Phytoplankton Biomass Related to Environmental Factors in the Ross Sea

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ABSTRACT

Three years of investigation in the western Ross Sea reveal that despite the general abundance of phytoplankton biomass, the ratios between biomass and nutrient availability are low due to high nutrient concentrations. The N/P ratio is practically identical to that of Redfield; however, during blooms the ratio can be severely altered due to very low phosphate concentrations. Phytoplankton biomass during summer shows a bimodal cyclic pattern with two blooms in early and late summer. The spatial and temporal distribution of these blooms follows the latitudinal distribution of daily irradiance, which determines the advance of sea-ice melting from south to north forming an upper mixed layer rich in nutrients. This mixed layer is well illuminated and warmer than the deeper layer, thereby favouring the development of the early bloom. Afterwards, in the mixed water column, biomass decreases and reaches the summer minimum. A new stabilization of the water column is followed by a second bloom, less extensive than the first. In all 3 years, similar cycles have been recorded, giving corroborative evidence for the existence of a second bloom.

Introduction

Studies on the ecology of phytoplankton in the Southern Ocean initially revealed the contrast between the large quantity of nutrients and the low concentration of phytoplankton (Holm-Hansen et al. 1977; El-Sayed et al. 1983; El-Sayed 1988). Jacques and Tréguer (1986) described the situation in the Southern Ocean as the Antarctic paradox, because of a high eutrophy which is capable of producing a quantity of biomass as small as that of most oligotrophic zones in the oceans. Geographic variety exists, moreover, between the coastal and open-sea areas (El-Sayed et al. 1983; Holm-Hansen and Mitchell 1991); in any case, phytoplankton blooms of remarkable intensity are reported in the Southern Ocean (El-Sayed 1984, 1988; Smith and Nelson 1985; Knox 1994).

As far as the Ross Sea is concerned, various studies have been carried out, such as those of Bunt and Lee (1970), Holm-Hansen et al. (1977), El-Sayed et al. (1983), and Wilson et al. (1986), also in areas close to Terra Nova Bay. The bay, however, has remained almost completely un-

known with regards to various oceanographic aspects, among which the hydrography and ecology of phytoplankton.

Research by the Italian Antarctic National Research Program (PNRA) was initially aimed at supplying a picture of the marine ecosystems of the western Ross Sea. The results of the first expedition (R/V Polar Queen, 1987-88) indicated a more extensive biomass and a more complex seasonal cycle (Innamorati et al. 1990c) than had been expected from the data reported in the literature. The second expedition was therefore organized to include a neritic group, to conduct a series of daily surveys at several given stations in Terra Nova Bay (M/N Barken and R/V Malippo, 1989-90), and an oceanic group, to carry out surveys on a large spatial scale in the Ross Sea (R/V Cariboo, 1989-90). The third expedition (M/N Italica, 1994-95) reexamined the temporal series in the bay. All data obtained during the three expeditions have been published in Data Reports (Innamorati et al. 1990a, 1990b, 1991, 1994a; Nuccio et al. 1994; Lazzara et al. 1997), and several preliminary results have been comunicated at congresses and workshops (Innamorati et al. 1992a,b; Lazzara and

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Nuccio 1994; Lazzara et al. 1995, 1996; Nuccio et al. 1992; Saggiomo et al. 1992).

Materials and Methods

The investigated area in 1987–88 (Fig. 1a), on board the R/V Polar Queen, covered a grid of 40 × 50 nmi with 40 stations spaced 5 nmi near the coast and 10 nmi offshore. Stations 16, 17, 49, 50 and 51 were all along 74°49′S up to 125 nmi from the coast.

During the 1989–90 expedition, the neritic group carried out its work at three stations (Fig. 1b): Terra Nova Bay (BTN; 74°41′42″S, 164°07′24″E), near the rocky shore, sampled at the surface daily; Mergellina (MRG), 250 m from the coast (74°41′33″S, 164°07′15″E; 50 m deep); Santa Maria Novella (SMN), at the centre of the bay (74°43′00″S, 164°16′00″E), where the bottom was 500 m deep. The oceanic group on board the R/V Cariboo, in the area from 60° to 75°S, sampled 27 stations (Fig. 1c), and several samples for
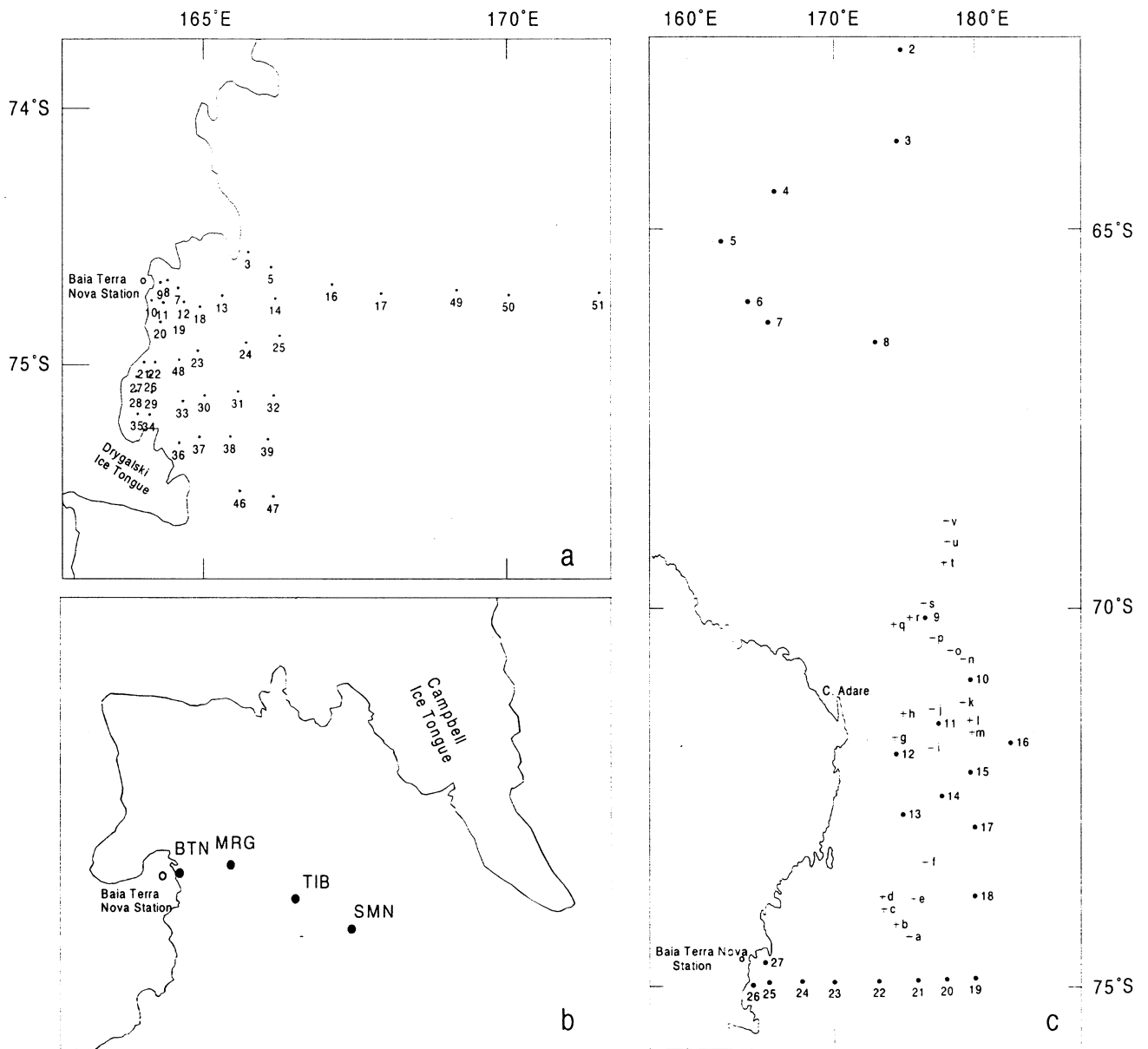

