FLORE
Repository istituzionale dell'Università degli Studi di Firenze

Spatial and temporal distribution of phytoplankton assemblages in the Ross Sea

(Article begins on next page)

CHAPTER 19

Spatial and Temporal Distribution of Phytoplankton Assemblages in the Ross Sea

C. Nuccio, M. Innamorati, L. Lazzara, G. Mori, and L. Massi[1]

ABSTRACT

The temporal evolution and spatial distribution of phytoplankton assemblages were investigated, in coastal and open waters of the western Ross Sea, during three austral summers. Terra Nova Bay shows a first massive bloom (up to 10^7 cell l^{-1}) of *Fragilariopsis* cf. *curta* between December and January in the receding ice-edge zone and another increase in February, also with the contribution of different species. Phytoplankton shows a patchy distribution, with areas of bloom dominated by diatoms (*Fragilariopsis, Nitzschia*) and *Phaeocystis* sp., and less rich zones, mainly dominated by dinoflagellates and other flagellates. The different phytoplankton assemblages show characteristics corresponding to different stages that alternate during the summer season in the different areas, but which are related to the temporal development of environmental conditions after the melting of the ice.

Introduction

Studies of the phytoplankton distribution in the Ross Sea, particularly in the south-western region, showed as typical features an intense and extensive spring bloom of *Phaeocystis* (El-Sayed et al. 1983; Knox 1994) related to the polynya dynamics (Arrigo and Weiss 1996) and the following diatom-dominated summer bloom (Knox 1994; Garrison et al. 1996). Diatom blooms dominated by few taxa (*Fragilariopsis, Nitzschia*) in the receding ice-edge zone were reported during the summer in the western Ross Sea (Wilson et al. 1986; Carbonell-Moore 1994). Very little information about phytoplankton composition and the dynamics of blooms in the northern open waters has been obtained up until now, except for the reported observations from some inshore stations of Terra Nova Bay (Andreoli et al. 1995).

Our investigations on phytoplankton spatial and temporal distributions in large areas of the northwestern Ross Sea were carried out during three austral summers (1987-88, 1989-90, 1994-95). Previous results had shown the spatial variability between areas of high biomass, with few diatoms (*Fragilariopsis, Nitzschia*) or *Phaeocystis* blooms in different layers of the water column, and less rich zones, the different characteristics of

some biomass indicators (chlorophyll, phaeopigments, particle size and number, cell densities) in different areas, and a new biomass increase in late summer (Innamorati et al. 1990c, 1992; Nuccio et al. 1992; Lazzara and Nuccio 1994).

The temporal evolution of the phytoplankton assemblages in Terra Nova Bay and their spatial distribution in the northern open waters of the Ross Sea are described for the first time in this chapter and are related to previous observations in order to depict the general features of their variations in these waters during summer.

Materials and Methods

The first cruise (R/V Polar Queen; Dec. 1987–Jan. 1988) was conducted on a grid of 40 stations in Terra Nova Bay and along a transect as far as 231 km offshore (Fig. 1a). A second cruise (R/V Cariboo; Nov. 1989–Feb. 1990) covered the route from 45° to 75°S sampling 27 stations (Fig. 1c). In all the stations of the two cruises, samples were collected with a rosette sampler at various depths from the surface down to 200 m. Furthermore, during the Cariboo cruise, continuous measurements of in vivo fluorescence of chlorophyll a (Backscat fluorometer Dr. Haardt) were carried

