Effect of permanent sea ice cover and different nutrient regimes on the phytoplankton succession of fjords of the Vestfold Hills Oasis, eastern Antarctica

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Abstract. Early season phytoplankton communities in both Omega and Taynaya Bays are characterized by diatoms sedimenting out of the overlying sea ice. Initial nitrate, phosphate and silicate levels are high and the bay waters are covered with ice and well mixed. In Taynaya Bay the ice cover is retained throughout the season while Omega Bay is ice free for 6–8 weeks. After ice break out in Omega Bay, the phytoplankton community changes from one dominated by diatoms to one dominated by the phytoflagellates, *Pyramimonas* spp., *Cryptomonas* sp. and *Gymnodinium* sp. In Taynaya Bay the ice remained and even though phytoflagellates became more common, diatoms still dominated. These differences in community composition result from differences in light climate, extent of stratification and nutrient levels.

Introduction

Coastal Antarctic environments are covered by sea ice for up to 11 months of every year so conditions for phytoplankton blooms are usually confined to a mere 6–8 weeks. Phytoplankton biomass beneath the coastal fast ice cover is usually very low and even in spring, it is mostly derived from cells sedimenting out of the melting sea ice (McMinn, 1996). While these cells may contribute to the ice edge phytoplankton blooms further offshore (Nelson and Smith, 1986; Nelson *et al.*, 1987), they make little contribution to blooms in coastal areas (McMinn and Hodgson, 1993; McMinn 1996).

Seas around Antarctica are characterized by high nutrient concentrations but low phytoplankton biomass (Knox, 1994). Only in the centre of intense ice edge blooms, or at the surface of strongly stratified fjords (McMinn *et al.*, 1995), have nutrients been seen to be depleted to anything like limiting levels. It has been suggested that this paradox can be explained by either iron limitation (Martin *et al.*, 1990), or by low light levels and deep mixing (Nelson and Smith, 1991). In coastal environments iron deficiency is unlikely to contribute to the high nutrient concentrations owing to the proximity of continental sources. Recent studies of Ellis Fjord (McMinn and Hodgson, 1993; McMinn *et al.*, 1995; McMinn, 1996) showed that nutrient depletion after water column stratification was likely to be the main factor driving the local species succession. In this investigation, we compare the species succession in two fjords with quite different hydrologies, and investigate the various environmental parameters that are likely to have determined the major changes in species composition.

Method

Long Fjord and Taynaya Bay are both located in the northern Vestfold Hills, eastern Antarctica (Figure 1), ~10 km from Davis Station. Omega Bay is a small, roughly circular embayment (~1 km diameter) on Partizan Island in Long Fjord. It is separated from the rest of the fjord by a shallow sill which in winter becomes blocked by sea ice. The bay is 7 m deep but is permanently stratified and anoxic (i.e. with an oxycline) beneath 5 m. Taynaya Bay is a much larger bay, located well to the west of the ice cap and connected to the sea by a narrow channel, the Barker Channel (Figure 1). This bay is up to 45 m deep but is also permanently stratified and anoxic (i.e. with an oxycline) beneath 25 m. A major difference between the two bays is the temporal extent of ice cover. Omega Bay becomes ice free for up to 8 weeks each year while most of Taynaya Bay retains an ice cover throughout the year. The permanently stratified bottom waters of both bays has allowed detailed examination of recent climate change from sediment cores (McMinn *et al.*, 1994, 1997).
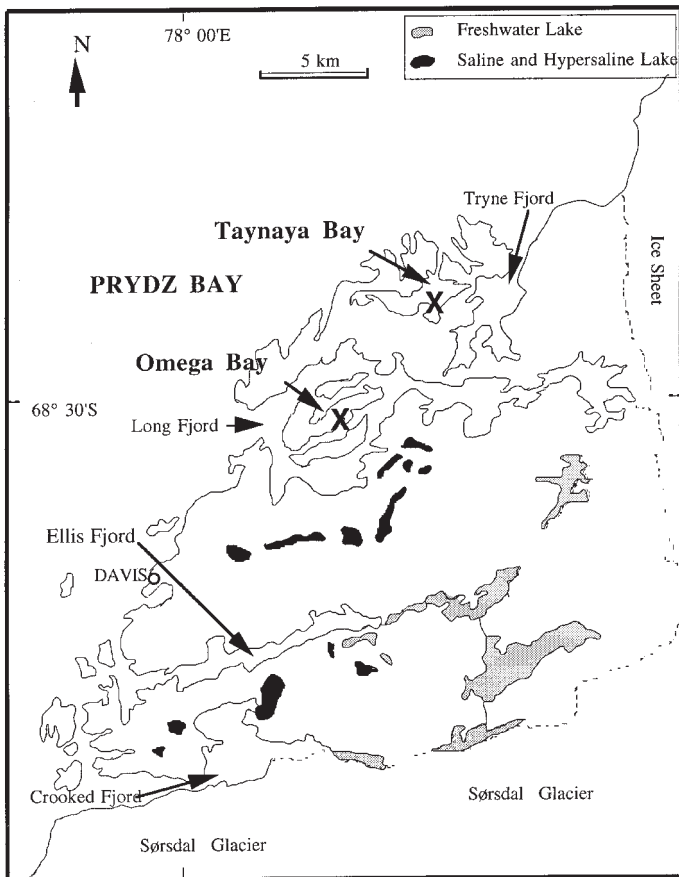
Fig. 1. Map of the Vestfold Hills showing the location of Taynaya Bay, Omega Bay and Long Fjord.

