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INTERANNUAL VARIATION IN DOMINANT PHYTOPLANKTON SPECIES AND BIOMASS NEAR DAVIS STATION, EAST ANTARCTICA

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Abstract: Phytoplankton biomass and speciation were monitored at an inshore site near Davis Station, East Antarctica (68°35′S, 77°58′E) during three consecutive summer seasons (December–February, 1992–5). Four distinct phytoplankton assemblages were identified in which the dominant species were: *Phaeocystis* sp., an undescribed *Cryptomonas* species, *Thalassiosira dichotomica*, and a mixed assemblage containing *Fragilariopsis* spp. and *Nitzschia* spp. Little interannual consistency was found in either the timing of the appearance or disappearance of the various assemblages. Similarly, the seasonal trends in biomass varied dramatically from year to year. Variations in the phytoplankton community can be ascribed, to some extent, to the random variation in a number of factors, including the date of fast ice break out, water column stratification, temperature and salinity, zooplankton grazing and strong winds. Periods of strong wind result in the introduction of offshore or deeper water masses into the shallow inshore environment, where the physical and chemical conditions allow blooms to develop.

1. Introduction

There has been little study of the interannual variation in phytoplankton speciation and biomass in the Antarctic region (SMITH and SAKSHAUG, 1990). An awareness of the natural variability of the phytoplankton community is important if the role of the Antarctic region in the global carbon cycle is to be understood. If biological production in some summers is much greater than in others, then the regional importance of the 'biological pump', which sequesters atmospheric carbon dioxide into the deep ocean, in the global carbon budget will also alter considerably from year to year.

We report here the results of a study of the phytoplankton community at an inshore site near Davis Base, East Antarctica (Fig. 1) conducted over three consecutive summer periods. A number of previous studies has investigated phytoplankton succession at this or nearby sites. PERRIN *et al.* (1987) sampled the nearshore phytoplankton throughout a complete annual cycle, and recorded that it was dominated at different times over summer by colonies of the nanoflagellate prymnesiophyte *Phaeocystis* sp., and a variety of diatom species. *Phaeocystis* sp. occurs as both individual, motile cells as well as large colonies consisting of many individuals embedded in an organic matrix. GIBSON *et al.* (1990) and DAVIDSON and MARCHANT (1992) undertook similar studies during the summers of 1987–8 and

1988–9 respectively, during which the colonial stage of *Phaeocystis* sp. and diatom species were again dominant. From these three studies, it appeared that the general cycle of phytoplankton succession was consistent between years. More recently, SKERRATT *et al.* (1995) reported the results of a study that used signature lipids to monitor seasonal and interannual variations in planktonic biomass and community structure near Davis. These authors found that considerable variation occurred in both the identity and amounts of the lipids present between years, indicating that the phytoplankton community did not, as suggested previously, undergo a predictable summer cycle.

In this paper we present phytoplankton speciation and biomass data from a site near Davis Station for the summer seasons of 1992–3, 1993–4 and 1994–5, along with supporting data, including water temperature and stratification, nutrient concentrations and weather conditions. The seasonality observed in both the phytoplankton biomass and assemblages present was unpredictable, and appeared to be related to some extent to the occurrence of periods of strong winds, which introduced new water masses and phytoplankton species into the inshore environment.

2. Materials and Methods

Water samples were obtained from five depths (under-ice or surface, 5 m, 10 m, 15 m and 20 m) at an inshore site approximately 1.5 km offshore from Davis Station, eastern Antarctica (68°35′S, 77°58′E, Fig. 1). Water depth at the site was 23 m. The site was covered by fast ice approximately 1.7 m thick at the beginning of each of the summer study periods. Meteorological data were collected by staff of the Australian Bureau of Meteorology at Davis Station.

Water samples were collected with a Go-Flo water sampler or a polycarbonate Kemmerer bottle. When the sample site was covered by ice the samplers were deployed through a hole drilled through the ice with an auger. After ice break out, samples were collected from a small boat anchored at the site. Phytoplankton samples were preserved with acidic Lugol's Iodine, and were stored in 1 *l* glass bottles. Water samples for chlorophyll *a* (chl *a*) analysis were transferred to 2 *l* plastic bottles, and were stored in the dark until they were processed. Nutrient samples were transferred to acid-washed polyethylene bottles, and were stored at −20°C until analysis was undertaken. During the 1994–5 season, nitrate analyses were performed on the filtrate from chl *a* analyses immediately after filtration.

