribution of diatoms found at Kerfix, and the location of the Kerfix site at the southern edge of the Polar Front, the diatom community structure and its variations from one summer season to another may not be surprising. It appears that they could well be attributed to lateral mixing of the water masses

at the sampling site, and particularly to southward meandering of the Polar Front (Park et al. in press) bringing “warmer” species from the north. Water masses of different histories are likely to stimulate the growth of different species (Hart 1942).

Cell carbon

Cell carbon values (summer maximum $8.91 \mu\text{g C l}^{-1}$) reflect the numerical poverty of phytoplankton populations. Dinoflagellates, which are the major contributors to carbon biomass, have previously been found to make 14% of cell carbon during late summer in Prydz Bay (Kopczyńska et al. 1995). Total carbon values at Kerfix are very low indeed compared with those in the latter area (average $317 \mu\text{g C l}^{-1}$), and other diverse regions such as a permanent station in Admiralty Bay (summer average $14.7 \mu\text{g C l}^{-1}$), (Kopczyńska 1996), or from Drake Passage (average $17.1 \mu\text{g C l}^{-1}$). However, it is interesting to note that the present carbon results are of the same order of magnitude as those from Drake Passage and Bransfield Strait obtained at the time of phytoplankton poverty in February/March 1981, at low water column stabilities (mixing to ~ 100 m) (Kopczyńska 1992).

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References

- Bathmann UV, Scharek R, Klass C, Dubischar CD, Smetacek V (1997) Spring development of phytoplankton biomass and composition in major water masses of the Atlantic sector of the Southern Ocean. *Deep Sea Res* 44:51–67
- Becquevort S (1997) Nanoprotozooplankton in the Atlantic sector of the Southern Ocean during early spring: biomass and feeding activities. *Deep Sea Res* 44:355–373
- Becquevort S, Mathot S, Lancelot C (1992) Interactions in the microbial community of the marginal ice zone of the north-western Weddell Sea through size distribution analysis. *Polar Biol* 12:211–218
- Berge G (1962) Discoloration of the sea due to *Coccolithus huxleyi* “bloom”. *Sarsia* 6:27–40
- Cassie V (1963) Distribution of surface phytoplankton between New Zealand and Antarctica, December 1957. *Trans-Antarct Exped 1955–1958 Sci Rep* 7:1–10
- Clarke A, Leakey RJG (1996) The seasonal cycle of phytoplankton, macronutrients, and the microbial community in a nearshore Antarctic marine ecosystem. *Limnol Oceanogr* 41:1281–1294
- Delille D, Fiala M, Razouls S (1996) Seasonal changes in bacterial and phytoplankton biomass in a subantarctic coastal area (Kerguelen Islands). *Hydrobiologia* 330:143–150
- Domanov MM, Lipski M (1990) Annual cycle of chlorophyll *a* and primary production in Admiralty Bay (Antarctica). *Pol Arch Hydrobiol* 37:471–478
- El-Sayed SZ (1971) Dynamics of trophic relationship in the Southern Ocean. In: Quan LO (ed) *Research in the Antarctic*. American Association for the Advancement Science, Washington, DC, pp 73–91
- Eppley RW, Reid FMH, Strickland JDH (1970) The ecology of the plankton off La Jolla, California, in the period April through September 1967. In: Strickland JDH (ed) *Estimates of phytoplankton crop size, growth rate and primary production, part III*. *Bull Scripps Inst Oceanogr* 17:33–42