All sampling, which was through holes in the sea ice produced by a Jiffey Drill, occurred between 6 November 1996 and 3 February 1997. Water samples were collected in a 1 l Kemmerer Bottle. Salinity and temperature were measured with a WTW conductivity meter. Underwater light measurements were made with a Biosphaerical 4π PAR quantum radiometer. One litre water samples for chlorophyll analysis were filtered onto 42 mm diameter Whatman GF/F filters, extracted for 12 h in 90% acetone and the absorbances then measured on a UV-VIS spectrophotometer following the method of Strickland and Parsons (Strickland and Parsons, 1972). Samples for species analysis were settled in Utermohl settling chambers and a minimum of 400 cells counted. Nutrients samples were frozen after collection and then measured on an Alpkem Autoanalyser following standard methods (Alpkem, 1992). Samples for diatom analysis were left in 30% H_2O_2 for 3 days, washed repeatedly and then mounted in Norland Optical Adhesive. All sampling was from above the permanent oxyclines.

Results

Temperature

The water column in Omega Bay remained well mixed with a uniform temperature of –3°C at each depth up to 29 December, 1996. After that date the surface waters became progressively warmer, reaching a maximum temperature of 6.7°C, while the temperature at 5 m reached only 1.1°C (Figure 2a).

In Taynaya Bay the water column remained well mixed until 5 December with temperatures of –2.0°C at all depths. Surface waters reached a maximum temperature of –0.1°C on 3 February while at 10 m, temperatures reached only –1.6°C (Figure 2b).

Salinity

Salinities above the oxycline (at 5 m) in Omega Bay were 53.2 pss until 12 December. After that date, salinities at 2 m decreased to a minimum of 25.7 pss on 3 February. Below this depth, salinities remained >52 pss (Figure 3a).

In Taynaya Bay surface salinities at the beginning of the season were 34.9 pss; these had decreased to 32.0 pss by 3 February. Salinities at 10 m remained in a tight band between 35.4 and 35.9 pss throughout the season (Figure 3b).

Nutrients

Omega Bay. Initial nitrate (i.e. nitrate + nitrite) concentrations were 8.4 mmol m^{-3} at 2.0 m and 9.8 mmol m^{-3} at 5.0 m (Figure 4). These decreased uniformly through the season to minima of 0.18 mmol m^{-3} at 2.0 m and 0.15 mmol m^{-3} at 5.0 m on 3 February. Early season (19 November) silicate concentrations were 86.3 mmol m^{-3} at 2.0 m and 87.6 mmol m^{-3} at 5.0 m (Figure 4). These had decreased to 24.6 mmol m^{-3} at 2.0 m and 42.2 mmol m^{-3} at 5 m by 3 February. Initial phosphate concentrations were 3.1 mmol m^{-3} at 2.0 m and 3.7 mmol m^{-3} at 5.0 m. These had decreased to 0.46 mmol m^{-3} at 2.0 m and 1.5 mmol m^{-3} at
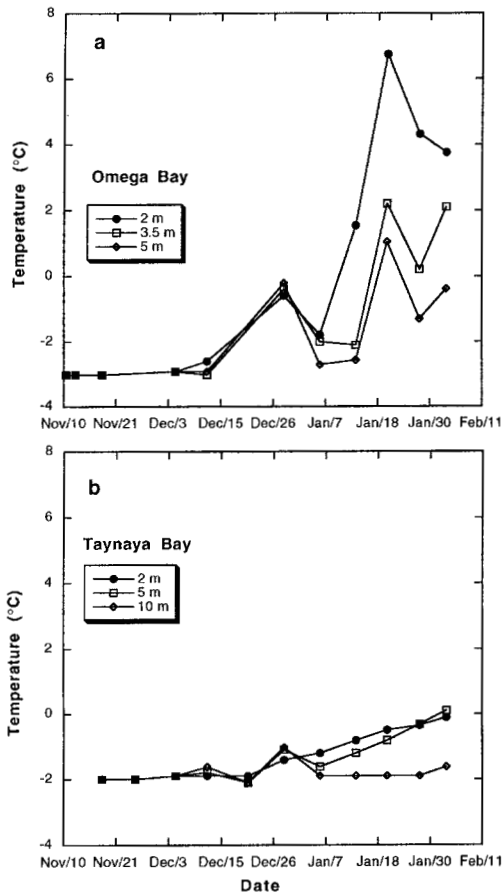
Fig. 2. Temperature profiles of Omega Bay (**a**) and Taynaya Bay (**b**).

5.0 m by 3 February. Unlike the nitrate (N) concentrations, the silicate (Si) and phosphate (P) concentrations showed a small rise in early January, followed by a continued fall.

The N:P ratio remained relatively constant from November to early January and then dropped sharply (Figure 5). The N:Si ratio, however, followed a more variable path, commencing in mid-November at ~0.8, rising to >1.4 by late November, dropping to <0.1 in mid-December and then rising again to >1.2 towards the end of January (Figure 5).

Taynaya Bay. Initial nitrate concentrations were 16.2 mmol m^{-3} at 2.0 m and 23.8 mmol m^{-3} at 10 m (Figure 4). These had decreased to 0.27 mmol m^{-3} at 2.0 m and 2.48 mmol m^{-3} at 10 m by 3 February. Silicate concentrations were initially 35.4 mmol m^{-3} at 2.0 m and 49.0 mmol m^{-3} at 10.0 m. These decreased to 10.0 mmol m^{-3} at 2.0 m and 13.4 mmol m^{-3} at 10.0 m. Phosphate concentrations were initially
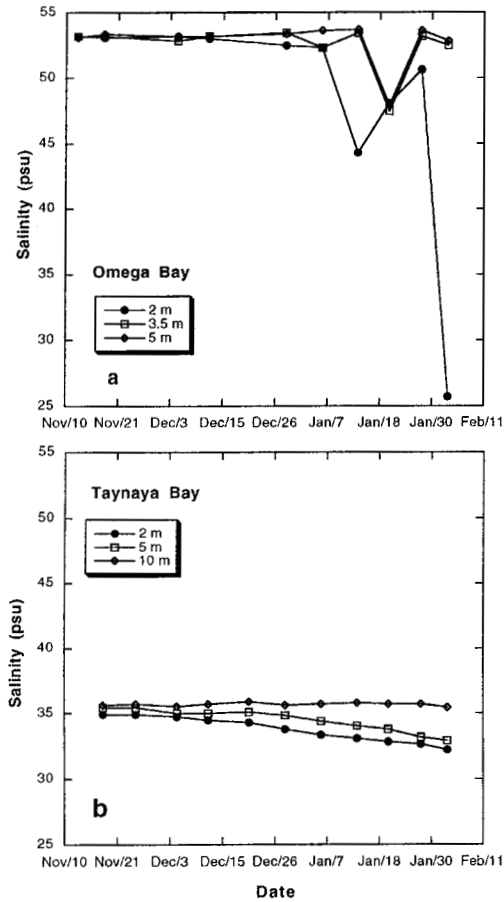
Fig. 3. Salinity profiles of Omega Bay (**a**) and Taynaya Bay (**b**).