Water temperature and electrical conductivity profiles were recorded using a Platypus submersible data logger (Platypus Engineering, Hobart, Australia). The conductivity data were converted to salinities and densities using the equations of FOFONOFF and MILLARD (1983). A measure of the extent of the stratification of the water column was obtained by calculating the average density increase per metre (units: kg m^{-3} m^{-1}).

The concentration of chl *a* was determined by a method similar to that of PARSONS *et al.* (1984). Two litres of water, or less during periods of high phytoplankton biomass, were filtered through a GF/F filter. The filter was cut up and placed in 90% (v/v) aqueous acetone, sonicated in an ultrasonicating bath for 5

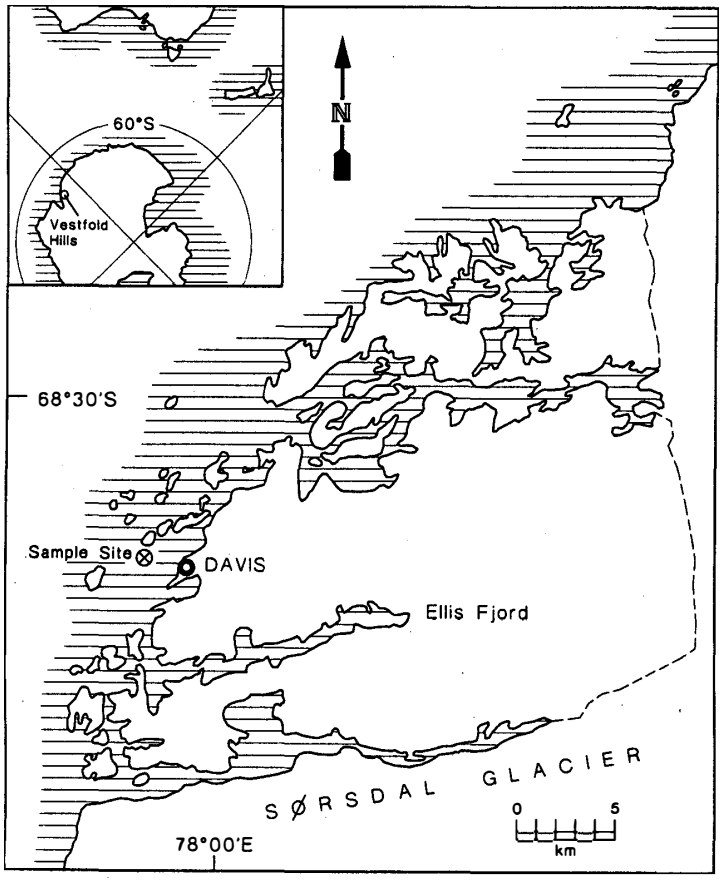

Fig. 1. A map of the Davis region showing the locality of the sampling site.

minutes, stored overnight in a freezer at −20°C, resonicated and finally centrifuged. Absorbance of the resulting solution was measured at 664, 647 and 630 nm. The equations given in PARSONS *et al.* (1984) were used to calculate the concentration of chl *a*.

Nutrient analyses were performed using a Technicon auto-analyser by the methods of STRICKLAND and PARSONS (1972) for samples collected in the 1992–3 season, and by wet chemistry techniques described in PARSONS *et al.* (1984) during the later seasons. Storage time before analysis was circa 2–3 months for samples from 1992–3, and 0–4 weeks during the subsequent seasons.

Phytoplankton samples were initially concentrated if necessary by sedimentation in a measuring cylinder, and then allowed to settle in 10 m*l* Utermöhl counting chambers (UTERMÖHL, 1958). Cells were counted using a Leitz Laborlux Inverted Microscope at ×400. At least 15 fields of view containing 300 cells were counted for each sample. Cells were generally identified to genus and, where possible, to species.

3. Results

1992–3

Seawater samples were collected on 10 occasions between 3 December 1992 and 20 January 1993. Break out of the fast ice cover occurred on 30 January 1993, after

the last set of samples had been collected for this summer.

Integrated chl *a* (Fig. 2) was very low in early December 1992, and rose slowly during the rest of the summer, reaching a maximum of 68 mg m^{-2} on 12 January 1993. No major increase in the concentration of chl *a* occurred after break out of the fast ice in late January or throughout February, which was after the end of sampling for this study for the summer (J. GREY, personal communication).