[1] Laboratorio di Ecologia, Dipartimento di Biologia Vegetale, Università di Firenze. Via P.A. Micheli, 1. 50121 Florence, Italy
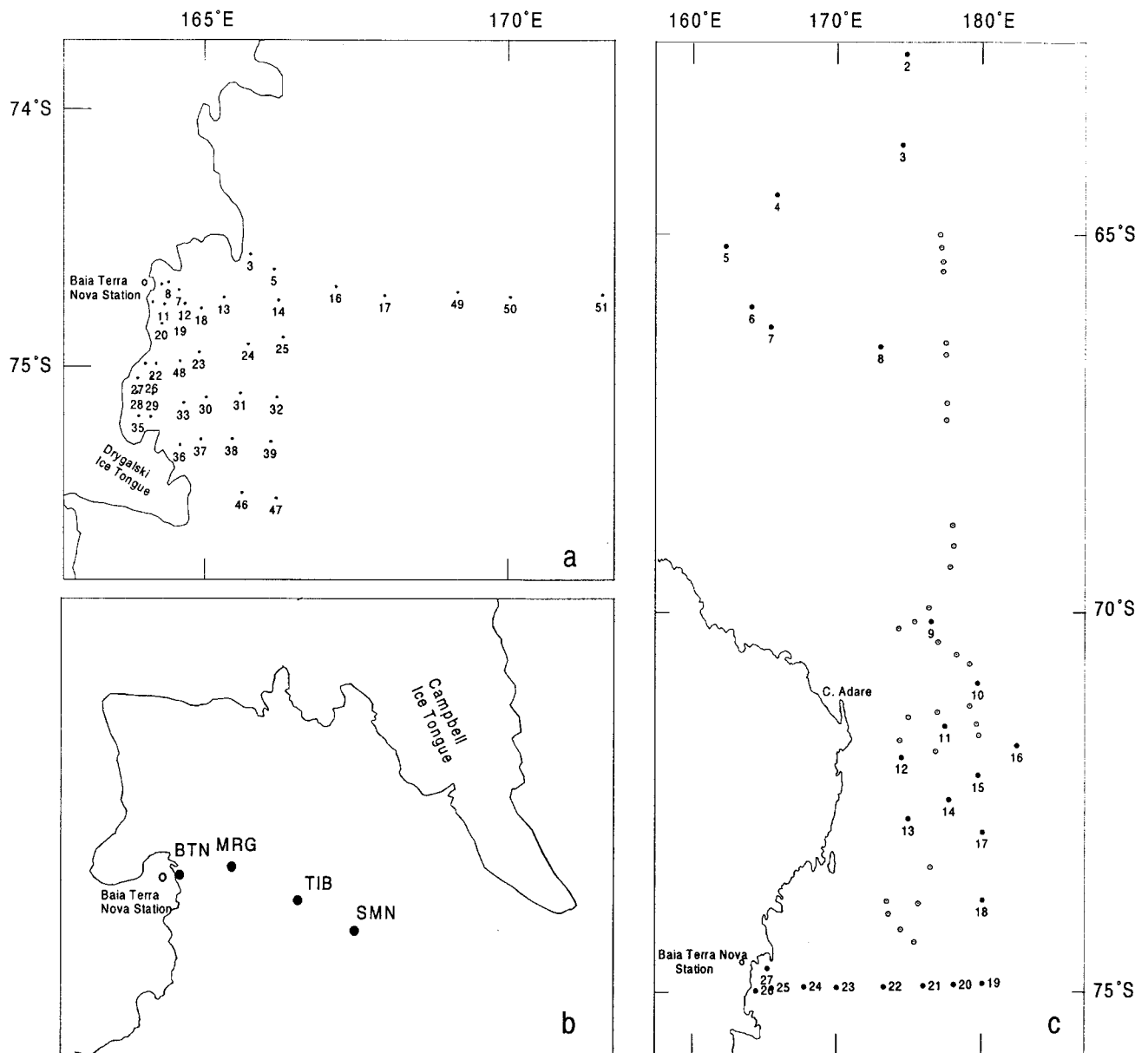
Fig. 1a–c. Maps of station locations. R/V Polar Queen cruise (Dec. 1987–Feb. 1988) in Terra Nova Bay (a); stations sampled from December to February 1989–90 and 1994–95: Baia Terra Nova (*BTN*), Mergellina (*Merg*), Santa Maria Novella (*SMN*), Tibertina (*TIB*) (b); R/V Cariboo cruise (Nov. 1989–Feb. 1990): stations (*closed circles*) sampled during the southwards route and samples (*open circles*) collected from surface layers during the way back (c)

out in the water pumped from a depth of 3 m and 79 samples were collected from this water going both southwards and northwards; only the samples from the way back (Fig. 1c) are discussed here. During this second expedition and in 1994–95, three (BTN, MRG, SMN) and two (BTN, TIB) stations (Fig. 1b), respectively, were sampled in Terra Nova Bay from December to February, so as to follow the temporal trend of the phytoplankton biomass and composition. Station BTN was

sampled near the rocky shore only on the surface, MRG at 0, 10, 25 m and SMN and TIB at 0, 10, 25, 50, 100, 200 m from the R/V Malippo using Niskin bottles. All the data acquired are detailed in Innamorati et al. (1990a,b, 1991, 1994). Chlorophyll concentrations were determined, after filtration (Whatman GF/F) and extraction in acetone (final dilution to 90%), by means of spectrophotometric analysis (Kontron, Uvikon 930), following Lorenzen (1967) as modified by Riemann (1978)

for separate determinations of chlorophyll a and phaeopigments. The sum of the two, named chlorophaeopigment (Chl), is used here. Surface and underwater downwelling, upwelling, and scalar quantum PAR irradiances were measured by means of a photoprobe equipped with three cosine and one spherical meters (LI-COR). Hydrographic data of the Polar Queen and Cariboo cruises are taken from Boldrin and Stocchino (1990) and Artegiani et al. (1992), respectively.