- Estrada M, Delgado M (1990) Summer phytoplankton distributions in the Weddell Sea. *Polar Biol* 10:441–449
- Fiala M, Oriol L (1990) Light-temperature interactions on the growth of Antarctic diatoms. *Polar Biol* 10:629–636
- Fiala M, Kopczyńska EE, Jeandel C, Oriol L, Vétion G (in press a) Seasonal and interannual variability of size fractionated phytoplankton biomass and community structure at station Kerfix, off Kerguelen Islands, Antarctica. *J Plankton Res*
- Fiala M, Semeneh M, Oriol L (in press b) Biomass, size fractionated phytoplankton and species composition in the Indian sector of the Southern Ocean during austral summer. *J Mar Systems*
- Fryxell GA, Kang S-H, Ashworth TK (1989) AMERIEZ 1988 and ODP leg 119: Antarctic phytoplankton summer and winter stage indicators. *Antarct J US* 24:156–157
- Hart TJ (1942) Phytoplankton periodicity in Antarctic surface waters. *Discovery Rep* 21:261–356
- Hasle GR (1968) Distribution of marine diatoms in the Southern Ocean. In: Bushnell VC (ed) *Primary productivity and benthic marine algae of the Antarctic and Subantarctic*. American Geographic Society, New York (Antarctic Map Folio series, folio 10), pp 6–8
- Hasle GR (1969) An analysis of the phytoplankton of the Pacific southern Ocean: abundance, composition, and distribution during the Bratigg Exp 1947–48. *Hvalradets Skr* 52:1–168
- Hasle GR (1976) The biogeography of marine planktonic diatoms. *Deep Sea Res* 23:319–338
- Heimdal BR (1983) Phytoplankton and nutrients in the waters north-west of Spitsbergen in the autumn of 1979. *J Plankton Res* 5:901–918
- Hewes CD, Holm-Hansen O, Sakshaug E (1985) Alternate carbon pathways at lower trophic levels in Antarctic food web. In: Siegfried WR, Condy PR, Laws RM (eds) *Antarctic nutrient cycles and food webs*. Springer, Berlin, Heidelberg New York, pp 277–283
- Jacobson DM, Anderson JM (1986) Thecate heterotrophic dinoflagellates feeding behaviour and mechanism. *J Phycol* 22:249–258
- Jacques G (1983) Some ecophysiological aspects of the Antarctic phytoplankton. *Polar Biol* 2:27–33
- Jacques G, Panouse M (1991) Biomass and composition of size fractionated phytoplankton in the Weddell-Scotia Confluence area. *Polar Biol* 11:315–328
- Jacques G, Descolas-Gros C, Grall J-R, Sournia A (1979) Phytoplankton distribution in the Antarctic sector of the Indian Ocean in late summer. *Int Rev Ges Hydrobiol* 64:609–628
- Jeandel C, Ruiz-Pino D, Gatja E, Poisson A, Brunet C, Charriaud E, Dehairs F, Delille D, Fiala M, Fravallo C, Miquel J-C, Park Y-H, Razouls S, Quéguiner B, Shauer B, Tréguer P (in press) Kerfix a permanent time series station in the Southern Ocean: a presentation. *J Mar Systems*
- Knox GA (1994) *The biology of the Southern Ocean*. Cambridge University Press, Cambridge
- Kopczyńska EE (1980) Small-scale vertical distribution of phytoplankton in Ezcurra Inlet, Admiralty Bay, South Shetland Islands. *Pol Polar Res* 1:77–96
- Kopczyńska EE (1981) Periodicity and composition of summer phytoplankton in Ezcurra Inlet, Admiralty Bay, South Shetland Islands. *Pol Polar Res* 2:55–70
- Kopczyńska EE (1988) Spatial structure of phytoplankton in the Scotia Front west of Elephant Island (Biomass III, October–November 1986). *Pol Polar Res* 9:231–242
- Kopczyńska EE (1991) Distribution of microflagellates and diatoms in the sea-ice zone between Elephant Island and the South Orkney Islands (December 1988–January 1989). *Pol Polar Res* 12:515–528

