

Seasonal variation in marine phytoplankton and ice algae at a shallow antarctic coastal site

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Abstract

The phytoplankton population near Davis, Vestfold Hills, Antarctica was monitored throughout 1982. Chlorophyll-a determinations and counts of living cells in both the water column and sea ice demonstrated a marked seasonality in phytoplankton abundance and species composition. From April to October nanoplanktonic organisms contributed most of the chlorophyll-a in both the sea ice and water column. Blooms of diatoms occurred in May, November and December in the bottom of the sea-ice and in January and February in the water column. *Phaeocystis pouchetii* was dominant during December in the water column. Large numbers of dead diatoms were found in winter. The concentrations of nitrate, dissolved inorganic phosphate and dissolved silicate increased throughout the year until December, when the concentrations of nitrate and silicate fell sharply, followed a month later by a reduction in phosphate concentration. The diversity of phytoplankton was greatest during the summer months.

Introduction

Numerous studies have been made of the standing crop and primary productivity of phytoplankton in antarctic waters (e.g. El-Sayed & Mandelli, 1965; El-Sayed, 1968; Holm-Hansen *et al.*, 1977; Fukuchi, 1980). In addition, considerable attention has been given to the taxonomy of the larger, more robust components of the phytoplankton, especially the diatoms. However, with few exceptions (e.g. Bunt, 1960; Hoshiai, 1977; Gruzov, 1977; Krebs, 1983), these investigations have been confined to the short summer period and there are few reports of organisms other than diatoms, despite Hasle's (1969) finding that a substantial component of the phytoplankton was of nanoplanktonic size. Only recently have detailed reports of antarctic nanoplankton, organisms of the size range 2–20 μm (*sensu* Sieburth *et al.*, 1978), appeared (e.g. Silver *et al.*, 1980; von Bröckel, 1981; Buck & Garrison, 1983; Marchant, 1985). These investigations indicate that the nanoplanktonic organisms

of antarctic waters are major contributors to the phytoplanktonic standing crop as is the case in other parts of the world (Hallegraeff, 1981; Booth *et al.*, 1982).

Organisms living in the sea ice of both the Arctic and Antarctic have been the subject of numerous investigations (Bunt, 1963; Bunt & Wood, 1963; Meguro *et al.*, 1967; Bunt & Lee, 1970; Horner, 1976; Palmisano & Sullivan, 1983; McConville & Wetherbee, 1983). However, most of these investigations have considered the sea ice community in relative isolation rather than dealing with the sea ice and water column together. Here we report a year-round investigation of microalgae in the sea ice and water column at a shallow antarctic coastal station.

Materials and methods

Monthly samples were collected 1 km offshore from the Australian antarctic station Davis

Table 1. Standing crop, nutrients, salinity, temperature, pH, sea ice thickness and snow cover at the monitoring site.

Date	Depth	Pigment concentration (mg m ⁻³)		Cell numbers (Cells × 10 ⁴ l ⁻¹)		Nutrients (g-at l ⁻¹)		Salinity ‰	Temp. °C	pH	Ice cm	Snow cm
		Total Chl-a	Nano- Chl-a	Phaeo- phytin	Total	Dead	NO ₃					
24.i.82	2.5 m	0.80	-	1.05	77	-	-	32.91	0.3	-	-	-
	Bottom	5.22	-	6.93	21	-	-	33.00	0	-	-	-
16.ii.82	2.5 m	0.37	-	0.24	12	-	-	33.33	-1.2	-	-	-
	Bottom	0.36	-	0.29	10	-	-	33.26	-1.2	8.17	-	-
05.iii.82	0 m	0.38	-	0.11	65	9.3	0.55	33.77	-1.6	8.06	4	0
	5 m	0.45	-	0.19	8	6.0	0.51	33.51	-1.6	8.05	-	-
08.iv.82	Bottom	0.87	-	0.55	5	5.9	0.55	33.67	-1.6	8.07	26	2
	Ice	1.16	0.67	0.16	42	-	-	-	-	7.96	-	-
07.v.82	0 m	0.16	0.06	0.04	2	8.8	1.01	34.07	-1.8	7.90	-	-
	5 m	0.12	0.06	0.05	2	10.5	0.84	33.20	-1.8	7.91	-	-
07.vi.82	Bottom	0.15	0.04	0.06	9	9.0	1.00	33.88	-1.8	7.93	68	6
	Ice	6.41	3.60	0	140	-	-	-	-	7.71	68	6
07.vi.82	0 m	0.35	0.18	0.01	6	-	-	34.09	-1.8	7.85	-	-
	5 m	0.19	0.19	0.03	14	-	-	34.13	-1.8	7.85	-	-
07.vi.82	Bottom	0.25	0.23	0.07	1	-	-	34.12	-1.8	7.86	91	8
	Ice	2.92	1.88	1.08	46	4.2	1.00	13.83	-	7.45	-	-
01.vii.82	0 m	0.39	0.17	0.02	5	17.1	0.96	33.63	-2.0	7.92	-	-
	5 m	0.17	0.13	0	7	13.9	1.05	34.07	-2.0	7.94	-	-
01.vii.82	Bottom	0.19	0.09	0.01	3	9.8	0.66	34.22	-2.0	7.94	107	18
	Ice	1.53	0.63	0	9	5.0	0.24	9.30	-	8.04	-	-
10.viii.82	0 m	0.19	0.12	0	2	10.3	0.82	34.66	-1.9	7.84	-	-
	5 m	0.15	0.11	0	7	9.2	0.64	34.16	-1.9	7.84	-	-
10.viii.82	Bottom	0.09	0.09	0.10	3	14.0	1.16	31.5	-1.9	7.85	115	35
	Ice	1.41	0.69	1.36	26	3.3	0.41	7.93	-	7.03	-	-
	0 m	0.19	0.10	0	2	13.9	1.17	34.58	-1.9	7.78	-	-

Table 1. Continued.