Samples (250 cm³) for microscopic analysis were fixed with Lugol (1987-88 and 1989-90) or neutralized (sodium carbonate) formaldehyde

(1994-95) to the final concentration of 1 and 4%, respectively. Seven hundred samples were analyzed by means of Nikon Diaphot and Zeiss IM35 inverted microscopes on sedimentation chambers (10, 25 or 50 cm³). Taxonomical identification was performed following: Hendey (1937); Manguin (1960); Hasle (1964, 1965a,b); Balech (1976); Sournia et al. (1979); Priddle and Fryxell (1985); Medlin and Priddle (1990). *Phaeocystis* sp. occurred in the non-motile stage, but the single individuals were counted.

Table 1 provides a list of recorded taxa. Some considerations on taxonomic terminology used

Table 1. List of the recorded taxa

Diatoms	Dinoflagellates
Actinocyclus actinochilus (Ehrenb.) Sim.	*Dinophysis* spp.
Achnanthes sp.	Gymnodiniaceae < 20 μm
Amphiprora cf. *kufferathii* Manguin	Gymnodiniaceae > 20 μm
Asteromphalus heptactis (Bréb.) Ralfs	Gymnodiniaceae > 100 μm
Asteromphalus hookerii Ehrenb.	*Gymnodinium* cf. *guttula* Balech
Asteromphalus hyalinus Karsten	*Gyrodinium lachryma* (Meun.) Kofoid & Swezy
Asteromphalus parvulus Karsten	*Gyrodinium* spp. > 20 μm
Centric diatoms spp.	Naked dinoflagellates < 20 μm
Chaetoceros cf. *"bulbosum complex"* sp.	Naked dinoflagellates > 20 μm
Chaetoceros cf. *criophilum* Castr.	*Oxytoxum criophilum* Balech
Chaetoceros cf. *dichaeta* Ehrenb.	*Prorocentrum* cf. *antarcticum* (Hada) Balech
Chaetoceros cf. *neglectum* Karsten	*Protoperidinium* cf. *adeliense* (Balech) Balech
Chaetoceros cf. *neogracile* Van Landingham	*Protoperidinium antarcticum* (Schim.) Balech
Chaetoceros spp.	*Protoperidinium applanatum* (Mangin) Balech
Cocconeis imperatrix A.S.	*Protoperidinium* cf. *archiovatum* (Balech) Balech
Corethron criophilum Castr.	*Protoperidinium* cf. *bellulum* (Balech) Balech
Coscinodiscus spp.	*Protoperidinium defectum* (Balech) Balech
Cylindrotheca closterium (Ehrenb.) Reim. & Lewin	*Protoperidinium* cf. *incertum* (Balech) Balech
Dactyliosolen tenuijunctus Manguin	*Protoperidinium* cf. *mediocre* (Balech) Balech
Eucampia antarctica (Castr.) Mangin	*Protoperidinium* cf. *rosaceum* (Balech) Balech
Fragilariopsis cf. *curta* (Van Heurck) Hustedt	*Protoperidinium* cf. *ps.antarcticum* (Balech) Balech
Fragilariopsis sp. 1 (8 μm)	*Protoperidinium* cf. *unipes* (Balech) Balech
Fragilariopsis spp.	*Protoperidinium* spp.
Grammatophora cf. *charcotii* M. Per.	Thecate dinoflagellates < 20 μm
Licmophora spp.	Thecate dinoflagellates > 20 μm
Melosira sp.	
Naviculacea sp. 20 μm	Prymnesiophyceae
Nitzschia sec. *Nitzschiella* sp.	*Phaeocystis* sp. (cf. *P. antarctica* Karsten)
Nitzschia cf. *subcurvata* Hasle	
Nitzschia sp. *(bilobatae sec.)*	Dictyochophyceae
Nitzschia spp.	*Dictyocha speculum* Ehrenb.
Odontella weissflogii (Jan.) Grunow	
Pennate diatoms > 20 μm	Other flagellates
Proboscia alata (Bright.) Sundström	*Cryptophycea* sp. 1
Pseudonitzschia spp.	*Cryptophyceans* spp.
Rhizosolenia chunii Karsten	Phytoflagellate sp. 7 μm
Rhizosolenia cf. *hebetata* Bailey	Phytoflagellate sp. 10 μm
Rhizosolenia truncata Karsten	Phytoflagellates < 10 μm
Thalassiosira cf. *antarctica* Comber	Phytoflagellates < 20 μm
Thalassiosira sp. 43 μm	Undetermined 20 μm (*Halosphaera* rosettes?)
Thalassiosira spp.	
Thalassiothrix antarctica (Schim.) Karsten	
Undetermined diatoms spp.	