Fig. 1a–c. Maps of the stations. a 1987–88. b Coastal stations SMN, MRG, BTN (1989–90), TIB, BTN (1994–95). c 1989–90

chlorophaeopigments analysis were collected on the way back from Terra Nova Bay using a pumping system, located at 3 m from the sea surface (Fig. 1c; stations a-v).

In 1994-95, two stations were sampled: BTN, as in 1989-90, and Tiburtina (TIB; 74°42'05"S, 164°10'01"E), with a depth of 300 m (Fig. 1b).

Hydrographic data of the 1987-88 cruise are from Boldrin and Stocchino (1990), and those of the R/V Cariboo cruise are from Artegiani et al. (1992). In 1989-90 and 1994-95 CTD data were acquired by means of the KMS profiler Meerestechnik, equipped with a Dr. Haardt Back-Scat fluorometer.

Seawater was sampled using Niskin bottles for phytoplankton microscopic analysis (fixed with Lugol or formaldehyde to a final concentration of 1 and 4%, respectively), for the analysis of nitrites, nitrates, phosphates and silicates (Hansen and Grasshoff 1983) as well as for pigment determinations, after filtration on Whatman GF/F. Data on nutrients for 1987-88 and for the 1989-90 R/V Cariboo cruises are from Catalano and Benedetti (1990) and Catalano et al. (1991). Liposoluble pigments were determined, after extraction with 90% acetone, using a Kontron Uvikon 930 spectrophotometer. The chlorophyll a + phaeophytin a (Phaeo) = chlorophaeopigments (Chl) concentration was determined following Lorenzen (1967) modified by Riemann (1978). During the three expeditions, chlorophaeopigment analyses at station BTN were begun at the end of December-beginning of January, on the ship's arrival (Fig. 7). In 1989-90 and 1994-95, samples for the microscopic analysis of phytoplankton densities were taken from the beginning of December (Fig. 7).

Measurements of solar global irradiance were carried out by means of a CM5 solarimeter (Kipp and Zonen) continuously recorded and daily integrated (CC1 Kipp and Zonen) in 1987-88 and 1989-90, and in 1994-95 by means of a PAR quantameter equipped by a data logger (LI-192SA; LI-100 LI-COR), storing data every 10 min. The conversion from PAR ($\mu M s^{-1} m^{-2}$ of photons) to global solar irradiance ($W m^{-2}$) was obtained by dividing the former by 1.96 (Morel and Smith 1974; Jerlov 1976).

Surface and underwater downwelling, upwelling, scalar quantum PAR irradiances were measured by means of a photoprobe (Innamorati et al. 1994b) equipped with three cosine and one spherical meters (LI 192SA, LI 193SA LI-COR).

The depth of the euphotic layer, z_e, was calculated from $E_e/E_0 = 0.01$, where E_e and E_0 are the downwelling quantum PAR irradiances at the euphotic depth and sea surface, respectively. For some stations, data for downwelling PAR were missing, so that, as the waters all belong to case I (Morel 1988), the euphotic zone depth was estimated from the orthogonal regression of log z_e vs. log Chl (Morel 1988) calculated on the overall data set, as described in Lazzara et al. (this Vol.).

Images for pack-ice cover (NOAA-HRTP AVHRR) in the Ross Sea during 1994-95 were obtained from the ENEA-PNRA receiving station at Terra Nova Bay.

Results

Irradiance and Ice Covering

Increasing daily irradiance during summer at these high latitudes is the main factor determining the melting of pack ice and subsequently all other physical and biological events. For about 35 days before and after the summer solstice, daily irradiance was greater in the direction of the poles, and decreased with latitude in the direction of the tropics (Fig. 2). The melting pattern of sea ice reflected that for irradiance; it began from the south and proceeded towards the north, encountering a certain delay in the coastal zone compared to ice in the open sea. At the beginning of
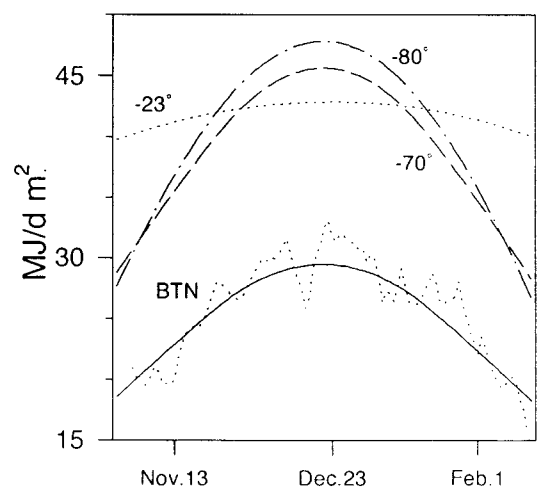

Fig. 2. Latitudinal variations of extraterrestrial daily irradiance (after Iqbal 1983) and mean of the global daily irradiance measured during the three expeditions at Terra Nova Bay with its interpolating function

December, in addition to the polynya of Terra Nova Bay, the central part of the Ross Sea was free of ice and, towards the beginning of January, this was also the case in coastal areas in the vicinity of the Terra Nova Bay Station (Fig. 3).