Date	Depth	Pigment concentration (mg m ⁻³)			Cell numbers (Cells × 10 ⁴ l ⁻¹)		Nutrients (g-at l ⁻¹)		Salinity ‰	Temp. °C	pH	Ice cm	Snow cm
		Total Chl-a	Nano- Chl-a	Phaeo- phytin	Total	Dead	NO ₃	PO ₄ ³⁻					
06.ix.82	5 m	0.11	0.08	0	1	0	12.5	1.5	31.3	-1.9	7.93		
	Bottom	0.12	0.08	0.06	9	2	15.1	1.24	37.7	-1.8	7.88		
	Ice	1.16	0.74	1.03	48	9	3.5	0.18	7.1	7.91	7.61	142	30
	0 m	0.21	0.06	0	0.7	2	16.7	1.25	36.7	34.83	-2.0	7.83	
13.x.82	5 m	0.10	0.08	0	6	2	17.1	1.02	37.6	34.51	-1.9	7.84	
	Bottom	0.20	0.01	0.20	5	9	16.7	1.27	38.8	34.55	-1.8	7.81	
	Ice	0.77	0.37	0.13	12	4	8.6	0.36	10.0	14.57	-	7.71	60
	0 m	0.40	0.20	0.12	5	1	14.9	0.97	32.3	34.58	-1.8	7.84	
01.xi.82	5 m	0.18	0.09	0.09	0.8	1	16.3	1.14	35.6	34.58	-1.8	7.84	
	Bottom	0.17	0.09	0.11	7	2	18.4	1.38	40.9	34.62	-1.8	7.81	
	Ice	0.56	0.32	0.44	130	26	2.8	0.15	6.3	5.96	-	7.75	55
	0 m	0.56	0.12	0.10	3	1	18.3	1.15	39.0	34.63	-1.8	7.80	
09.xiii.82	5 m	0.37	0.09	0	28	1	16.6	1.20	37.9	34.50	-1.8	7.82	
	Bottom	0.35	0.10	0.20	51	0.8	15.3	1.06	34.9	34.58	-1.8	7.75	
	Ice	0.95	0.40	0.09	160	0	3.0	0.40	4.9	-	8.04	194	0
	0 m	3.52	0.61	0	21	0	4.9	1.76	11.0	-	-1.7	8.21	
10.i.83	5 m	4.52	0.29	0	120	0	7.3	0.68	17.7	-	-1.1	7.93	
	Bottom	5.95	1.55	6.20	83	0	6.2	1.17	14.2	34.30	-1.2	7.94	
	0 m	2.52	1.21	-	480	0	3.2	0.43	13.8	31.87	1.1	-	
	5 m	5.89	0.89	-	520	0	0.5	0.32	17.5	33.03	1.3	-	
02.ii.83	Bottom	9.73	1.60	-	280	0	1.1	0.43	10.4	33.15	1.2	-	
	0 m	-	-	-	2 000	0	1.5	0.54	10.6	-	1.8	-	
	5 m	-	-	-	2 000	0	1.4	6.41	12.7	-	1.6	-	
	Bottom	-	-	-	2 100	0	6.4	6.20	6.9	-	0.6	-	

- No sample taken.