The phytoplankton in early December was dominated at all depths by *Fragilariopsis* spp. and *Nitzschia* spp. (Fig. 3). Total cell counts were comparatively low, reaching a maximum of 8.4×10^5 cells l^{-1} at 2 m on 3 December 1992. *Phaeocystis* sp., which was present as mucilaginous colonies containing many hundreds of individual cells, became the dominant species throughout the water column in the middle of December, and remained the most common phytoplankton species for the remainder of the summer at 15 and 20 m. Maximum abundance recorded was 4.8×10^6 cells l^{-1} on 31 December 1992 at 20 m. An as yet undescribed species of *Cryptomonas* (J. VAN DEN HOFF, personal communication) was the dominant taxon from 2 to 10 m from late December 1992 till the end of the study for the summer, with a maximum abundance recorded of 1.4×10^7 cells l^{-1} on 5 January 1993 at 2 m. The vertical division between the *Phaeocystis*- and *Cryptomonas*-dominated assemblages (Fig. 3) was initially sharp, with low numbers of *Phaeocystis* cells in the upper water and similarly few *Cryptomonas* cells beneath 10 m. The demarcation between the two assemblages became less clear cut later in January 1993.

Water temperature and stratification data for 1992–3 are shown in Fig. 4. Water temperature at 10 m rose steadily throughout the summer, reaching a maximum of 0.10°C on 20 January 1993. The water column was weakly stratified throughout the study period, with the maximum again recorded on 20 January 1993. The only day of strong winds (defined as those days with an average wind speed of greater than 23 knots) occurred on 20 December 1992. Nutrient concentrations at 10 m (Fig. 5) were initially near winter values (nitrate circa 25 μM, phosphate circa 2.0 μM and silicate circa 65 μM), and generally decreased during the summer.

1993–4

Seawater samples were collected on 11 occasions between 15 December 1993 and 24 February 1994. Break out of the fast ice cover during this summer occurred on 23

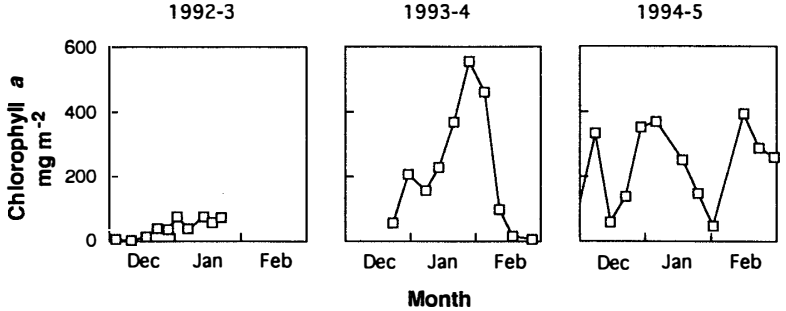

Fig. 2. Water column chl a *integrated from 0 to 23 m measured in (a) 1992–3, (b) 1993–4, and (c) 1994–5.*