As a result of ice melting and warming of surface temperatures, salinity and density decreased, determining a stratification and stability of the water column that favoured the development of phytoplankton.
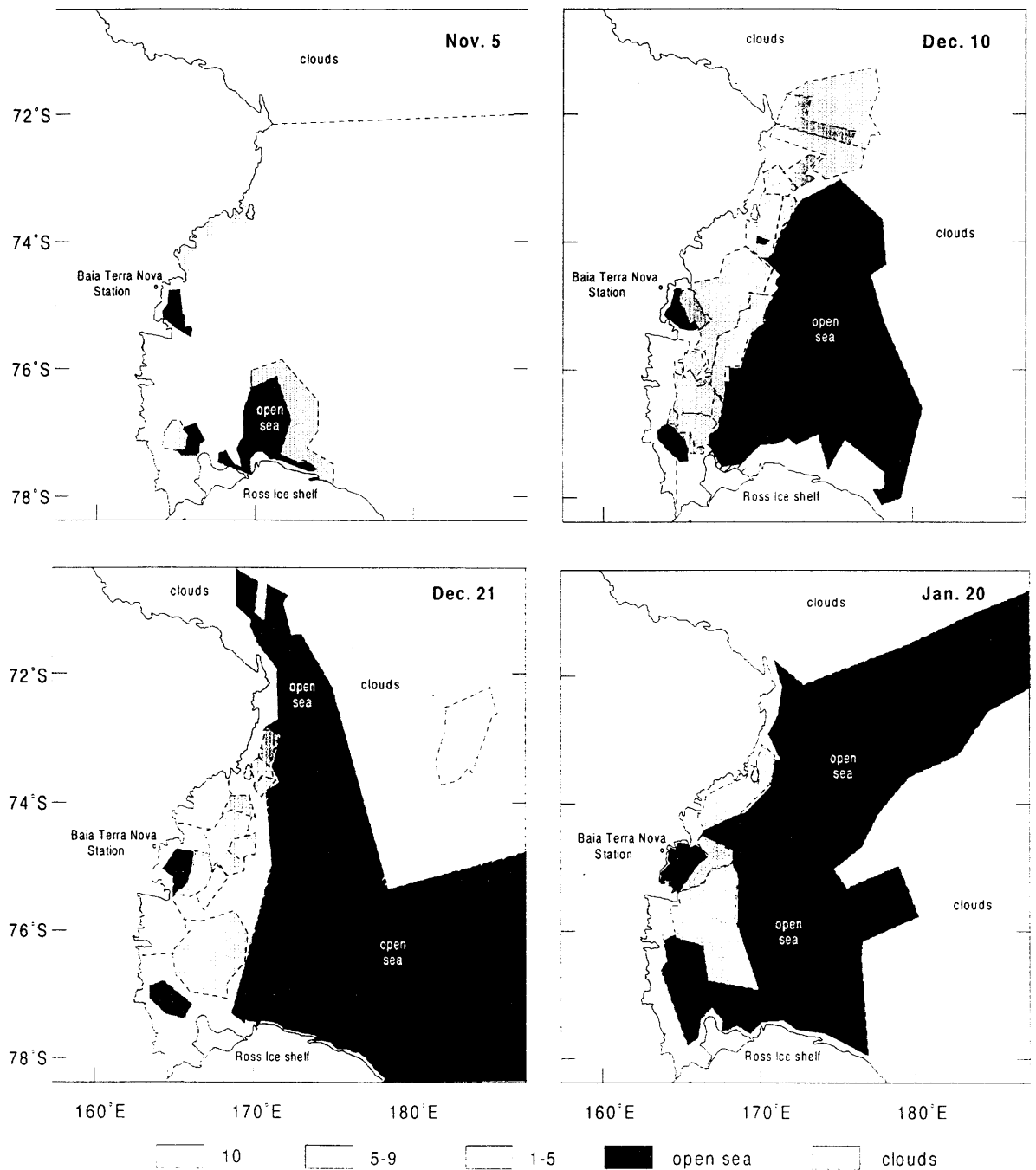

Fig. 3. Pack-ice cover dynamics in the Ross Sea. (After 1994–95 NOAA-HRTP AVHRR daily images)

Vertical Structure of the Water

The characteristics of the water column of the stations in Terra Nova Bay (Fig. 1b) are very similar, and their temporal evolution was well represented by that of the SMN station (Fig. 4).

In the early days of January (Fig. 4a), the irradiance determined the melting of ice, formation of the pycnocline, heating of the water, which exceeded 2 °C at the surface, and formation of the thermocline. Up until the second half of January, stratification remained well defined in the waters that were ice-free. Starting from the second half of January (Fig. 4b), the new mixing and the decreased supply of fresh water tended to render the column homogeneous. In early February (Fig. 4c), due to the melting of floating ice, a new stratification phase occurred which was less developed than the preceding one. In fact, in the bay there had been a continuous accumulation and freeing again of large slabs of pack ice coming from the south, brought by winds and currents, and directed northward. The temperature decreased to −0.6 °C.

This same type of succession in the structure of the water column was noted also at other stations in the Ross Sea, beginning from the north in a southerly direction (Fig. 1c). Therefore, these stations were grouped and classified in a sequence according to the time elapsed since the liberation of the ice and, therefore, to the type of structure of the water column, independent of the chronological sequence with which they were detected. Other factors may also have affected the structure of the water column; nonetheless, in our opinion irradiance controlling ice melting was the determining factor.

The observed phases were the following:

1st phase: stations 5 to 8 (Fig. 5a); pack ice barely broken by the ship; this was a phase prior to the beginning of the sampling at SMN; it indicated the beginning of stratification.

2nd phase: stations 25 to 27 (Figs. 5b, 4a); the sea still had some ice present, complete stratification; the upper mixed layer (UML) was about 25 m thick; the surface temperature varied from 0 to 0.5 °C and, when stability continued, reached >1 °C.

3rd phase: stations 11 to 19 (Figs. 5c, 4b); the sea had been free of ice for about 2 weeks; the pycnocline was greatly reduced or non-existent, and was not influenced by the thermocline;

a remixing of the surface layers with the underlying ones occurred.