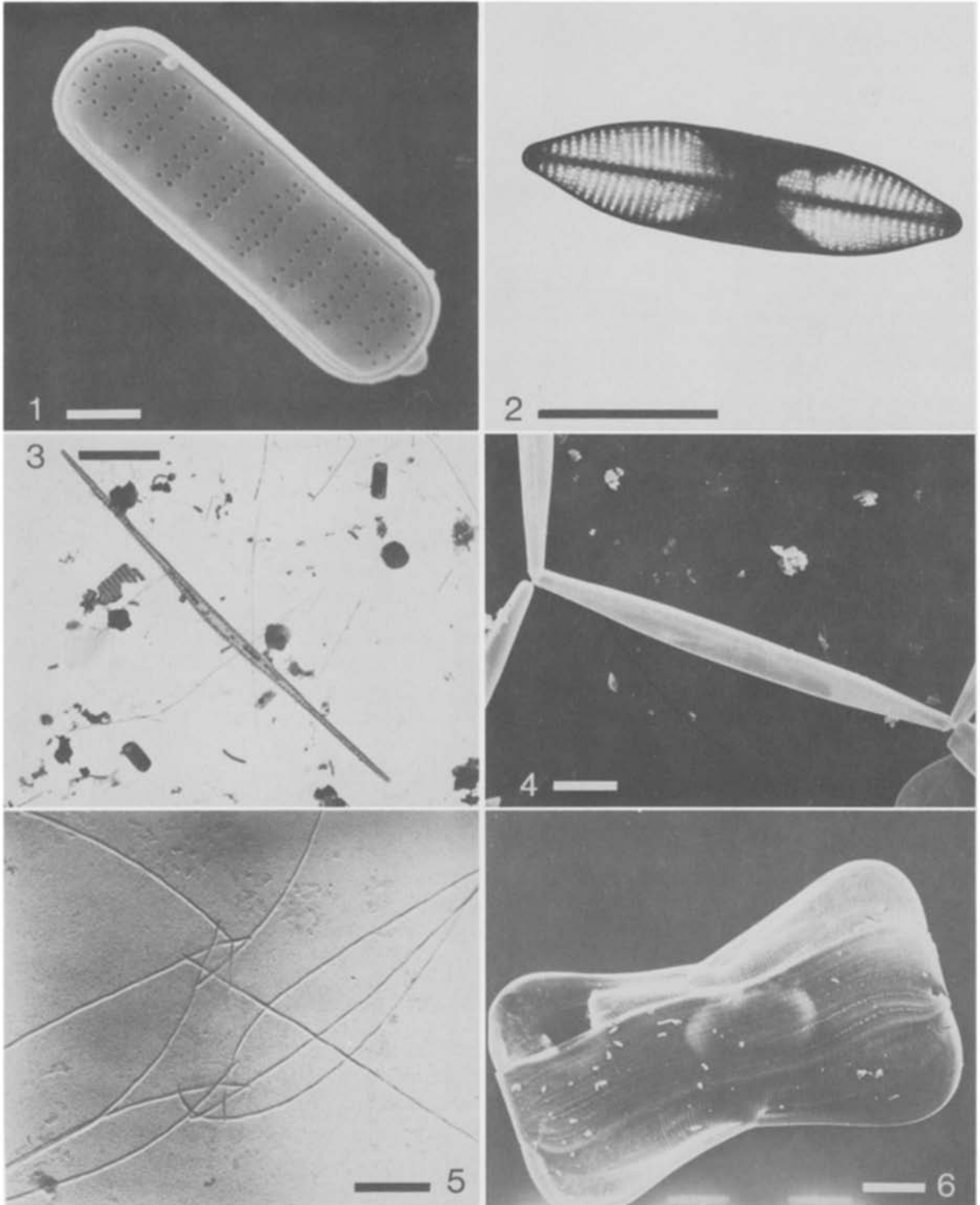


Fig. 1. Scanning electron micrograph (SEM) of *Nitzschia cylindrus*, one of the most common diatoms found at the inshore site. Scale bar=1 μm .

Fig. 2. Transmission electron micrograph (TEM) of *Navicula* sp. 1, common in the sea ice during May. Scale bar=10 μm .

Fig. 3. *Nitzschia lanceolata*, a common diatom in the water column in summer: TEM. Scale bar=10 μm .

Fig. 4. *Nitzschia frigida*, abundant in the sea ice in spring: SEM. Scale bar=10 μm .

Fig. 5. Pentagonal arrays of thread-like material from the prymnesiophyte *Phaeocystis pouchetii*: TEM. Scale bar=1 μm .

Fig. 6. The diatom *Amphiprora kjellmanii* which occurred in the sea ice during spring: SEM. Scale bar=10 μm .

(68°35'S, 77°58'E) from January 1982 to February 1983. In winter, a Kemmerer bottle was used to collect water samples from the surface (or ice-water interface), and at depths of 2.5 m, 5 m and at the bottom (8 m). Brash ice, under the consolidated sea ice, occurred only in April and May when it was collected as part of the interface sample. During summer when there was open water, sampling was undertaken from an amphibious vehicle. For the rest of the year the collections were made through a 10 cm diameter hole cut in the ice with a SIPRE corer. The ice core was kept for investigations of the sea ice community.

Approximately 4 l of water from each depth were stored at 0°C until analysed. The thickness of ice and snow, together with water temperature, were recorded. Observations of the extent, structure and development of the sea ice algal community were made three times per month by SCUBA diving.

From each sample 1 l of water or ice was melted at about 20°C and reduced to 5.5 ml by gentle filtration through a 0.8 µm sized Millipore filter. Drops of the concentrate were placed on formvar-coated electron microscope grids, fixed with OsO₄ vapour for 25 s, dried, washed gently with distilled water and stored in a desiccator for later examination by transmission electron microscopy.

Counts of living organisms were made using a modified Lund cell on an optical microscope equipped with phase contrast optics at 200 and 400× magnification. The remaining concentrate was fixed in 1% glutaraldehyde for subsequent microscopical studies. For scanning electron microscopy this glutaraldehyde fixed material was attached to glass coverslips with polylysine (Marchant & Thomas, 1983), dehydrated with acetone, critical point dried and gold coated.

Chlorophyll-a and phaeophytin concentrations were determined using the methods detailed in UNESCO (1966). The nanoplanktonic contribution to the total chlorophyll was ascertained by determining the chlorophyll concentration of plankton samples that had been passed through a 20 µm mesh nylon gauze. The pH of this filtered water was measured.