1.5 mmol m^{-3} at 2.0 m and 2.2 mmol m^{-3} at 10 m. These had decreased to 0.29 mmol m^{-3} at 2.0 m and 0. mmol m^{-3} at 10 m by 3 February. There was a reasonably well defined rise in both nitrate and silicate concentrations in early January; this trend was less clear in the phosphate data (Figure 4).

N:P ratios remained at ~12 until early January from which date they dropped sharply and then remained at <1 until the end of the season. N:Si ratios showed a similar trend to the N:P ratios, with initial values constant at ~0.5 until early January, followed by a sharp drop to values of <0.05 (Figure 5).

Pigments

Omega Bay. Chlorophyll *a* concentration at the beginning of the season, i.e. 13 November, was extremely low, with values of only 0.04 mg Chl *a* m^{-3} at 2 m and
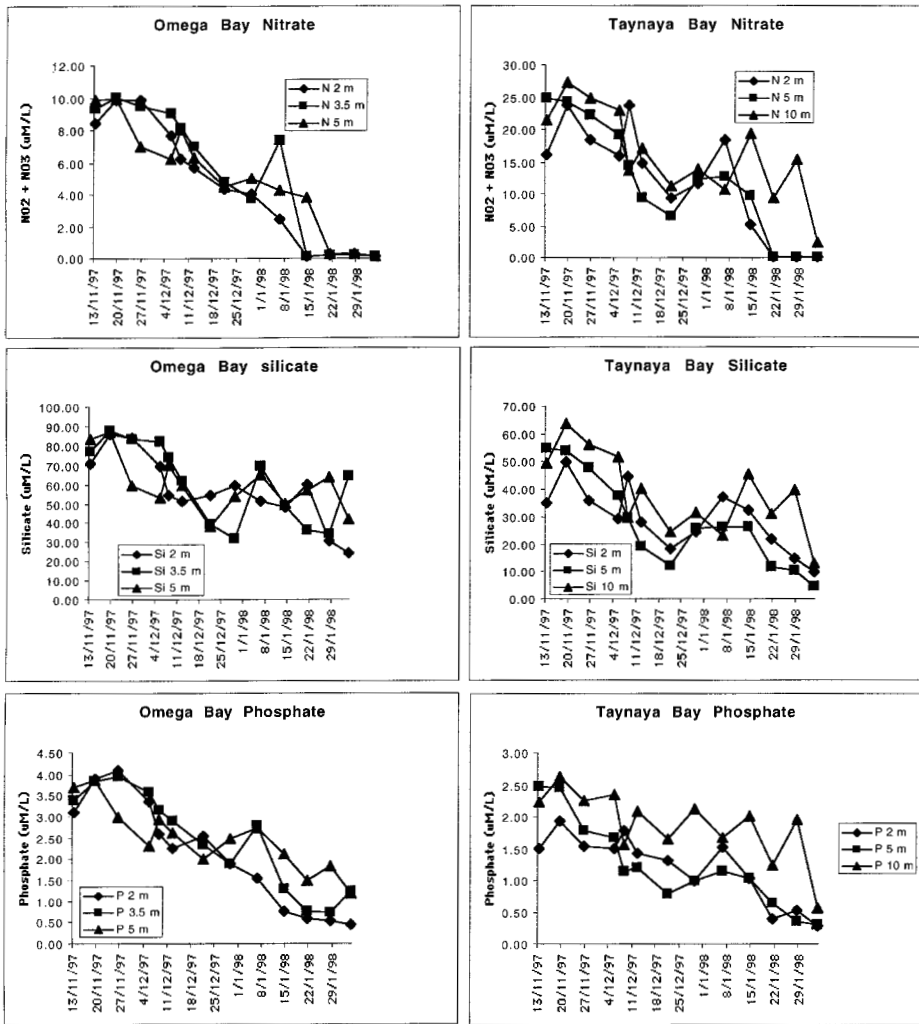
Fig. 4. Concentration of nitrate (nitrate + nitrite), silicate and phosphate at 2 m, 3.5 m and 5 m in Omega Bay and 2 m, 5 m and 10 m in Taynaya Bay.