4th phase: stations 20 to 23 (Figs. 5d, 4c); the sea had been free of ice for about 1 month; in some cases, the temperature of the surface layer exceeded 1.5 °C, forming a thermocline that produced only a weak pycnocline. Such stratified conditions were typically produced by heating of the surface layers (Fig. 5d), while at the stations of Terra Nova Bay, they originated essentially from the decrease in salinity (Fig. 4c).

The latitudinal succession of the phases was consistent with that of daily irradiance (Fig. 2). It began from the south, where it was greater and where the most advanced phases were found. It then proceeded in a northerly direction, where, due to less intense irradiance, more time was needed to melt the pack ice and where the initial phases were found. However, because of the faster advancement in the melting of ice towards the north and slower melting towards the west, as reported in Fig. 3 and also by Smith and Nelson (1985), stations 25, 26 and 27 were ice-free almost simultaneously with those of Terra Nova Bay, but later compared with those of equal latitudes off shore.

Nutrients

During the first phase, nutrients (nitrates and phosphates) had a high concentration that was almost homogeneous throughout the water column (Fig. 5e). Subsequently, in the surface layer they were strongly consumed by the phytoplankton biomass, thus contributing to the formation of a nutricline (Figs. 4d,g, 5f,j). Later, the production of phytoplankton decreased, as a result of the lack of nutrients, causing an alteration in the ratios between nutrients in the water, compared to those necessary for phytoplankton assimilation. This alteration was caused primarily by phosphate concentration, which was so low that it could no longer be detected by the analytical method (Figs. 4d, 5f). Therefore phytoplankton biomass was reduced (Figs. 4h, 5j,k), also because of zooplankton grazing activity (Fonda Umani et al. 1992; Knox 1994). Thus, there was a decrease in the consumption of nutrients, whose concentrations were enhanced (Figs. 4e, 5g), as a result of a mixing of the water column probably caused by winds and waves, which rehomogenized the water column

Early January   Second half of January   Early February

Fig. 4a–i. Representative types of vertical profiles of salinity (‰), temperature (°C) and density (kg m^{-3}) (a, b, c); phosphate (µM), nitrate (µM) and nitrite (µM) (d, e, f), Chl (mg m^{-3}) and Phaeo/Chl ratio (g, h, i) at SMN, 1989–90. z_e represents the euphotic zone depth
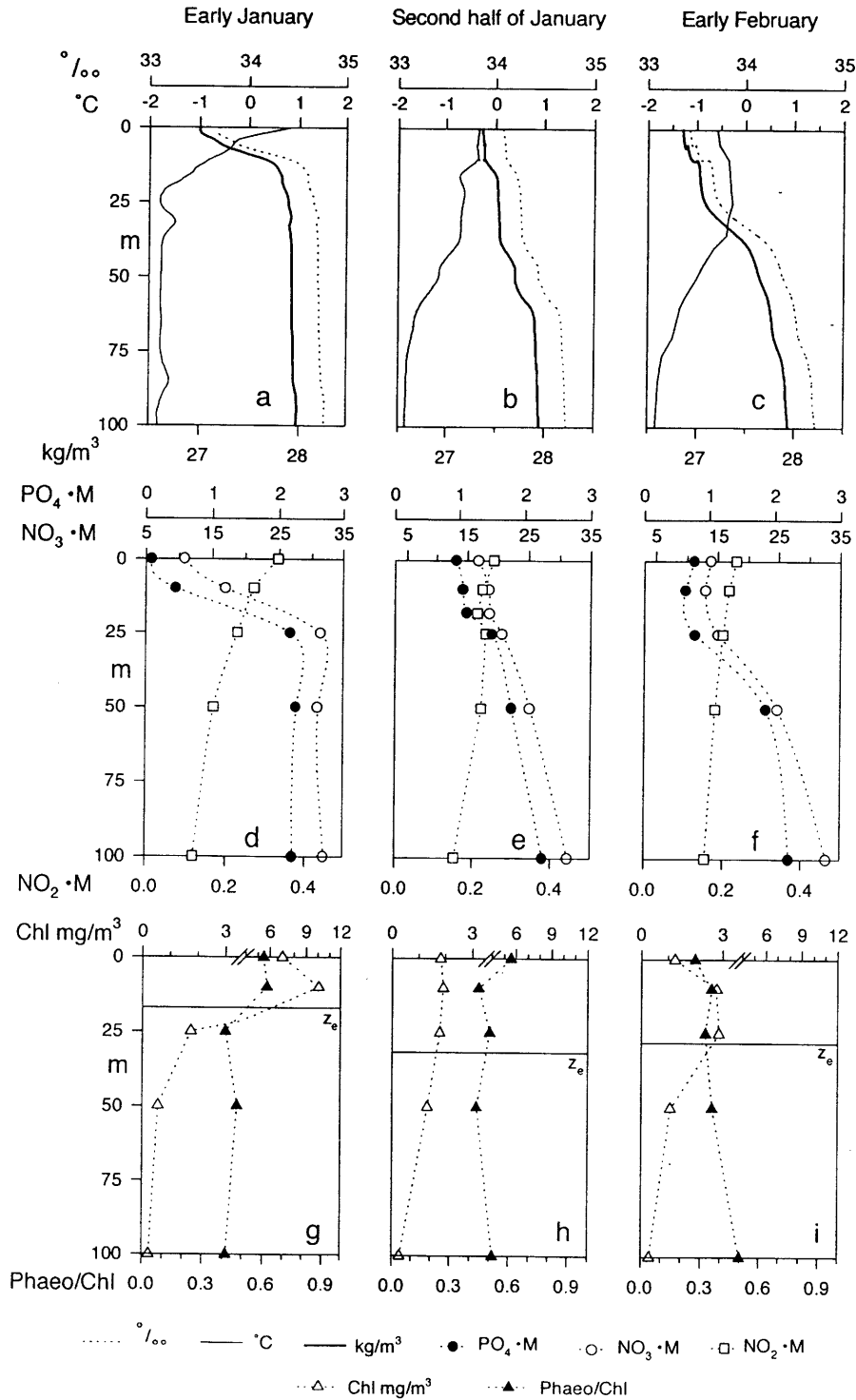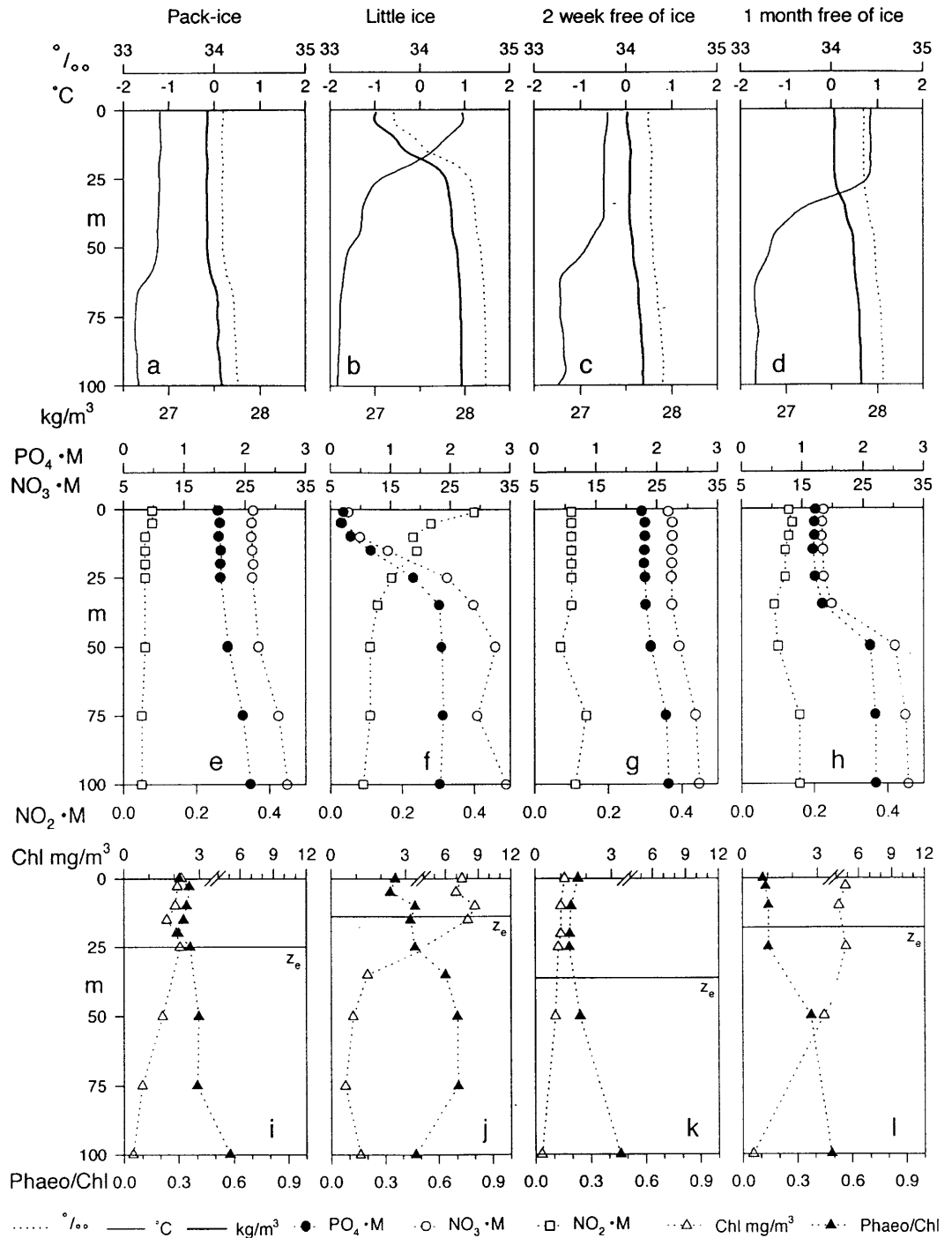
Fig. 5a–i. Representative types of vertical profiles of salinity (‰), temperature (°C) and density (kg m^{-3}) (a, b, c, d); phosphate (μM), nitrate (μM) and nitrite (μM) (e, f, g, h), Chl (mg m^{-3}) and Phaeo/Chl ratio (i, j, k, l) at the 1989–90 offshore stations. z_e represents the euphotic zone depth