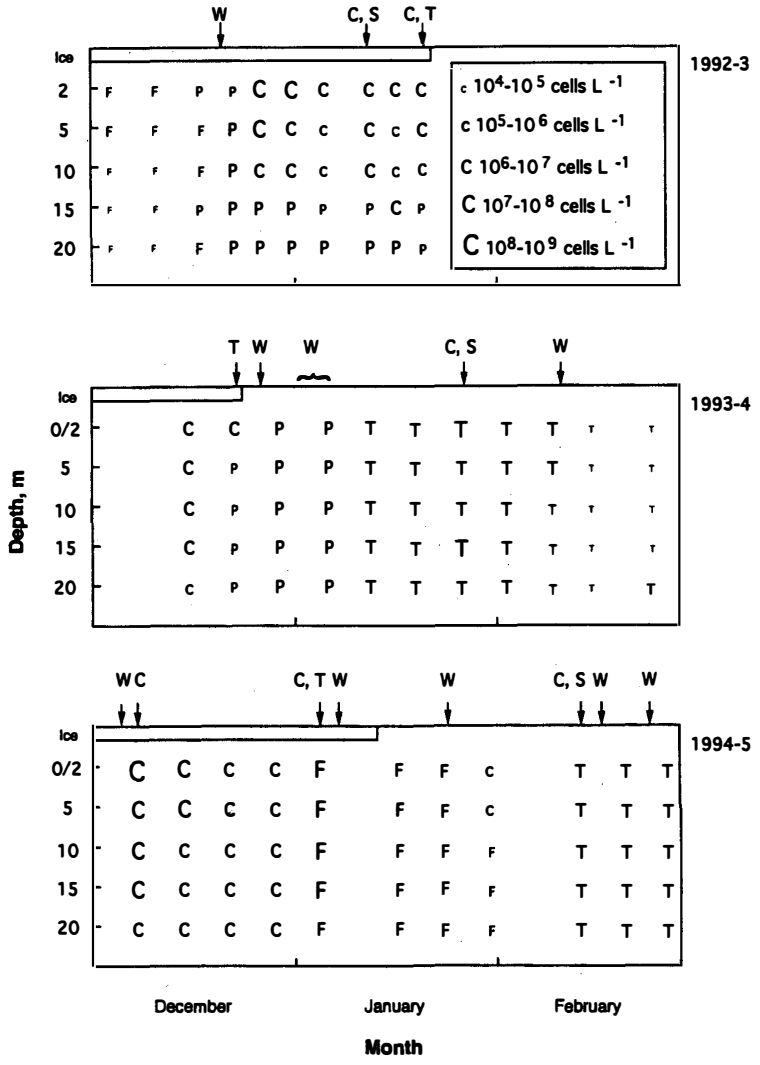

Fig. 3. Dominant phytoplankton assemblages recorded during December to February: (a) 1992–3, (b) 1993–4, and (c) 1994–5. The dominant phytoplankton species are denoted by C: Cryptomonas *sp.; T:* Thalassiosira dichotomica*; F:* Fragilariopsis *spp.*/Nitzschia *spp.; and P:* Phaeocystis *sp. The letters at the top of the graphs denote dates of strong winds (W), of maximum temperature (T), of maximum stratification (S) and chl* a *maxima (C).*

December 1993.

Integrated chl *a* was again low early in the study, but rose steadily to a peak of 555 mg m^{-2} on 26 January 1994, before falling to near zero by the end of February (Fig. 2). A drop in chl *a* occurred on 6 January 1994 after an extended period of strong winds.

The phytoplankton during the 1993–4 summer was initially dominated by the undescribed *Cryptomonas* species (maximum abundance: 3.6×10^6 cells l^{-1}, 22 December 1993 at 2 m) (Fig. 3). *Phaeocystis* sp. soon became dominant, and remained the most common taxon until early January 1994 (maximum abundance: 5.8×10^6 cells l^{-1}, 29 December 1993 at 15 m). For the rest of the summer, the most common species was the centric diatom *Thalassiosira dichotomica*, which reached a