0.0003 mg Chl *a* m^{-3} at 5 m. This increased to a maximum of 2.20 mg Chl *a* m^{-3} at 2.0 m and 0.39 mg Chl *a* m^{-3} at 5 m on 8 December and subsequently declined. There was a late increase to 1.90 mg Chl *a* m^{-3} at 2.0 m and 2.40 mg Chl *a* m^{-3} at 5 m on 6 January (Figure 6). Chlorophyll *c* concentration showed a similar distribution to chlorophyll *a*, although there was no late season increase. Chlorophyll *b* concentration was mostly low throughout the season but there was a late season increase coincident with the increase in chlorophyll *a* (Figure 6).
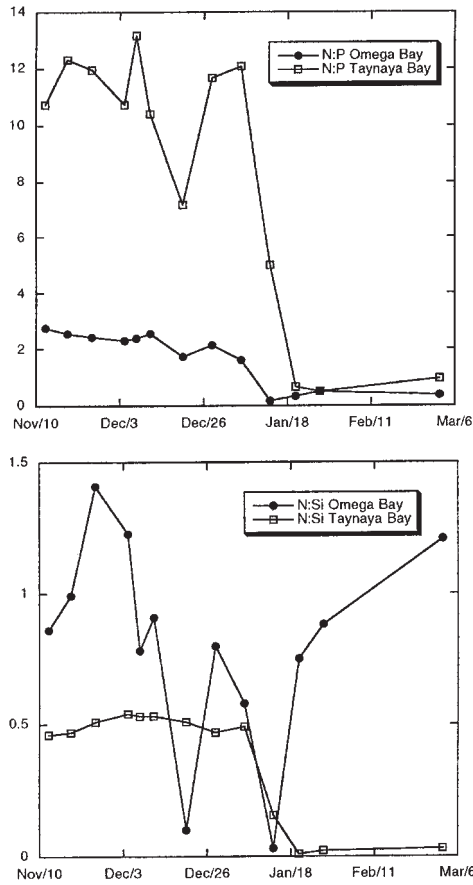
Fig. 5. N:P ratios at 2 m in Omega and Taynaya Bays, N:Si ratios at 2 m in Omega and Taynaya Bays.

Taynaya Bay. Chlorophyll *a* concentration reached a peak on 26 November, with values of 1.70 mg Chl *a* m^{-3} at 2.0 m and 0.22 mg Chl *a* m^{-3} at 10 m. Chlorophyll *c* distribution followed that of chlorophyll *a*. Chlorophyll *b* remained low throughout the season (Figure 6).

Species distribution

Omega Bay. Cell numbers from Omega Bay were integrated to a depth of 5 m. There were two peaks in cell abundance, one on 5 December (99 × 10^9 cells m^{-2}) and a second (53 × 10^9 cells m^{-2}) on 21 January. These corresponded to maximum unintegrated cell abundances of 4.7 × 10^6 cells l^{-1} and 1.6 × 10^6 cells l^{-1} from the same dates both at 5 m (Figure 7).
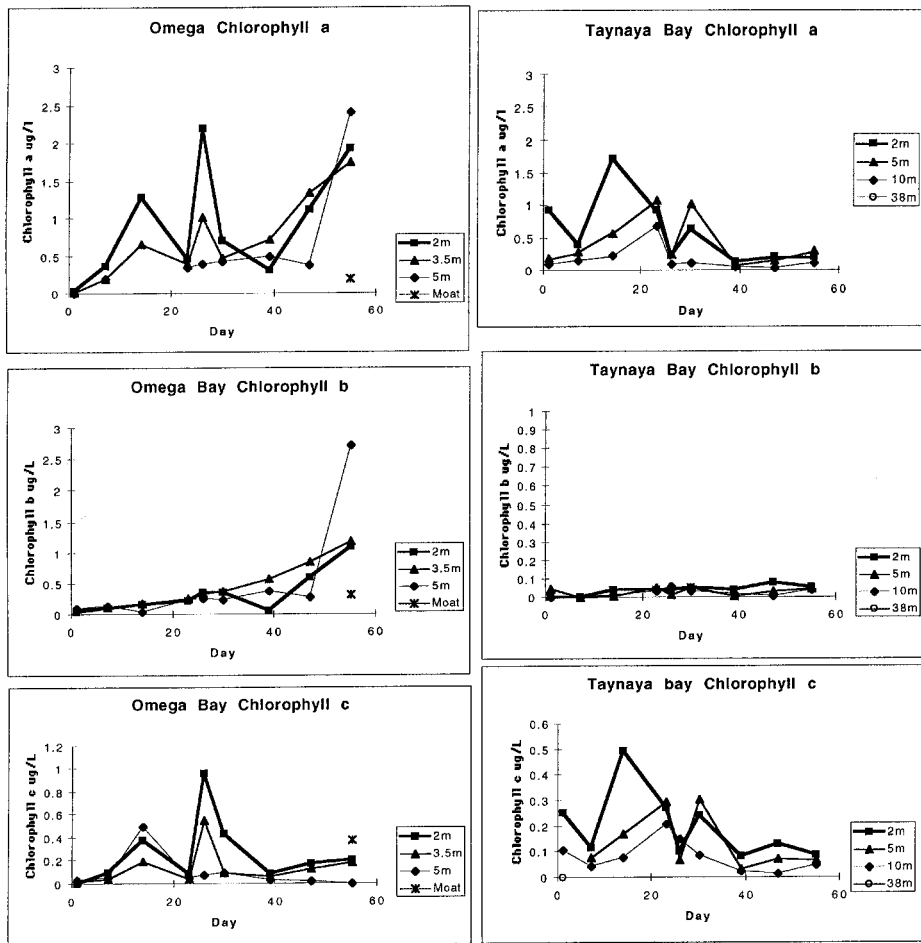
Fig. 6. Pigment concentration. Chlorophyll *a*, *b* and *c* concentrations at 2 m, 3.5 m and 5 m in Omega Bay and 2, 5 and 10 m in Taynaya Bay.