structure (Figs. 4b, 5c). In the end, a second increase in the phytoplankton biomass occurred (Figs. 4i, 5l), again accompanied by the consumption of nutrients and the development of a nutricline (Figs. 4f, 5h).

Similar dynamics were verifiable also for silicates, the concentrations of which were very high during the periods preceding (80 μM) and following (65 μM) the first bloom. Since diatoms were dominant in this period, a large consumption (8 μM) of silicates was recorded. The concentration decreased again, also during the second increase in phytoplankton biomass (down to 55 μM).

The nitrite distribution in the surface layer (Figs. 4d-f, 5d-f), behaved differently from other nutrients; its concentration increased as the phytoplankton biomass increased (Figs. 4g-i, 5i-l).

Dynamics of the Biomass

The temporal evolution of environmental conditions, Chl, and Phaeo/Chl is shown in Fig. 6. In Fig. 7, the temporal evolution of phytoplankton biomass, assessed as Chl and cell densities, at Terra Nova Bay during the three summers is reported. From Figs. 4, 5 and 6 it is clear that the biomass maxima were in agreement with phases 2 and 4 of the water-column stratification, with a marked pycnocline and nutricline, and high absolute biomass values, up to 18 mg m^{-3} of Chl and 10^7 cell dm^{-3}.

The lack of Chl analyses at the beginning of December was sufficiently compensated for by the data on cell densities. The cycle in the development of biomass began with a minimum at the beginning of December (Fig. 7d,f), which subsequently increased to a maximum between December and January, and decreased once more to a second minimum between January and February. In all three expeditions, biomass showed this second minimum in close agreement with phase 3, during which there was also a diminishing of the stratification and nutrient concentrations (Figs. 4b,e,h, 5c,l, and 6 between 25 January and 1 February), which made it similar to phase 1. On the whole, the evolution of the biomass assumed the form of an undulatory cycle. However, after having performed one complete oscillation, it started a second. Indeed, Figs. 7; 4c,f,i, 5d,h,l and Fig. 6 between 1 February and 8 February show that there was a second increase in biomass. It is

also evident that this second phase (Fig. 5d,h,l) was preceded by conditions (Fig. 5c,g,k) similar to those of phase 1 (Fig. 5a,e,i). In addition (Fig. 7e), the decrease shown by Phaeo compared to Chl in correspondence with the resumption of cell multiplication could be an indication that a young assemblage was in a developing phase.