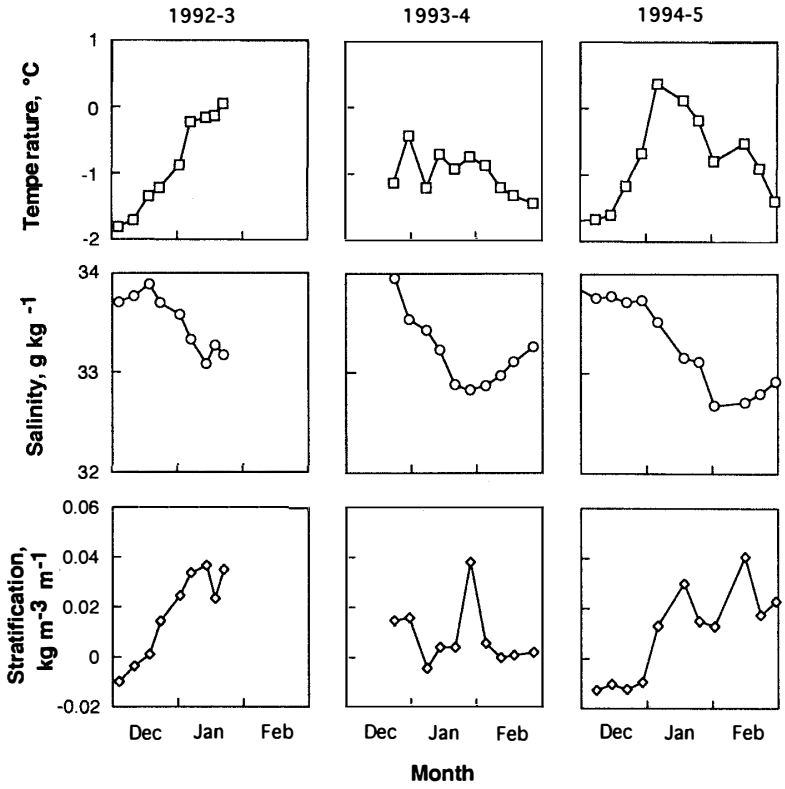

Fig. 4. Temperature (°C) and salinity (g kg^{-1}) at 10 m and average water column stratification (kg m^{-3} m^{-1}) measured during (a) 1992–3, (b) 1993–4, and (c) 1994–5.

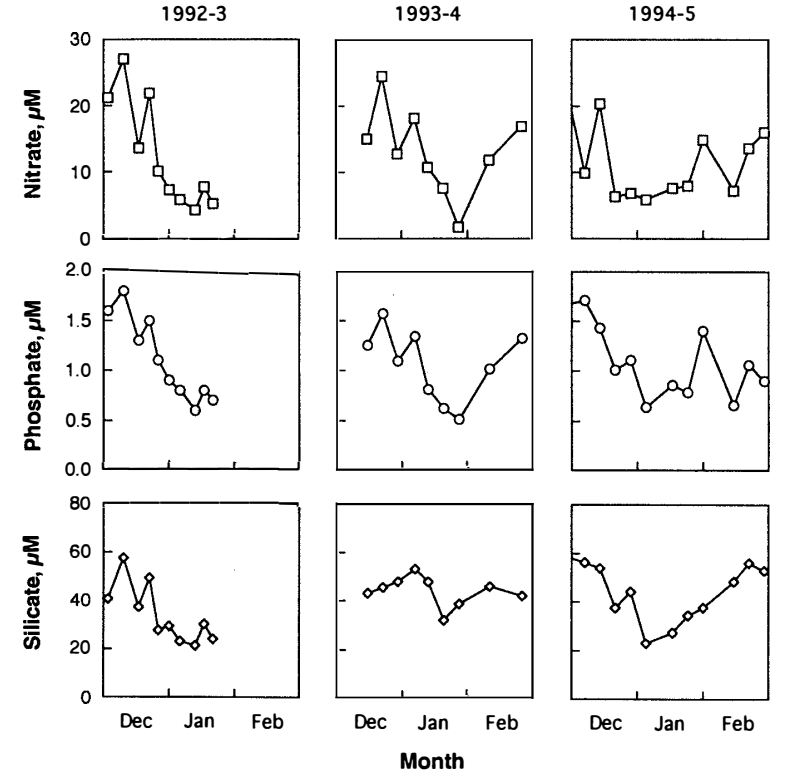

Fig. 5. Nutrient concentrations (normalied to a salinity of 35 g kg^{-1}) measured at 10 m, (a) 1992–3, (b) 1993–4, and (c) 1994–5.

population of 1.2×10^7 cells l^{-1} at 15 m on 26 January 1994. Few *Fragilariopsis* spp. and *Nitzschia* spp. cells were observed during this season.

Maximum water temperature at 10 m, −0.42°C, was recorded on 29 December 1993 (Fig. 4). Water temperature remained less than −0.5°C for the rest of the study. Maximum stratification of the water column occurred on 26 January 1994. Days of strong wind occurred on 26 December 1993, 2, 4, 5 and 6 January 1994, and 10 February 1994.

Nutrient concentrations at 10 m followed similar trends to those observed in 1992–3 (Fig. 5). An increase in nutrient concentrations occurred after the period of high winds in early January. Nitrate and phosphate then fell rapidly, soon reaching concentrations similar to those observed in the other summers. Silicate, however, remained relatively high (compared to nitrate and phosphate) until the peak in biomass occurred (26 January 1994). By this date silicate had dropped to a similar concentration to that measured in late January during the other summers of this study.

1994–5

Seawater samples were collected on 11 occasions between 7 December 1994 and 27 February 1995. Break out of the fast ice cover during this summer occurred on 13 January 1995.

Chl *a* concentration during the 1994–5 summer exhibited three maxima (Fig. 2). The concentration rose sharply in early December, but dropped just as sharply after the peak on 7 December. It rose again to another peak in early January before falling to a low level in late January, rose again in mid-February and then finally fell late in the month. The concentration at each of the peaks was in the range 300–400 mg m^{-2}.