Diatom abundance remained approximately constant throughout the season, with maxima on 19 November (0.63×10^9 cells m^{-2}), 21 December (0.59×10^9 cells m^{-2}) and 21 January (0.50×10^9 cells m^{-2}). The abundance of *Pyramimoas gelidicola* peaked on 5 December (4.3×10^9 cells m^{-2}) and 21 January (3.4×10^9 cells m^{-2}). These correspond to unintegrated values for these dates of 2.1×10^6 cells l^{-1} and 1.2×10^6 cells l^{-1}. *Cryptomonas cryophila* exhibited a unimodal distribution with a peak of 1.1×10^9 cells m^{-2} on 14 January. It did not appear in the water column until 12 December. Dinoflagellate abundance followed the general phytoplankton abundance trends with peaks on 5 December (0.79×10^9 cells m^{-2}) and 6–21 January (0.30×10^9 cells m^{-2}). Although *Gyrodinium* and *Protoperidinium* species were present, the dinoflagellate flora was overwhelmingly dominated by *Gymnodinium* spp.

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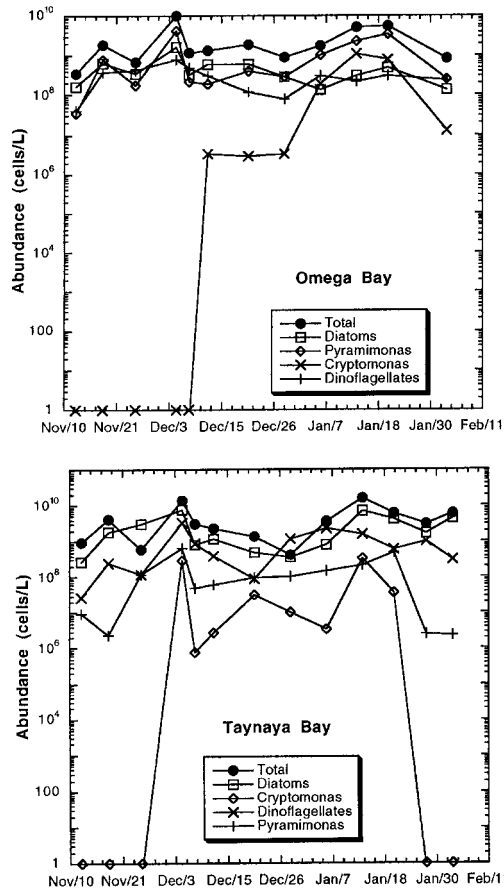
Fig. 7. Species composition of Omega Bay and Taynaya Bay. Abundance is presented logarithmically.

Desmids, likewise, had a bimodal distribution with peaks on 5 December (1.9×10^9 cells m^{-2}) and 14 January (1.1×10^9 cells m^{-2}) (Figure 7). The most abundant microheterotrophs were tintinids. Their abundance was also bimodal with peaks of 0.36×10^9 cells m^{-2} on 5 December and 1.1×10^9 cells m^{-2} on 14 January (Figure 8).

Taynaya Bay. Cell numbers from Taynaya Bay were integrated to a depth of 10 m. There were two main peaks in cell abundance, one on 5 December (14×10^9 cells m^{-2}) and a second on 14 January (16×10^9 cells m^{-2}). These correspond to maximum unintegrated cell abundances of 4.2×10^6 cells l^{-1} and 4.7×10^6 cells l^{-1} from the same dates and both from a depth of 5 m (Figure 7). Diatom abundances follow the general trends of cell abundances with maxima on 5 December and 14 January. However, phytoflagellates show different patterns of
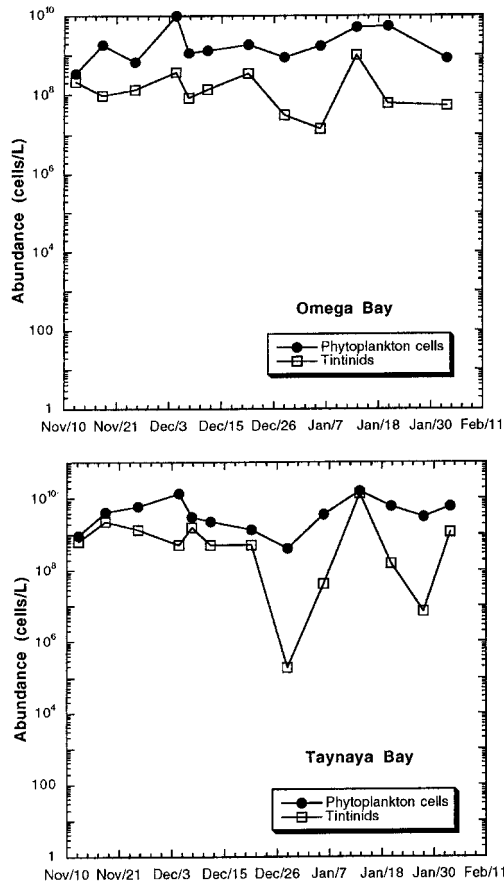
Fig. 8. Abundance of tintinids in Omega and Taynaya Bays. Total is the combined abundance of all protists. Abundance is presented logarithmically.

abundance. The abundance of *Pyramimonas gelidicola* rose from low values in early November, reaching an early peak (0.65×10^9 cells m^{-2}) by 5 December, then declined until again peaking in abundance on 21 January (0.49×10^9 cells m^{-2}). Unlike diatoms and *Pyramimonas*, *Cryptomonas cryophila* was completely absent until 12 December. Its abundance peaked on 14 January (0.34×10^9 cells m^{-2}) but had disappeared by 28 January.

Dinoflagellates, predominantly *Gymnodinium* spp., showed a similar distribution pattern to diatoms. They peaked in abundance on 5 December (3.4×10^9 cells m^{-2}), declined, and then peaked again (2.3×10^9 cells m^{-2}) on 6 January (Figure 7).

Tintinids, the dominant microheterotrophs, reached peak abundance (14×10^9 cells m^{-2}) on 14 January (Figure 8).

Diatom distribution

The diatom flora has been further differentiated into species (Table I).