This temporal pattern does not seem to be limited to Terra Nova Bay. A situation of scarce biomass and absence of nutricline and pycnocline were reported in the area between 74° and 67°S, in the early days of January 1990 (stations 11–19, Fig. 1c; Fig. 5c,g,k). Successively from January 13 to 16 (74°–73°S), 17 to 20 (72°–70°S), and from 21 to 22 (70°–67°S) enhancement of biomass up to an average of 2.5, 1.4 and 0.9 mg m^{-3} of Chl (Fig. 8), respectively, was recorded, which characterised the zone as also being affected by the second end-of-season blooming. As in the first bloom, this second bloom occurred in different times and at different latitudes.

Phytoplankton Assemblages

As far as the phytoplankton assemblages are concerned, those of the first bloom (Figs. 4a,d,g, 5b,f,j) were similar in all of the Ross Sea. They appeared at different times and were always characterized by diatoms dominated by the genus *Fragilariopsis* (Nuccio et al., this Vol.). The role of sympagic microalgae in this bloom is controversial and some authors (Krebs et al. 1987; Knox 1994) contend that blooms might be due to sympagic cells rather than free-living organism. However, as regards the interrelationship between sympagic and free-living organisms, the active colonization of the sea-ice environment by the water-column organisms should also be considered. Further, if it is feasible to think that the sympagic algae make a contribution, it is difficult to believe that they determine the entire pelagic bloom.

During the summer minimum, phytoplankton assemblages generally showed a greater species diversity. However, diatoms were still dominant close to the coast; offshore the assemblages become predominantly composed of phytoflagellates (Nuccio et al., this Vol.). Near the coast phytoplankton assemblages of the second bloom were dominated by *Fragilariopsis* cf. *curta* and some other diatoms. Offshore, diatoms of the genus *Nitzschia* dominated, together with *Phaeocystis* sp. (Nuccio et al., this Vol.).
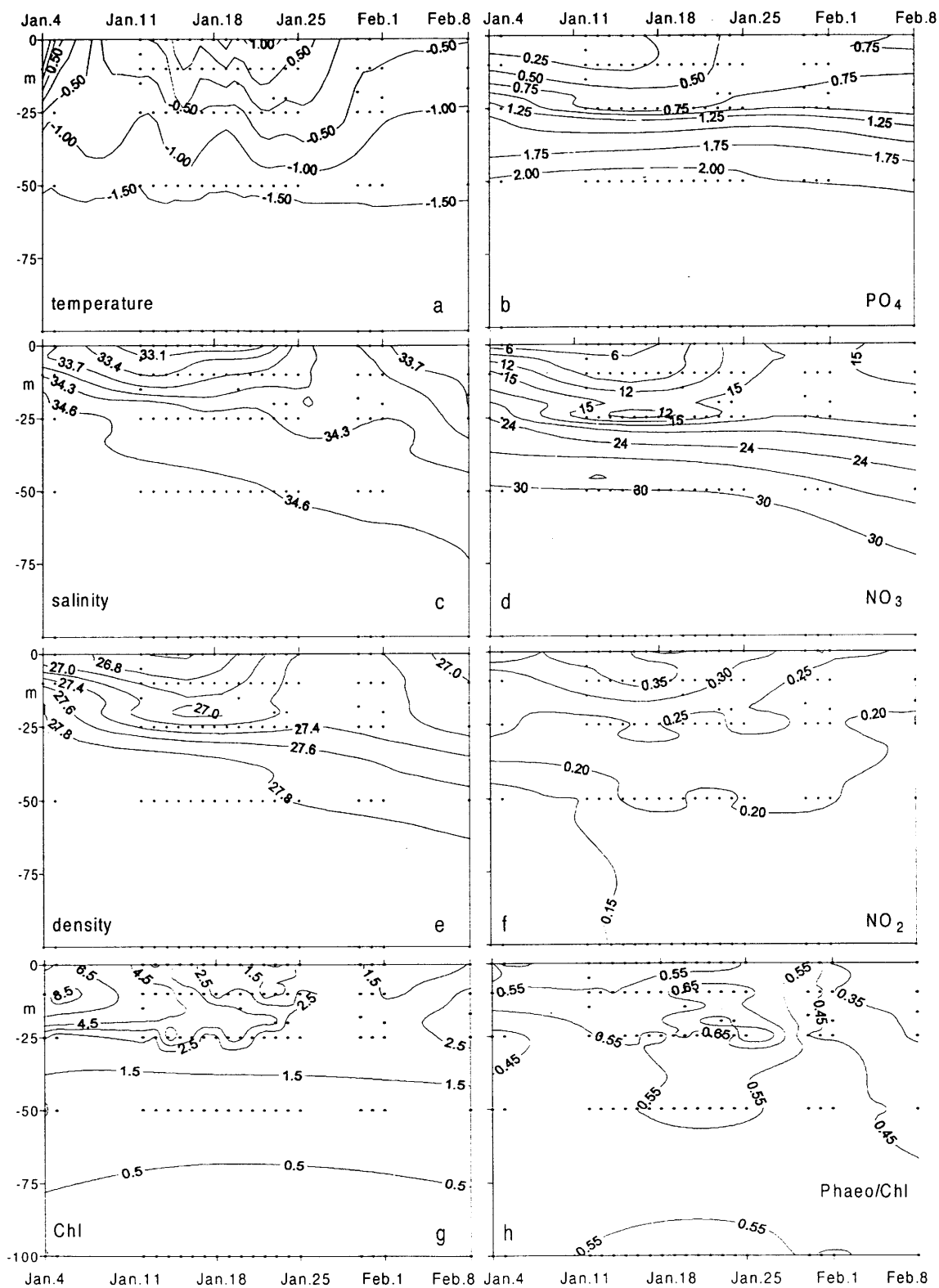
Fig. 6a–h. Isopleths of: a temperature (°C); b phosphate (μM); c salinity (‰); d nitrate (μM); e density (kg m^{-3}); f nitrite (μM); g Chl (mg m^{-3}) and h Phaeo/Chl ratio at SMN from January 4 to February 8, 1990
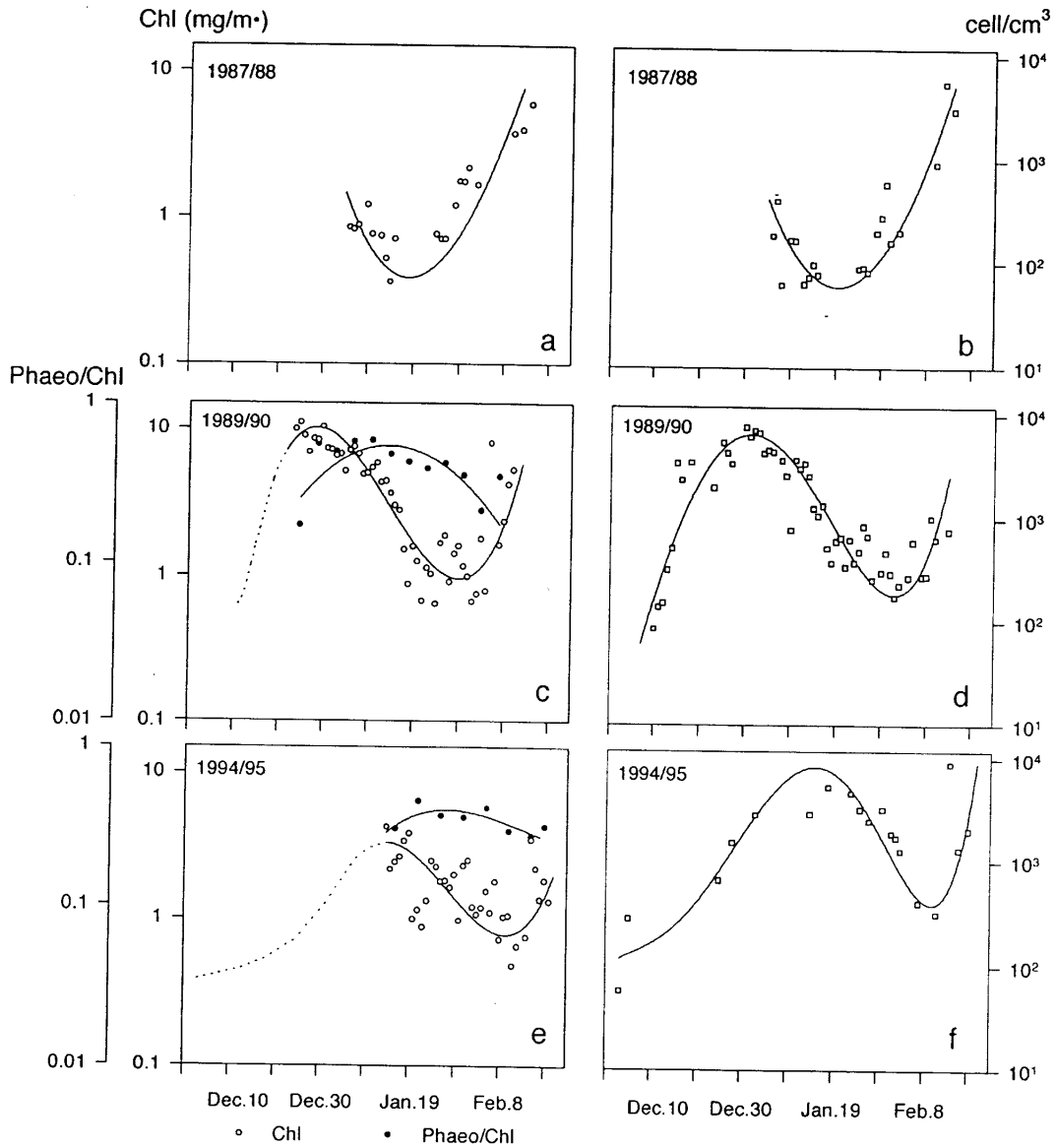
Chl (mg/m·)