The unnamed *Cryptomonas* species was again dominant during December 1994, with a particularly dense bloom recorded on 7 December 1994 (1.0×10^8 cells l^{-1} at 2 m) (Fig. 3). This bloom faded away, and was replaced by *Fragilariopsis* spp. and *Nitzschia* spp., which were the most common species throughout most of January (maximum abundance: 1.3×10^7 cells l^{-1}, 4 January 1995 at 10 m). *Cryptomonas* sp. continued to be present, but at lower abundances, throughout this period. By the end of January 1995, the diatom bloom had largely disappeared, and *Cryptomonas* sp. was again briefly numerically dominant in the surface waters on 30 January, but at a much reduced abundance (7×10^5 cells l^{-1}, 0 m). A further diatom bloom consisting largely of *Thalassiosira dichotomica* occurred during February, reaching a maximum abundance of circa 5×10^6 cells l^{-1} on 13 February throughout the water column. Non-colonial cells of *Phaeocystis* sp. were observed only occasionally throughout the 1994–5 summer, and the large colonies found in the blooms of 1992–3 and 1993–4 were completely absent.

Water temperature increased steadily during December 1994, reaching a maximum at 10 m of 0.37°C on 4 January 1995 (Fig. 4). The temperature dropped steadily after ice break out before rising briefly in early February. Maximum stratification of the water column occurred on 13 February 1994. Days of strong wind occurred on 5 and 8 December 1993, 7, 8 and 24 January 1994, and 16 and 24 February 1994.

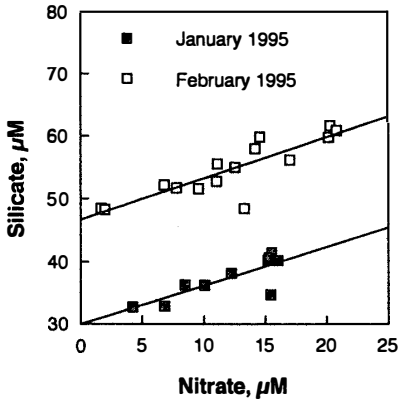

Fig. 6. Silicate concentration plotted against nitrate concentration (both normalised to a salinity of 35 g kg^{-1}) for January 1995 and February 1995, showing the presence of water with relatively high concentrations of silicate after a period of strong winds late in January.

Nutrient concentrations at 10 m followed similar trends to the other summers (Fig. 5). A significant drop in nitrate, but not phosphate or silicate, concentration occurred on 7 December 1994, coincident with the bloom of *Cryptomonas* sp. Concentrations of all of the nutrients decreased until mid-January 1995 before beginning to rise. Nitrate and phosphate decreased again in early February 1995, before recovering by the end of the month. Plotting the concentration of nitrate against that of silicate for the last six sampling dates (Fig. 6) revealed that the water in February 1995 was considerably enriched in silicate with respect to nitrate. Silicate was similarly enriched with respect to phosphate during February 1995.

4. Discussion

During the three summer study periods four major phytoplankton assemblages were observed in the inshore waters near Davis Station. Single species of phytoplankton were dominant in three of these assemblages (*Phaeocystis* sp., an undescribed *Cryptomonas* species and the diatom *Thalassiosira dichotomica*), while the fourth assemblage consisted of a mixture of *Fragilariopsis* spp. and *Nitzschia* spp. The dominant species typically accounted for 60–80% of the total phytoplankton cell counts in a sample.

The species in the four assemblages have been recorded in many other studies of Antarctic phytoplankton. *Phaeocystis* has a cosmopolitan distribution, but is particularly common around the Antarctic continental margin where it often dominates the phytoplankton in December-January (BÖLTER and DAWSON, 1982; GARRISON *et al.*, 1987; HOLM-HANSEN *et al.*, 1989; DAVIDSON and MARCHANT, 1992). The species observed in the present study could not be identified accurately, but was probably *Phaeocystis antarctica*, which has recently been described from the Antarctic region (MEDLIN *et al.*, 1994). *Cryptomonas* spp. have also been recorded as the dominant phytoplankton species in many studies around the Antarctic continent (TAYLOR and LEE, 1971; JACQUES and PANOUSE, 1991; BUMA *et al.*, 1992; KOPCZYNSKA, 1992). As mentioned previously, the species observed near Davis was as yet

undescribed (J. VAN DEN HOFF, personal communication). The distribution of this particular species in the Antarctic region is unknown, though it was common in Ellis Fjord, Vestfold Hills (Fig. 1), during January in 1992 (MCMINN and HODGSON, 1993) and 1995 (J. GIBSON, unpublished results).