Omega Bay. The seasonal distribution of diatoms is dominated by the release of ice-associated diatoms into the water column in early December. Dominant species include the ice-associated taxa *Berkelaya adeliense*, *Nitzschia stellata* and *Thalassiosira australis*. *Navicula glaciei* is also most abundant during this time, sometimes forming an almost monospecific bloom, but it is also present in large numbers both before and after the ice melt. *Fragilariopsis cylindrus* is the most abundant diatom prior to ice melt in November, while *F.curta* co-dominates with *N.glaciei* afterwards.

Taynaya Bay. As in Omega Bay, the seasonal distribution of diatoms is dominated by the release of ice-associated diatoms from the ice into the water column in early December. Species which show this distribution include *B.adeliense*, *N.glaciei*, *T.australis*, *N.stellata* and *N.lecointei*. *Fragilariopsis cylindrus* also peaks in abundance in early December but is abundant both before and after the peaks of other ice-associated diatoms. Its abundance is probably not solely related to release from the ice. *Fragilariopsis curta* is uncommon early in the season but is the dominant species in January and February.

Discussion

Both Omega and Taynana Bays had a similar bimodal phytoplankton distribution. In the early part of the season, i.e. November to early December, light levels were low as a consequence of the sea ice cover, the water column was mostly well mixed and nutrient concentrations were uniformly high. Much of the phytoplankton was in the form of diatoms contributed from the melting and break-up of the sea ice. The melting of the sea ice and the increasing temperatures caused the water column in both bays to become increasingly stratified from this time onwards. Nutrient levels also declined from early season highs to minima at the end of summer. The second phytoplankton bloom coincided with increasing stratification but decreasing nutrient levels. In Omega Bay this bloom was characterized by blooms of phytoflagellates, in particular *Pyramimonas gelidicola*, *Cryptomonas cryophila* and *Gymnodinium* sp. In Taynaya Bay these taxa became increasingly abundant but the community was still dominated by diatoms, in particular *Fragilariopsis curta* and *Navicula glaciei*. This difference is reflected in the pigment analysis, which shows a strong late season development of chlorophyll *b* concentrations in Omega Bay but not Taynaya Bay, indicating the presence of the prasinophyte, *Pyramimonas*.

Prior to the ice melting, the most abundant diatom species in both bays were *Fragilariopsis cylindrus* and *Navicula glaciei*; however, after 6 January, these species were replaced by *F.curta*. Each of these species is strongly related to sea ice communities (McMinn, 1996, 1998), but *F.curta* is also associated with reduced salinities resulting from ice melt (Leventer, 1998). Its abundance in both bays

Table I. Seasonal diatom abundance (%)

Date (depth in m)	13 Nov 97			19 Nov 97			26 Nov 97		5 Dec 97			8 Dec 97			12 Dec 97			21 Dec 97			29 Dec 97			6 Jan 98			14 Jan 98			28 Jan 98			3 Feb 98		
	2	3.5	5	2	3.5	5	2	3.5	2	3.5	5	2	3.5	5	2	3.5	5	2	3.5	5	2	3.5	5	2	3.5	2	2	3.5	2	2	3.5	2	2	3.5	2
Omega Bay diatoms																																			
Achnanthes spp.	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Berkelaya adeliense	0	1	2	0	0	0	2	0	0	1	4	0	0	0	0	1	0	3	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	2
Chaetoceros spp.	2	1	0	1	0	0	2	0	5	5	3	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	2	0	2	2	2	2
Cocconeis spp.	0	0	0	0	0	0	0	0	1	1	1	0	0	3	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	3	2	10	5	1	1
Cylindrotheca cloisterium	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entomoneis kjellmannii	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
Eucampia antarctica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	4	0	0	0	0	0	0	1	0	0
Fragilaria spp.	1	0	0	0	0	0	0	0	0	0	5	0	2	2	1	1	0	1	0	0	2	2	2	0	0	0	2	2	3	4	2	2	2	3	8
Fragilariosis cylindrus	10	28	41	3	3	3	8	0	0	5	1	2	1	0	1	5	2	2	0	0	1	0	3	58	12	23	72	36	36	18	23	42	10	7	14
Fragilariopsis curta	3	2	0	0	2	0	0	2	5	1	0	0	1	0	0	0	1	2	0	0	0	0	0	1	1	0	0	0	0	1	5	2	3	0	4
Navicula directa	2	0	0	0	0	0	0	0	1	6	4	1	0	3	0	4	1	0	0	0	1	0	3	1	1	0	1	3	5	0	0	0	10	3	4
Navicula glaciei	48	23	48	23	42	37	19	41	41	67	82	94	86	90	97	86	89	74	100	95	85	83	74	38	84	66	23	59	60	16	29	14	20	36	35
Navicula spp.	26	38	3	6	0	0	10	2	1	5	1	3	2	0	0	2	0	8	0	0	3	0	0	2	2	3	1	3	5	25	2	2	36	34	14
Nitzschia lecontei	0	2	6	0	0	0	13	0	0	5	1	3	2	0	0	4	1	8	0	1	0	0	0	2	0	0	1	3	5	11	0	2	2	1	1
Nitzschia stellata	4	4	0	67	52	60	24	57	7	8	3	2	8	0	4	2	0	3	0	0	0	0	0	2	2	3	0	0	4	2	2	2	1	2	5
Nitzschia subcurvata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	1	0	0	0	0	0	0	0	14	0	0	9	2	0
Nitzschia teaniformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinnularia quadreata	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Porosira spp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	7	8
Stauophora sp.	2	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	2	2	0	0	0	0	0	0	0	0	7	1	6	4
Synedra spp.	1	0	0	0	0	0	0	0	0	0	0	2	0	2	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	3	0	3	0	0	0
Synedropsis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	8	12	9	0	1	0	0	1	0	0	0	0	0	0	0
Thalassiosira ambigua	0	1	0	0	0	0	24	0	1	1	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	4	0	2
Thalassiosira australis	0	0	0	0	0	0	0	0	46	9	2	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalassiosira gracillis	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Thalassiosira gravida	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table I. continued