Samples for salinity determination were stored unfrozen in tightly stoppered plastic bottles until they were analysed with an Anton Parr DMA55 density meter. Salinity was calculated using the formula: $\text{salinity} = 1315.789474 \times \text{density} - 1313.421053$ (Appendix I in Whitfield & Jagner, 1981).

Nutrient analysis was carried out on samples of filtered water that had been frozen in 500 ml plastic Whirlpaks. Nitrate, dissolved inorganic phosphate and dissolved silicate were determined using the procedure outlined in Grasshoff *et al.* (1983; 143–150, 126, 175–180 respectively).

Results

Counts of living cells and measurements of chlorophyll-a indicate that the algal concentration was higher in the sea ice community than in the water column (Table 1). There were two major peaks of phytoplankton abundance in the ice during the year. The first occurred in May and was dominated by two pennate diatoms, *Nitzschia cylindrus* (Grun.) Hasle and *Navicula* sp. 1 (see Figs 1 & 2). A 1 cm thick brown layer on the undersurface of the ice was first observed during April and developed to a thickness of 4 cm by May. The second peak of algal abundance in the sea ice occurred during November-December when *Amphiprora kjellmanii* (Cleve) in Cleve & Grunow (Fig. 6), *Synedra* sp. 1 (an epiphyte of *A. kjellmanii*) and *Nitzschia frigida* (Grun.) in Cleve & Grunow (Fig. 4) were present in large numbers. These organisms had a patchy distribution on the underside of the sea-ice, being most abundant where the ice was free of snow cover. Two peaks of cell abundance in the water column occurred during summer. The 1982/83 summer peak was caused by high concentrations of the dinoflagellate *Gymnodinium* sp., the prymnesiophyte *Phaeocystis pouchetii* (Har.) Lagerh. (Fig. 5) and *Nitzschia lanceolata* Wm. Smith (Fig. 3).

Other cells that occurred commonly in the water column were *Chaetoceros simplex* Ostenfeld (Fig. 7), *Dactyliosolen antarcticus* Castracane (Fig. 8), *Thalassiosira* sp. 1 (Fig. 9), *Cocconeis fasciolata* (Ehr.) Brown (Fig. 10), *Asteromphalus parvulus* Karsten (Fig. 11), *Thalassiosira gracilis* (Karsten) Hustedt (Fig. 12), *Navicula* sp. 2 (Fig. 13), *Navicula muticopsis* Van Heurk (Fig. 14), *Chaetoceros atlanticus* var. *bulbosum* (Ehr.) Hargraves (Fig. 15), and *Pleurasigma* sp. 1 (Fig. 16).

Nanoplankton chlorophyll-a accounted for a major part of the total chlorophyll in the sea ice community throughout the year (as shown in Table 1), and particularly from April until October in the water column (see Fig. 17). The contribution of