cell/cm³

Fig. 7a–f. Chl (a, c, e) and cell density (b, d, f) temporal dynamics at Terra Nova Bay during the 3 years. Data are averages of daily samplings in the surface layer. *Continuous lines* are the interpolating function; *dotted lines* are the reconstruction of Chl dynamics based on cell density dynamics. *Filled symbols* in c and e represent the Phaeo/Chl temporal evolution ratio with its interpolating function. Data were averaged every 4 days

Discussion

The results obtained during the three expeditions show that phytoplankton biomass was generally very high, and during the summer two blooms developed. In Terra Nova Bay, the first was between December and January and the second in February. Satellite images (Arrigo and McClain 1994a,b) and the bimodal annual pattern of phytoplankton depicted by Knox (1990) support these conclusions. The annual cycle of phytoplankton in

the Ross Sea would therefore not appear as the classic unimodal pattern reported in the literature for polar regions.

The N/P ratio in the water was generally similar to the Redfield's theoretical level N/P = 16, and shows (Innamorati and Giovanardi 1992) the minimum variance we have registered. This balance between nutrients is altered during phytoplankton blooms when DIN and DIP concentrations decrease strongly; their ratio increases up to N/P >200, probably as a consequence of a prefer-
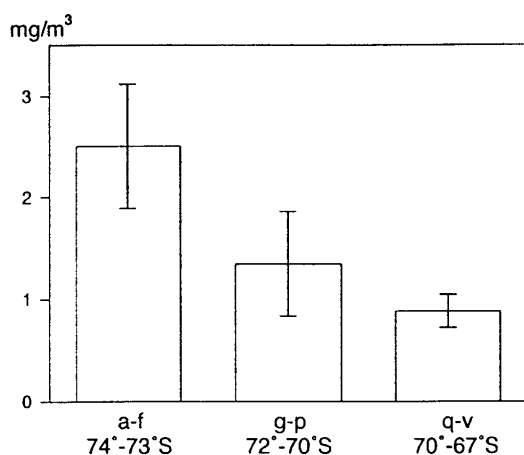
Fig. 8. Histograms representing the mean Chl concentrations of the three groups of stations (a-f, g-p, q-v) during the return journey to New Zealand at the end of January 1990. The corresponding range of latitudes is reported for each group of stations. The *error bars* indicate the ± one standard deviation range

Fig. 9. Distribution of log(Chl/P) vs. log(Chl/N). P = phosphate; N = nitrate + nitrite The 45° straight lines represent the 32, 16 and 8 N/P ratios. The –45° straight lines represent the 0.03, 0.3, 3 and 30 Chl √NP ratios

ential consumption of DIP (luxury consumption?), as noted in the upper layer of other seas we have investigated (Innamorati and Giovanardi 1992). At these very high ratios it is plausible to assume that phosphate must be recycled many times compared to nitrate (e.g. 200/16 = 12.5 times) in order to be assimilated in the N/P = 16 ratio.