Thalassiosira dichotomica is a small centric diatom (diameter 12–26 μM) found around the margin of the Antarctic continent (MEDLIN and PRIDDLE, 1990). This species was reported to be an important member of the phytoplankton in Ellis Fjord late in February 1992 (MCMINN and HODGSON, 1993). Assemblages dominated by *Fragilariopsis* spp. and/or *Nitzschia* spp. have been recorded from many parts of the Southern Ocean (HASLE, 1969; WILSON *et al.*, 1986; KANG and FRYXELL, 1992; KOPCZYNSKA *et al.*, 1995). The species present in the blooms near Davis included *Fragilariopsis kerguelensis, Fragilariopsis cylindrus* and *Nitzschia lecontei.*

The seasonal cycle of phytoplankton assemblages observed near Davis exhibited considerable variation over the three summers. For example, *Thalassiosira dichotomica* was not observed in any abundance in 1992–3 (though it may have bloomed after the end of the sampling period), and *Phaeocystis* sp. was absent in 1994–5. *Cryptomonas* sp. was dominant throughout the water column in December 1993 and 1994, but during January (and only to a depth of 10 m) in the 1992–3 summer, and the *Fragilariopsis/Nitzschia* assemblage was present in December in 1992–3 and January 1994–5, but was poorly represented in 1993–4. Some trends, however, were observed. *Cryptomonas* sp. was generally, but not exclusively, associated with the presence of sea ice, *Phaeocystis* sp. was present (when observed) at the end of December and early January, which was consistent with previous studies (PERRIN *et al.*, 1987; GIBSON *et al.*, 1990; DAVIDSON and MARCHANT, 1992), and *Thalassiosira dichotomica* blooms were initiated during periods when the water was relatively enriched with silicate compared to the other macronutrients.

The results of this study are consistent with those of SKERRATT *et al.* (1995), who, from a study utilising signature lipids to characterise the phytoplankton community at Davis, reported considerable interannual variation in the community over the period 1988–1993. The occurrence of *Phaeocystis* sp. was found to be sporadic, and it was concluded that this species was not always a major component of the phytoplankton in the coastal region of Antarctica (SKERRATT *et al.*, 1995). SKERRATT *et al.* (1995) reported lipids and pigments attributable to cryptomonads during each summer of their study, but did not observe *Thalassiosira dichotomica* specifically.

Earlier studies of the phytoplankton near Davis observed some of the assemblages found in the present study (PERRIN *et al.*, 1987; GIBSON *et al.*, 1990; DAVIDSON and MARCHANT, 1992), but, remarkably, no *Cryptomonas* sp. or *Thalassiosira dichotomica* were reported. The absence of *Cryptomonas* sp. from the earlier studies is difficult to explain, but was possibly due to collection of samples from deeper depths rather than from the upper water column closer to the ice, which appears to be the preferred habitat of this species. In contrast, *Thalassiosira dichotomica* is clearly associated with periods of high relative silicate concentrations, and this situation might not have occurred in the earlier years.

Phytoplankton biomass, as reflected in the concentration of chl *a*, also varied dramatically between the summers of this study. Peak integrated chl *a* in 1993–4 was

approximately 1.4 times greater than in 1994–5, and 8 times higher than in 1992–3. Data from near the same site in earlier summers indicated that similar interannual variation occurred previously (PERRIN *et al.*, 1987; DAVIDSON and MARCHANT, 1992; MCTAGGART, 1994; F. SCOTT, personal communication). Assuming that the ratio of chl *a* to photosynthetically fixed organic carbon is relatively constant, the amount of carbon fixed in Antarctic nearshore waters would therefore appear to vary considerably from year to year.

The interannual variation in the phytoplankton assemblages and the biomass present at the site can be attributed to a number of factors. The presence of an ice cover will effect the light levels available for photosynthesis as well as influencing the phytoplankton species present. *Cryptomonas* sp. was observed at greatest abundances when the ice cover was still present. Observations in the laboratory indicated that this species is negatively phototactic, and thus adapted to living in the low light conditions experienced in the under ice environment. The ice cover also appeared to effect the flow of water currents. The persistent biological stratification observed during January 1993 suggests that little turbulence occurred in the flow under the ice.