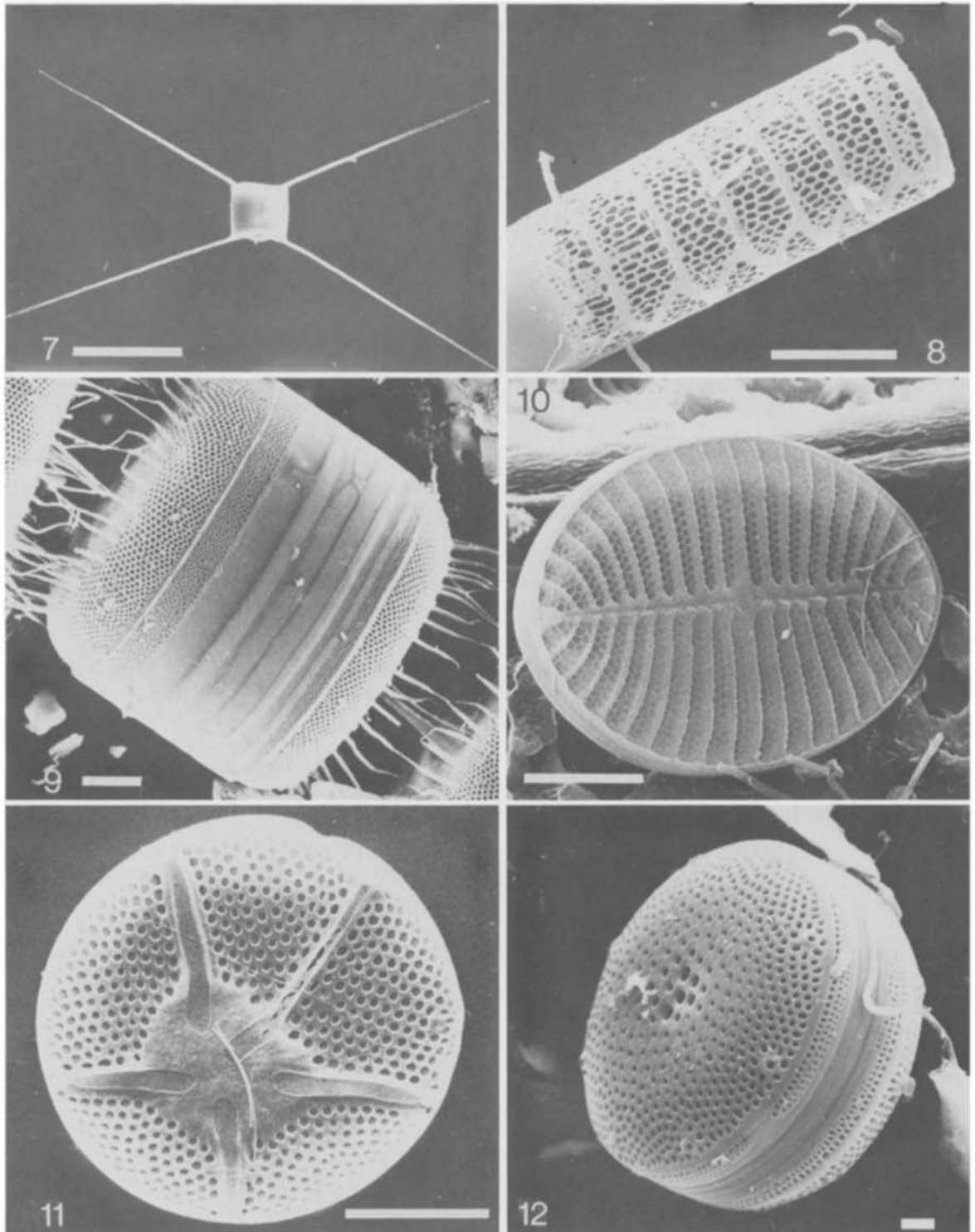


Fig. 7. The small diatom *Chaetoceros simplex*: SEM. Scale bar=10 μm .

Fig. 8. Aerolate girdle bands of the lightly silicified diatom *Dactyliosolen antarcticus*: SEM. Scale bar=5 μm .

Fig. 9. *Thallasiosira* sp.: Scale bar=10 μm .

Fig. 10. *Cocconeis fasciolata*: SEM. Scale bar=10 μm .

Fig. 11. *Asteromphalus parvulus*: SEM. Scale bar=10 μm .

Fig. 12. *Thallasiosira gracilis*. Note both the variation in the distribution of aerolae on the valve from numerous at the margin to less numerous near the centre, and the variation in size between marginal and central aerolae: SEM. Scale bar=1 μm .