- Kopczyńska EE (1992) Dominance of microflagellates over diatoms in the Antarctic areas of deep vertical mixing and krill concentrations. *J Plankton Res* 14:1031–1054
- Kopczyńska EE (1996) Annual study of phytoplankton in Admiralty Bay, King George Island, Antarctica. *Pol Polar Res* 17:151–164
- Kopczyńska EE, Goeyens L, Semeneh M, Dehairs F (1995) Phytoplankton composition and cell carbon distribution in Prydz Bay, Antarctica: relation to organic particulate matter and its ^{13}C values. *J Plankton Res* 17:685–707
- Kopczyńska EE, Weber LH, El-Sayed SZ (1986) Phytoplankton species composition and abundance in the Indian Sector of the Antarctic Ocean. *Polar Biol* 6:161–169
- Kozlova OG (1964) Diatom algae of the Indian and Pacific sectors of the Antarctic. Nauka, Moscow
- Laubscher RK, Perissinotto R, McQuaid CD (1993) Phytoplankton production and biomass at frontal zones in the Atlantic sector of the Southern Ocean. *Polar Biol* 13:471–481
- Ligowski R (1983) Phytoplankton of the Olaf Prydz Bay (Indian Ocean, East Antarctica) in February 1969. *Pol Polar Res* 4:21–32
- Ligowski R, Kopczyńska EE (1991) Distribution of net phytoplankton in the sea-ice zone between Elephant Island and the South Orkney Islands (December 1988–January 1989) *Pol Polar Res* 12:529–546
- Lutjeharms JRE, Walters NM, Allanson BR (1985) Oceanic frontal systems and biological enhancement. In: Siegfried WR, Condy PR, Laws RM (eds) *Antarctic nutrient cycles and food webs*. Springer, Berlin, Heidelberg, New York, pp 11–21
- Park Y-H, Charriaud E, Ruiz-Pino D, Jeandel C (in press) Seasonal and interannual variability of the mixed layer properties and steric height at station Kerfix, southwest of Kerguelen Islands. *J Mar Systems*
- Parke M, Manton I, Clarke B (1955) Studies of marine flagellates. II. Three new species of *Chrysochromulina*. *J Mar Biol Assoc UK* 34:579–609
- Parke M, Manton I, Clarke B (1956). Studies of marine flagellates. III. Three further species of *Chrysochromulina*. *J Mar Biol Assoc UK* 35:387–414
- Pondaven P, Fravalo C, Ruiz-Pino, Tréguer P, Quéguiner B, Jeandel C (in press) Modelling the silica pump in the permanently open ocean zone of the Southern Ocean. *J Mar Systems*
- Sakshaug E, Holm-Hansen O (1984) Factors governing pelagic production. In: Holm-Hansen O, Bolis L, Gilles R (eds) *Marine phytoplankton and productivity*. Springer, Berlin Heidelberg New York, pp 1–18
- Smayda TJ (1978) From phytoplankton to biomass. In: Sournia A (ed) *Monographs on oceanographic methodology*, 6, *Phytoplankton manual*. UNESCO, Paris, pp 273–279
- Smetacek V, Passow U (1990) Spring bloom initiation and Sverdrup's critical depth model. *Limnol Oceanogr* 35:228–233
- Smetacek V, Scharek R, Nothig E-M (1990) Seasonal and regional variation in the pelagial and its relationship to the life history cycle of krill. In: Kerry KR, Hempel G (eds) *Antarctic ecosystems: ecological change and conservation*. Springer, Berlin Heidelberg New York, pp 103–114
- Smetacek V, Baar HJW de, Bathmann UV, Lochte K, Rutgers Loeff MM van der (1997) Ecology and biogeochemistry of the Antarctic Circumpolar Current during austral spring: a summary of Southern Ocean JGOFS cruise ANT X/6 of r.v. Polarstern. *Deep Sea Res* 44:1–21
- Smith WO (1987) Phytoplankton dynamics in marginal ice zones. *Oceanogr Mar Biol Annu Rev* 25:11–38
- Smith WO, Nelson DM (1986) Importance of ice-edge phytoplankton production in the Southern Ocean. *BioScience* 36:251–257
- Socal G, Nöthig EM, Bianchi F, Boldrin A, Mathot S, Rabitti S (1997) Phytoplankton and particulate matter at the Weddell/Scotia Confluence (47°W) in summer 1989, as a final step of a temporal succession (EPOS project). *Polar Biol* 18:1–9
- Sournia A, Grall J-R, Jacques G (1979) Plankton diatoms and dinoflagellates along a meridian transect in the Southern Indian Ocean (Campagne "Antiprod I" du Marion Dufresne, mars 1977). *Bot Mar* 22:183–198
- Steyaert J (1973a) Distribution of plankton diatoms along an African-Antarctic transect. *Invest Pesq* 37:295–328
- Steyaert J (1973b) Difference in diatom abundance between two summer periods of 1965 and 1967 in Antarctic inshore waters (Bread Bay). *Invest Pesq* 37:517–532
- Thomsen HA, Buck KR, Coale SL, Garrison DL (1988) Nanoplanktonic coccolithophorids (Prymnesiophyceae, Haptophyceae) from the Weddell Sea, Antarctica. *Nord J Bot Sect Phycol* 8:419–436
- Tréguer P, Jacques G (1992) Dynamics of nutrients and phytoplankton and fluxes of carbon, nitrogen and silicon in the Antarctic Ocean. *Polar Biol* 12:149–162
- Utermöhl H (1958) Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitt Int Ver Theor Angew Limnol* 9:1–38
- Villafane VE, Helbling EW, Holm-Hansen O (1995) Spatial and temporal variability of phytoplankton biomass and taxonomic composition around Elephant Island, Antarctica, during the summers of 1990–1993. *Mar Biol* 123:677–686
- Weber LH, El-Sayed SZ (1987) Contributions of the net, nano- and picoplankton to the phytoplankton standing crop and primary productivity in the Southern Ocean. *J Plankton Res* 9:973–994
- Whitaker TM (1982) Primary production of phytoplankton off Signy Island, South Orkneys, the Antarctic. *Proc R Soc Lond* 214:169–189