The maximum concentrations of chl *a* in the present study were often associated with peaks of water column temperature and/or stratification (Fig. 3). The highest water temperatures generally occurred while the sea ice was still present. In 1993–4, when the ice broke out relatively early, water temperatures were lowest of the three summers. Water temperature rose to a maximum in 1994–5 just before the break out of the sea ice, but dropped steadily during the rest of the summer. Higher temperatures will result in an increase in phytoplankton productivity (*e.g.* MORRIS, 1980), though the range of temperature differences observed in this study was small.

Water column stratification is a result of both warming of the surface water by solar radiation and, more importantly in the Antarctic environment, surface water dilution by freshwater input from melting sea ice, icebergs and the polar ice cap. Stratification will increase the time a cell spends in an environment with higher available light for photosynthesis. That maxima in the chl *a* concentrations were observed during each of the summers on the same day as maximum stratification reflects the importance of this parameter. The salinity of the water itself is also likely to have some small effect, as lower surface salinities might select for particular species.

The phytoplankton assemblages observed near Davis Station will also be the result of the interplay between development of blooms in the inshore environment and transport of such blooms out of the area and then replacement by new assemblages from offshore or deeper waters. A relatively strong westerly current, part of the cyclonic Prydz Bay Gyre, flows along the coast offshore from Davis. Under calm conditions, it appears that the current flows uniformly, with the water entering the inshore water near Davis having undergone a similar history to that which it replaces. Thus the phytoplankton species and biomass present at the sampling site will exhibit only slow change. However, during periods of strong offshore winds, this flow is disrupted, and water from either offshore or from deeper in the water column are introduced into the inshore flow. These water masses can contain different phytoplankton species, which can then develop in the inshore

environment. This process can also result in an increase in nutrient levels in the water as well as in unexpected temperature changes.

The best example of this process in this study occurred in late January 1995. An intense bloom of *Thalassiosira dichotomica* developed after periods of high wind brought in water containing high relative silicate concentration (Figs. 5 and 6). It is probable that *Thalassiosira dichotomica* was also transported into the inshore flow during this water exchange. This water was also significantly warmer than that it had replaced (Fig. 2). The bloom continued for at least three weeks, indicating that the strong wind episode had brought water either from upwelling or surface advection into the coastal flow over a considerable area.

The changes in the phytoplankton community observed during the 1992–3 summer, on the other hand, show the effect of the lack of wind. During this summer a low level *Fragilariopsis/Nitzschia* bloom was initially present, which was replaced firstly by *Phaeocystis* sp. and then, in the upper waters, by *Cryptomonas* sp. The maintenance of the biological stratification during January indicated that little wind-induced mixing occurred in the water column. Primary production appeared to be relatively low during this summer, as the concentration of chl *a* was significantly lower than in the subsequent summers.

Finally, it must be remembered that zooplankton grazing can also play an important role in structuring the phytoplankton community. It is possible that the low biomass observed in 1992–3 was not only a result of reduced primary productivity, but also reflected increased grazing. Zooplankton can also effect phytoplankton succession, as blooms of a particular phytoplankton species can be removed by grazing, and, conversely less palatable species of phytoplankton (such as *Phaeocystis* sp.) might be able to bloom due to reduced competition for light and nutrients.

In spite of the interannual variation observed in this study, a general picture can be developed of the phytoplankton cycle in the waters offshore from Davis Base. Various phytoplankton species are dominant at different times of the summer depending on the cycle of the development of assemblages in the inshore region and the introduction of new assemblages from offshore or deeper waters. The biomass produced will be a function of such environmental parameters including light (mediated to a large extent by the presence of sea ice), water temperature and salinity, water column stratification, zooplankton grazing pressure and nutrient availability. Strong wind events will facilitate the interchange of water masses and communities. Such events as wind and sea ice break out are irregular both in time and space, and it is possible that a particular assemblage can be removed from the inshore region before it has reached peak biomass. The species assemblages present, the timing of the succession of the assemblages, and the biomass present inshore near Davis will therefore differ from year to year as the ice, winds and other environmental parameters vary.

Acknowledgments

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