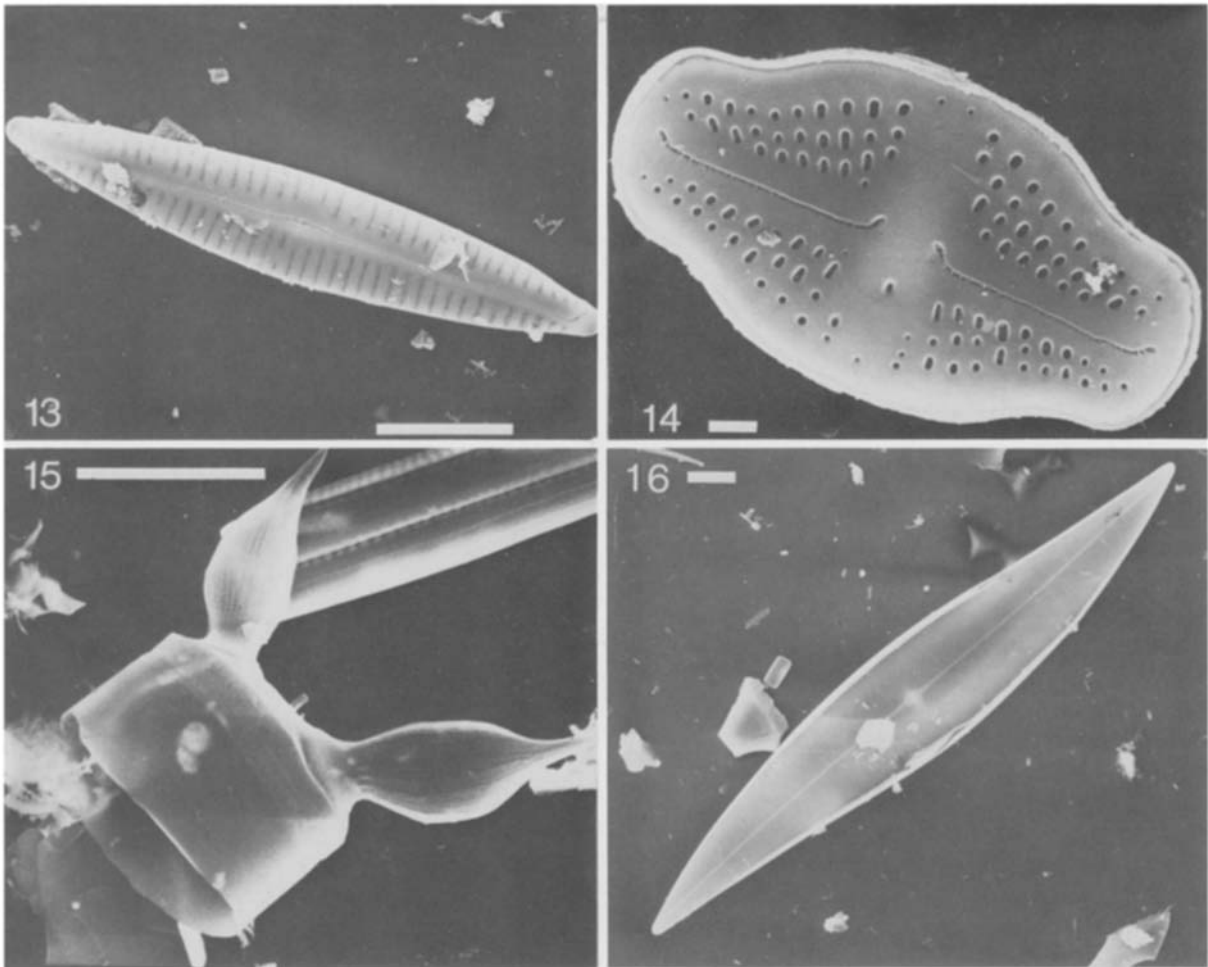


Fig. 13. *Navicula* sp. 2: TEM. Scale bar=10 μ m.

Fig. 14. Valve view of *Navicula muticopsis*: SEM. Scale bar=1 μ m.

Fig. 15. *Chaetoceros atlanticus* var. *bulbosum*: SEM. Scale bar=10 μ m.

Fig. 16. *Pleurasigma* sp. 1: SEM. Scale bar=10 μ m.

nanoplankton chlorophyll to total chlorophyll was at a minimum in the water column at the time of the diatom blooms in November and December.

Thirty-eight taxa of phytoplankton were identified from the water column (Table 2), and 20 from the sea ice (Table 3). A number of unidentified organisms was also found which will be considered elsewhere. Considerable seasonality is evident in the diversity of species in the water column (Table 2) with the greatest diversity in summer and autumn. No such trends were evident in the ice. Counts of living cells of eight of the most abundant taxa are presented in Table 4 which shows the

marked temporal distributions of these species, with the exception of *Nitzschia cylindrus* which was common in both ice and water samples throughout the study period. The succession of algal species was rapid in the summer. *Gymnodinium* sp. 1 occurred in high numbers in the ice for only a week before *P. pouchetii* bloomed throughout the water column. This bloom lasted from the third week of December to the first week of January, after the ice broke out from the sampling area. *Nitzschia lanceolata* became dominant in the water column during January and February 1983.

Large numbers of dead cells were observed

Table 2. Species occurrence of phytoplankton and ice algae in the water samples.

Species	1982												1983		
	Date	24.i	16.ii	05.iii	08.iv	07.v	07.vi	01.vii	10.viii	06.ix	13.x	01.xi	09.xii	10.i	02.ii
<i>Achnanthes</i> sp.1	+	+	+	+	+	-	+	-	-	-	-	-	+	-	-
<i>Amphiprora kjeltmanii</i> (Cleve) in Cleve & Grunow	-	-	-	-	-	-	-	-	-	-	-	+	+	-	+
<i>Amphora</i> sp.1	-	-	-	-	-	+	-	+	-	-	+	+	+	+	+
<i>Asteromphalus parvulus</i> Karsten	+	-	+	+	+	-	-	-	-	-	-	-	-	-	-
<i>Chaetoceros atlanticus</i> var. <i>bulbosum</i> (Ehr.) Hargraves	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-
<i>Chaetoceros borealis</i> Bailey	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chaetoceros criophilum</i> Castracane	-	+	-	+	+	-	-	-	-	-	-	-	-	-	-
<i>Chaetoceros debilis</i> Cleve <i>Chaetoceros dichaeete</i> Ehrenberg	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
<i>Chaetoceros simplex</i> Ostenfeld <i>Chaetoceros schimperianum</i> Karsten	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+
<i>Chaetoceros</i> sp.1	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
<i>Chaetoceros</i> sp.2	+	+	+	+	+	-	-	-	-	-	-	-	+	-	-
<i>Cocconeis fasciolata</i> (Ehr.) Brown	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+
<i>Corethron criophilum</i> Castracane	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Coccinodiscus</i> sp.1	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-
<i>Dactyliosolen antarcticus</i> Castracane	-	+	+	+	+	+	-	-	-	-	-	-	-	+	+
<i>Distephanus speculum</i> (Ehr.) Haeckel	+	+	-	-	-	+	-	-	-	-	-	-	+	-	+

Table 2. Continued.

Species	1982												1983		
	Date	24.i	16.ji	05.iii	08.iv	07.v	07.vi	01.vii	10.viii	06.ix	13.x	01.xi	09.xii	10.i	02.ii
<i>Eucampia</i> sp.1	+	+	-	-	-	-	-	-	-	-	-	-	+	-	-
<i>Gymnodinium</i> sp.1	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
<i>Navicula muticopsis</i> Van Heurk	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
<i>Navicula</i> sp.1	-	-	+	-	-	+	-	-	+	-	-	+	+	-	+
<i>Navicula</i> sp.2	-	-	+	-	-	+	-	-	-	+	+	-	-	-	-
<i>Nitzschia angulata</i> Hasle	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
<i>Nitzschia closterium</i> (Ehr.) Wm. Smith	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
<i>Nitzschia cylindrus</i> (Grun.) Hasle	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-
<i>Nitzschia frigida</i> (Grun.) in Cleve & Grunow	-	-	-	-	-	+	-	-	-	-	-	+	+	+	+
<i>Nitzschia lanceolata</i> Wm. Smith	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Nitzschia longissima</i> (Breb. in Kutz.) Grunow	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
<i>Peridinium</i> sp.1	+	+	-	-	+	+	-	-	-	-	-	-	+	-	-
<i>Phaeocystic pouchetii</i> (Har.) Lagerh.	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-
<i>Pleurasigma</i> sp.1	+	+	-	-	-	-	+	-	-	-	+	+	+	-	-
<i>Pyramimonas</i> sp.1	-	-	-	+	+	-	-	-	-	-	-	-	-	+	+
<i>Rhizosolenia</i> sp.1	-	+	+	-	-	+	-	-	-	-	-	-	+	+	-
<i>Synedra</i> sp.1	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
<i>Thalassiosira grandis</i> (Karsten) Hustedt	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Thalassiosira</i> sp.1	+	-	-	-	-	+	-	-	-	-	-	+	+	-	-
<i>Trigoniium arcticum</i> (Brightw.) Cleve	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 3. Species occurrence of phytoplankton and ice algae in the ice samples.