The relation between the actual phytoplankton biomass, i.e. Chl, and the potential biomass, i.e. nutrients available in the water, can be represented by the nutrition ratios Chl/P and Chl/N. These ratios are generally lower than any we have found in other seas (Innamorati and Giovanardi 1992), but during blooms they increase up to Chl/P >100 and Chl/N >1 (Fig. 9); similar values are often found in eutrophic areas, such as the NW Adriatic Sea.

The low Chl/P and Chl/N ratios in non-bloom periods can be due to limiting factors other than major nutrient availability, such as low temperature (Eppley 1972; Knox 1994), scarcity of light due to vertical instability (Sverdrup 1953), scarcity of iron (Martin et al. 1990) or silicates (Sullivan et al. 1993). During bloom periods, on the contrary, phytoplankton biomass is very high, similar to production (Lazzara et al., this Vol.), suggesting that limiting factors may disappear. Our observations suggest that the main factor which determines a bloom is the daily irradiance that, as it increases, melts the ice and warms the water rich in nutrients, forming a less dense and eutrophic UML.
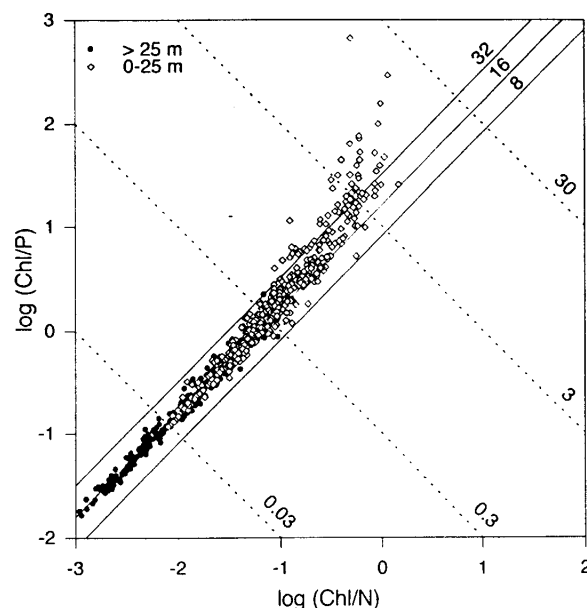
Therefore the stability of the UML favours the availability of light to phytoplankton. Together with an increase in water temperatures, these conditions will favour high phytoplankton growth rates.

The spatial distribution of blooms in the Ross Sea follows the latitudinal pattern of increasing daily irradiance (Fig. 2), which determines the advancement of the melting of the sea ice from the south northward. Blooms in the Ross Sea do follow the melting of the sea ice as regards time and movement (Fig. 3). In the same way, the phases described in Figs. 4 and 5 occur in sequence, beginning and developing in different times at different latitudes, but always starting with the disappearance of the covering of the sea ice.

The major events influencing phytoplankton dynamics can be summarized as follows:

- the irradiance controlling melting of ice produces low-salinity surface waters and an UML is formed which allows phytoplankton growth; phytoplankton biomass reaches its maximum while nutrient concentrations (nitrate, phosphates and silicates) attain their minimum.
- the UML disappears as a consequence of meteorological events, and a well-mixed water condition emerges. In this period a minimum of phytoplankton biomass is recorded.

- a short period of stratification occurs, due to thermocline formation off-shore and low salinity layer in coastal waters, which sustains a second bloom.

In the peak phase (Figs. 4a,d,g, 5b,f,j) the euphotic zone can become less deep than that of the UML so that, in this layer, phenomena of photolimitation occur as the biomass itself severely reduces the PAR. At the same time, an increase in nitrite is observed in the UML. High concentrations of nitrite have been observed as a peculiarity of the Antarctic Ocean (Jacques and Tréguer 1986). In accordance with Harris (1986), this could be the consequence of the scarcity of light, which does not supply the phytoplankton with sufficient energy to reduce the nitrate to nitrite and this to ammonium, so that the cells accumulate nitrite and release it into the water. This mechanism could also be favoured by the concentrations of nitrate (7-$8\,\mu M$), which are high compared to the extremely low levels of phosphate.

The summer minimum (Figs. 4b,e,h, 5e,g,k) occurs as a result of the sharp decrease in the concentration of nutrients, in particular of phosphate, intense feeding activity of the zooplankton (Fonda Umani et al. 1992; Knox 1994), and, above all, because of the disappearance in the stratification. Since the summer minimum occurred during all 3 years of our study, we believe that it is induced by meteorological conditions.

Offshore this phase is fairly long (mid-December–mid-January) and it is therefore probable that this was the condition which was most frequently sampled during the early Antarctic scientific expeditions, providing a picture of scarcity of biomass in the Ross Sea, to which the heterogeneity of the temporal and spatial distribution of the biomass may also have contributed.

The cycle proceeds with an ultimate stabilization of the water column (Figs. 4c,f,i, 5d,h,l) which may have different origins. Offshore, due to the persistance of good weather conditions in the periods of December and January, and in the absence of a marked haline and pycnic discontinuity, the thermocline is formed. In the coastal stations in February, there is, on the other hand, a decrease in salinity at the surface which is probably caused by the melting of floating sea ice transported by the currents northwards. The vertical stabilization is regularly followed by a second bloom, less extensive than the first, which occurs about half way through January at the offshore stations (Lazzara and Nuccio 1994) and towards the beginning of February in Terra Nova Bay.

The evidence for the presence of this second bloom is given by the fact that in all 3 years (Fig. 7), we have observed a minimum phase followed by an increase of phytoplankton biomass. The off-shore sampling also showed a substantial increase in phytoplankton biomass; in areas characterized by average surface values of $0.3\,mg\,m^{-3}$ at the end of December (Innamorati et al. 1991), an average value of $2.5\,mg\,m^{-3}$ was recorded half-way through January (Fig. 8).

The fate of this second bloom is not known. It is probable that it will cease in the ascending phase because of a decrease in irradiance, and a fall in temperatures with the consequent reforming of ice. In any case, the evolution of environmental conditions and biomass define this second resurgence of cell multiplication as the development of a second bloom, the progress of which reaches fairly high quantitative levels of biomass. Finally, the temporal series in Terra Nova Bay and the spatial series in the Ross Sea both contribute to depict a model of temporal successions (as shown in Fig. 7d,f), which we believe can be extended to the entire Ross Sea.

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