	13 Nov 97		19 Nov 97		26 Nov 97			5 Dec 97			8 Dec 97			12 Dec 97			21 Dec 97		29 Dec 97			6 Jan 98			14 Jan 98			28 Jan 98			3 Feb 98		
	11	38	5	10	2	5	10	2	5	10	2	5	10	2	5	10	2	5	2	3.5	2	2	5	10	2	5	10	2	5	10	2	3.5	2
Taynaya Bay diatoms																																	
Achnanthes spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
Berkelaya adeliense	0	0	1	3	1	4	6	4	3	7	5	2	2	3	3	2	0	0	1	2	1	1	0	1	0	0	0	0	0	0	2	0	0
Fragilariopsis curta	6	6	4	8	8	2	3	2	0	1	2	2	12	4	3	2	41	39	73	49	44	60	88	60	93	75	93	5	90	94	11	63	87
Fragilariosis cylindrus	47	80	45	15	5	42	60	13	22	40	16	55	49	13	23	48	19	38	7	23	23	11	6	36	1	6	4	63	1	0	2	11	3
Navicula glaciei	5	4	6	2	1	15	5	14	12	10	27	11	5	7	23	10	21	10	8	9	17	8	1	0	0	0	0	13	0	0	3	3	0
Nitzschia cloisterium	0	0	1	0	1	9	1	0	1	0	1	1	1	6	2	0	1	2	1	0	2	1	0	0	0	0	0	2	0	0	2	0	0
Nitschia polaris/neglecta	2	0	0	0	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Nitschia stellata	2	0	1	2	1	0	0	9	2	7	27	15	1	32	35	29	8	2	5	9	2	8	1	1	0	0	0	4	0	0	11	11	1
Nitzschia lecointei	18	1	18	24	15	9	4	0	14	7	15	0	1	4	0	1	0	0	9	2	1	0	1	0	0	0	0	0	0	0	0	0	0
Nitzschiella delicatissima?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Nitzschiella subcurvata	0	0	1	2	3	2	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	3	0	0	3	3	0	0	0
Nitzschia teaniformis	0	2	0	0	2	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinnularia quadrataea capitata	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudonitzschia lineola	2	0	0	7	1	0	2	0	0	1	0	0	0	1	0	0	0	2	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0
Pseudonitzschia prolongatoides	3	6	1	5	1	1	0	2	4	0	2	1	7	7	4	3	5	3	0	1	2	2	0	0	1	0	0	0	0	0	0	17	4
Pseudonitzschia turgiduloides	0	0	1	4	0	1	2	0	0	1	0	1	0	1	0	3	0	0	1	0	0	0	2	0	0	7	0	0	2	0	0	0	0
Thalassiosira ambigua	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	36	0
Thalassiosira australis	11	1	6	13	23	8	7	29	28	13	11	7	11	17	3	1	1	1	0	0	0	0	0	0	1	4	0	2	0	0	8	0	0
Thalassiosira diatomica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	18	4	2
Synedropsis cf *hyperbola?*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0
Synedra spp.	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

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suggests that it is responding to meltwater-induced stratification and not to changing light levels.

All nutrients show strong depletion over the summer (Figure 4). However, the relative depletion rates indicate that at times, different processes are operating in the two bays. Redfield *et al*. noted that growing phytoplankton take up nutrients from the water column in fixed proportions and proposed C:N:P:Si ratios of 106:16:1:15 (Redfield *et al*., 1963). Jennings *et al*., however, suggested a more appropriate ratio for the Southern Ocean would be 62:11:1:24 (Jennings *et al.*, 1984).

Initial N:P ratios in Omega Bay were between 2 and 4 and in Taynaya Bay, ~12; those from Omega Bay were well below the 11 nominated for normal phytoplankton growth (Jennings *et al*., 1984) while those from Taynaya Bay were quite close. Unlike N:P ratios, N:Si ratios are far more variable as they depend on the abundance of diatoms which can show both temporal and spatial variations. The N:Si ratios from Omega Bay were relatively high, in the range 0.8 to 1.4, while those from Tayanaya Bay were lower, initially ~0.5 but dropping to 0.05 later in the season. These compare with a suggested normal values of 0.45 (Jennings *et al*., 1984) or 1.07 (Redfield *et al*., 1963), and field measurements at nearby Ellis Fjord of 0.56 (McMinn *et al*., 1995).

These ratios indicate that N was usually the limiting nutrient in Omega Bay, although minor occurrences of Si limitation may have occurred early and late in the season. The general trend of N limitation is further reinforced by the trend lines in the whole nutrient dataset (Figure 9), which show residual Si and P when all the N has been used.

Initial nitrate levels were considerably higher in Taynaya Bay than in Omega Bay and initial N:P ratios were mostly between 10 and 14, suggesting that the phytoplankton were not initially strongly limited be either of these two nutrients. The initial N:Si ratios of ~0.40 are low. However, both the N:P and N:Si ratios drop sharply after 6 January and this implies N limitation after this date. As with Omega Bay, trends in the whole nutrient dataset show residual Si and P when the N has been exhausted, indicating that N is usually the limiting nutrient (Figure 9).