Species	1982											
	Date	08.iv	07.v	07.vi	01.vii	10.viii	06.ix	13.x	01.xi	09.xii		
<i>Achnanthes</i> sp.1	-	-	-	-	-	+	-	-	-	-		
<i>Amphiprora kjellmanii</i> (Cleve) in Cleve & Grunow	-	+	-	-	-	+	+	+	+	+		
<i>Amphora</i> sp.1	-	+	-	+	-	-	-	-	-	-		
<i>Asteromphalus parvulus</i> Karsten	-	-	+	-	-	-	-	+	-	-		
<i>Chaetoceros atlanticus</i> var. <i>bulbosum</i> (Ehr.) Hargraves	-	-	-	-	-	-	+	-	-	-		
<i>Corethron criophilum</i> Castracane	-	+	+	+	-	-	-	-	-	-		
<i>Dactyliosolen antarcticus</i> Castracane	+	+	+	+	-	-	-	-	-	-		
<i>Gymnodinium</i> sp.1	-	-	-	-	-	-	-	-	-	+		
<i>Navicula</i> sp.1	-	+	+	+	+	+	+	+	+	-		
<i>Nitzschia closterium</i> (Ehr.) Wm. Smith	+	+	-	-	-	-	+	-	-	-		
<i>Nitzschia cylindrus</i> (Grun.) Hasle	+	+	+	+	+	+	+	+	+	+		
<i>Nitzschia lanceolata</i>	-	+	+	+	+	+	+	+	+	+		
<i>Nitzschia longissima</i> (Breb. in Kutz.) Grunow	-	+	+	+	-	-	+	-	-	-		
<i>Nitzschia frigida</i> Grunow in Cleve & Grunow	-	+	-	-	-	+	+	+	+	+		
<i>Nitzschia seriata</i> Cleve	-	-	-	-	-	-	+	-	-	-		
<i>Odontella litigiosa</i> (Van H.) Hoban comb. Mov.	-	-	+	+	-	-	-	-	-	-		
<i>Pleurasigma</i> sp.1	-	+	-	-	-	-	-	-	+	+		
<i>Rhizosolenia</i> sp.1	-	+	-	-	-	-	-	-	+	-		
<i>Synedra</i> sp.1	-	-	-	-	-	-	-	-	+	-		
<i>Thalassiosira</i> sp.1	-	-	-	-	-	+	-	-	-	-		

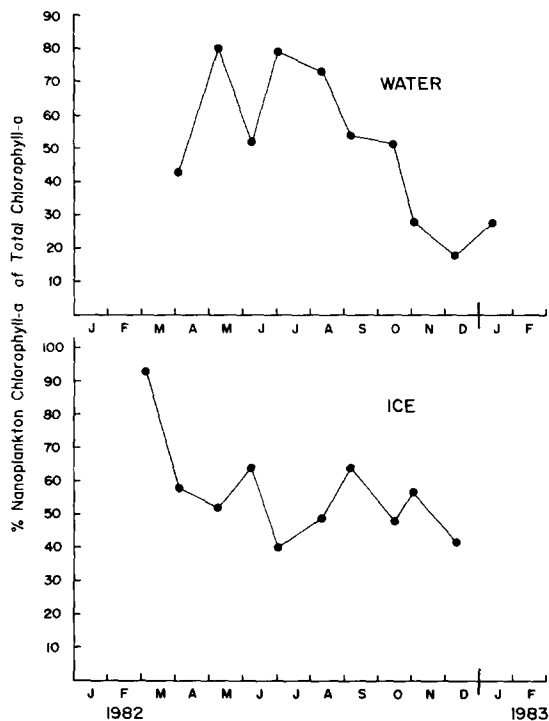


Fig. 17. The contribution of nanoplankton to total chlorophyll-a in the ice and water samples.

throughout the year, especially in June in both the water column and bottom samples. Phaeophytin, a degradation product of chlorophyll-a, was abundant in the ice samples in winter and in the bottom samples in January and December 1982 (Table 1).

The concentrations of nitrate, inorganic phosphate and inorganic silicate in the water column increased through the year with minor fluctuations until December when the silicate and nitrate levels decreased sharply. A month later the concentrations of phosphate declined (Fig. 18). The concentrations of nutrients in the water column were higher than in the sea ice throughout the year, except in June.