Sommer (1986) reported that many Antarctic diatoms had a particularly strong affinity for silica and that consequently, silica concentrations as low as 80 mmol m^{-3} could effect growth (Sommer, 1986). Of the species he documented, only *Fragilariopsis cylindrus* is common in the fjord environments examined here. However, he recorded a silica half saturation constant of 8.4 and a nitrate half saturation constant of 4.2 for this species. Of the nutrient concentrations recorded in both fjords, nitrate is consistently below levels necessary to avoid growth limitation from early January onwards. Silicate levels in Omega Bay are mostly above 30 mmol m^{-3} and are therefore at levels unlikely to cause serious limitation. Lower silicate concentrations in Taynaya Bay, however, could lead to minor limitation. Iron limitation affects nitrate uptake (Dohler, 1992; Timmermans *et al*., 1994) and this could possibly have contributed to the decrease in the N:Si ratios observed here. However, elsewhere around Antarctica, iron has not been found to be limiting in near shore marine environments (Helbling *et al*., 1991).

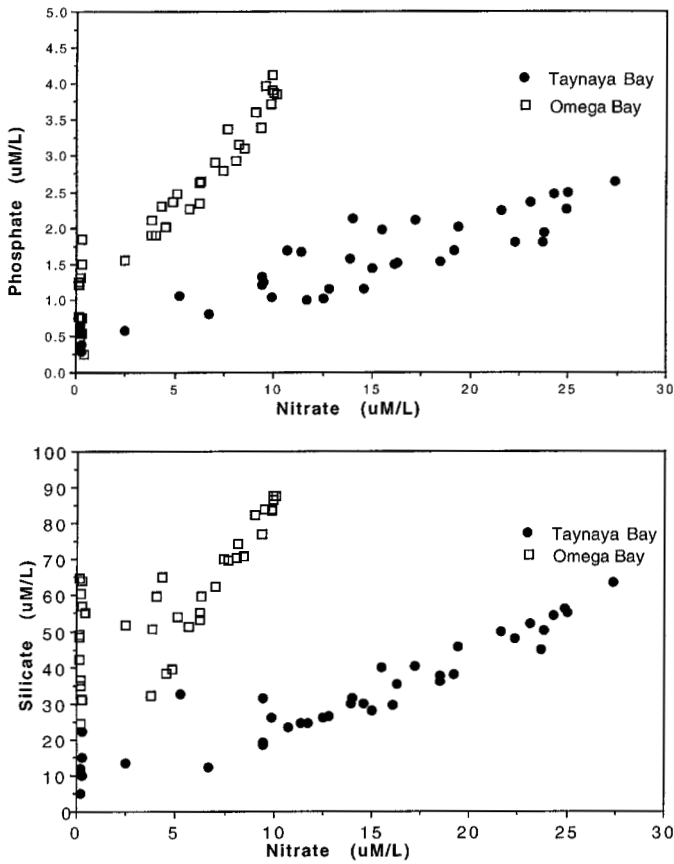There was a small mid-season rise in nutrient concentrations at both sites

Fig. 9. N versus P and N versus Si plots of complete nutrient dataset for Omega and Taynaya Bays.

(Figure 5). This occurrence approximately coincided with a peak in tintinid numbers, which is possibly associated with remineralization resulting from increased microheterotroph activity. However, measurement of bacterial numbers and ammonium concentration would be necessary to validate this suggestion. While ammonium concentration was not measured, it is likely that it became an increasingly important source of N throughout the season. Priddle *et al.* have even suggested that Southern Ocean phytoplankton production is primarily dependant on ammonium rather than nitrate as a nitrogen source (Priddle *et al.*, 1997). Recent evidence suggests that at low temperatures, phytoplankton have a decreased affinity for nitrate but not ammonium, and this would result in an increasing dependence on ammonium as a nitrogen source (Reay *et al.*, 1999).

Despite both bays exhibiting different salinities, nutrient concentrations and light environments (i.e. ice cover), the taxonomic composition of the two communities was surprisingly similar. There were, however, a number of important differences. Early season communities in both bays were almost identical,

being strongly influenced by the overlying sea ice algal mats. However, after 6 January in Omega Bay, *Cryptomonas* sp., *Pyramimonas gelidicola* and *Gymnodinium* spp. bloom and become more abundant than diatoms. While these taxa are also common in Taynaya Bay, they are never more abundant than diatoms.

Little is known about the light requirements of the principal phytoflagellates found in the two bays. However, it is well established that most ice-associated diatoms are extremely shade adapted (Palmisano *et al.*, 1985; Grossi *et al.*, 1987). Light levels beneath the fast ice between October and December are typically <10 μM photons m^{-2} s^{-1} (McMinn and Ashworth, 1998). Photoadaptive index values (E_k) of between 10 and 20 μM photons m^{-2} s^{-1} are characteristic of diatom species associated with the bottom ice community (Palmisano *et al.*, 1985; McMinn and Ashworth, 1998), while values between 37 and 42 μM photons m^{-2} s^{-1} were reported for a *Navicula glaciei* dominated community (Robinson *et al.*, 1997). Weddell Sea diatom-dominated pack ice communities had average E_k values of 60 μM photons m^{-2} s^{-1} (Gleitz and Kirst, 1991). It seems likely that the shift from a diatom to a phytoflagellate-dominated phytoplankton community that has also been reported from both Ellis Fjord (McMinn and Hodgson, 1993) and from Davis (Perrin and Marchant, 1987), resulted, at least in part, from the increased light levels once the ice had broken out.

The effect of the differing salinities between the two bays on the phytoplankton succession is difficult to gauge. Initially, the salinities were quite different while the community structure was quite similar. Later in the season, the melting ice and increasing stratification led to reduced surface salinities in both bays. However, surface salinites in Omega Bay dropped to as low as 25.7 pss while those in Taynaya Bay remained at or above 32.0 pss. Ice-related diatoms, such as *F.curta,* are known to be able to adapt to changing salinities (Vargo *et al.*, 1986; Arrigo and Sullivan, 1992) but the response of the phytoflagellates is unknown.

It is possible that ice cover alone accounts for the difference in species successions between the two bays. However, it is likely that differing nutrient status and salinities between the two bays also played a significant role.

Acknowledgements

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