The water temperature changed only 3.3°C throughout the year; from April to November the range was only 0.2°C. After November the water temperature rose rapidly, reaching a maximum in January following the breakout of the sea ice.

The sea ice thickness and snow depth increased until October when the snow cover began to decrease. The sea ice continued to thicken until it broke out in December (Table 1).

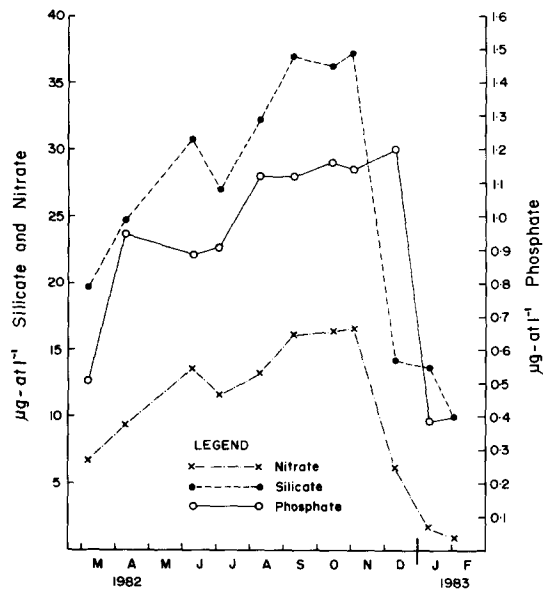


Fig. 18. Seasonal changes in the averaged concentrations of nitrate, silicate and phosphate in the water column.

Discussion

The annual cycle of phytoplankton abundance and species composition showed marked seasonality. Abundance was greatest during summer, from late December to early March, with high average daily hours of sunlight, water temperatures exceeding -1.5°C and an absence of sea ice. At the time of the sea ice breakout in late December and early January, the prymnesiophyte *Phaeocystis pouchetii* was the most abundant phytoplankton. Our methods led to an underestimate of the abundance of *P. pouchetii*, due to difficulties in accurately enumerating living cells in the gelatinous colonies. Similar difficulties have been reported by Baker (1954) and Horner (1973). Underwater visibility decreased from 20 m to less than 1 m in 3 d at the time of the *P. pouchetii* bloom. This alga, known to be abundant in antarctic waters (Kashkin, 1963), was not detected in either the water column or the ice before the bloom. We observed *P. pouchetii* to be the most abundant alga at the edge of the fast ice at an oceanic site in 63°S , 85°E on 21 November 1982, and Buck & Garrison (1983) found it to be the most common phytoplankton at the ice edge of the Weddell Sea, suggesting that this alga may fol-

low the retreat of the ice edge south during the austral summer.

Following *P. pouchetii*, *Nitzschia lanceolata* became numerically dominant in the water column, reaching a density of 5.8×10^7 cells l^{-1} in February (Table 4). Bunt (1960) and Buinitskii (1977) found similar cell densities at coastal sites near Mawson ($67^{\circ}36'S$, $62^{\circ}25'E$) and Mirny ($66^{\circ}33'S$, $93^{\circ}01'E$). This alga dominated the water column until just after sea ice formed in early March.

Not unexpectedly, the lowest phytoplankton biomass in both the water column and the sea ice occurred during winter, July to early October, when light penetration through the sea ice and temperatures were minimal.

During October areas of sea ice became cleared of snow cover and patches of algae developed on the under-surface of the ice, below these clear areas. From October onwards there was a proliferation of algae in both the sea ice and the water column. It has been shown experimentally by Sullivan *et al.* (1985), and again in this study, that snow cover has a strong influence on the standing crop of the sea ice algal community by limiting light availability. Light is clearly of major importance in stimulating the spring-summer bloom of ice algae and phytoplankton.

The concentrations of nutrients in the water column are increased by their exclusion from the forming sea ice. Nutrients entrapped in brine pockets in the ice are released into the water column in late spring when the sea ice begins to melt (Allen, 1871; Grainger, 1977). The sudden drop in nutrient concentration coincided with the November-December diatom blooms. The sea ice contained lower nutrient levels than did the water column probably due to the exclusion of the salts during ice formation (Martin, 1979).

For most of the year the nanoplankton accounted for the major part of the chlorophyll of the water column, particularly in winter when it sometimes approached 100% of the total phytoplankton chlorophyll-a. Only during blooms of *P. pouchetii* and large diatoms did the relative nanoplanktonic contribution decrease. In the ice the situation was similar with the nanoplankton contribution decreasing during the diatom blooms in May and November-December.

Thus, as in parts of other oceans, in antarctic seas the nanoplankton account for a major part of

the total phytoplankton chlorophyll except when blooms of diatoms occur.

The marked seasonal diversity of algal species composition found in the water column has not been reported before. Changes in light levels have been shown to be of critical importance for the growth of under-ice algae and would also be a major controlling factor in the diversity of phytoplankton. In addition, water temperature, salinity and nutrients, all of which exhibit seasonal fluctuations (Table 1), have been shown to have considerable effect on the phytoplankton and ice algal abundance and species composition (Horner, 1977; Legendre *et al.*, 1981).

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