need to be emphasized here. *Fragilariopsis* cf. *curta* is the form in valvar view that prevailed over all the others in the 1987–88 and 1989–90 samples and *Fragilariopsis* spp., the denomination used for the 1994–95 samples, includes both this form in valvar view and a great number of long chains in girdle view which ultimately could not be identified. *Nitzschia* sec. *Nitzschiella* sp. (from now on called *Nitzschia* sp. 1 for brevity) is a tiny form resembling *Cylindrotheca closterium*,

but which we prefer not to assign yet to this latter species, that is quite recognizable, for its larger size, in the 1994–95 samples. *Fragilariopsis* sp. 1 is a very small form (length 7–9 μm) often in doublets, which we assume belongs to *Fragilariopsis cylindrus*. Detailed floristic lists are provided in Innamorati et al. (1994) and Nuccio et al. (1994).

The average ($\bar{x}$) cell densities (Table 2; Fig. 10) and Chl concentrations (Fig. 4) in the 0–25 m layer

Table 2. Biovolume and carbon content of selected diatoms and temporal variation at station SMN of their cell densities, biovolume and biomass in the layer 0–25 m

	μm³	C pg cell⁻¹		μm³	C pg cell⁻¹
Fragilariopsis cf. *curta*	465	39.80	*Pennate diatom* 40 μm	1855	113.61
Nitzschia sp. 1	68	9.27	*Pennate diatom* 90 μm	3463	182.35
Pseudonitzschia spp.	524	43.58	*Rhizosolenia truncata*	39891	1162.69
Eucampia antarctica	28000	889.09	*Thalassiosira* 43 μm	25415	826.15

cell 10³ l⁻¹	Dec.31	Jan.05	Jan.12	Jan.17	Jan.23	Jan.30
Fragilariopsis cf. *curta*	3500	3356	1888	804	564	710
Nitzschia sp. 1	670	215	13	3	0	1
Pseudonitzschia spp.	278	676	724	26	1	9
Total	4448	4247	2625	833	565	720
% of total cell density	95	98	90	83	80	83
Eucampia antarctica	2	0	0	0	0	0
Pennate diatom 40 μm	4	2	7	0	5	9
Pennate diatom 90 μm	2	5	1	1	0	1
Rhizosolenia truncata	1	0	0	0	0	0
Thalassiosira 43 μm	0	0	0	0	1	1

μm³ 10⁶ l⁻¹	Dec.31	Jan.05	Jan.12	Jan.17	Jan.23	Jan.30
Fragilariopsis cf. *curta*	1627.5	1560.5	877.9	373.9	262.3	330.1
Nitzschia sp. 1	45.6	14.6	0.88	0.2	0	0.068
Pseudonitzschia spp.	145.7	354.2	379.4	13.6	0.5	4.7
Total	1818.8	1929.3	1258.1	387.7	262.8	334.8
Eucampia antarctica	56	0	0	0	0	0
Pennate diatom 40 μm	7.4	3.7	12.9	0	9.3	16.7
Pennate diatom 90 μm	6.9	17.3	3.5	3.5	0	3.5
Rhizosolenia truncata	39.9	0	0	0	0	0
Thalassiosira 43 μm	0	0	0	0	25.4	25.4
Total	110.2	21	16.4	3.5	34.7	45.6

Carbon μg l⁻¹	Dec.31	Jan.05	Jan.12	Jan.17	Jan.23	Jan.30
Fragilariopsis cf. *curta*	140.0	134.2	75.5	32.2	22.6	28.4
Nitzschia sp. 1	6.0	1.9	0.12	0.03	0	0.009
Pseudonitzschia spp.	12.2	29.7	31.8	1.1	0.04	0.4
Total	158.2	165.8	107.4	333.3	22.6	28.8
Eucampia antarctica	1.8	0	0	0	0	0
Pennate diatom 40 μm	0.5	0.2	0.8	0	0.6	1.0
Pennate diatom 90 μm	0.4	0.9	0.2	0.2	0	0.2
Rhizosolenia truncata	1.2	0	0	0	0	0
Thalassiosira 43 μm	0	0	0	0	0.8	0.8
Total	3.9	11.0	1.0	0.2	14.0	2.0

were obtained as: $\bar{x} = \dfrac{1}{2z_n}\sum(x_a+x_b)(z_a-z_b)$, where x_a and x_b are the pairwise values in the adjacent sampling depth z_a and z_b at or above the depth z_n considered. The percentages of phytoplankton classes reported for the 0–25- or 10–50-m layers (Figs. 2, 5, 6, 8) were calculated from the cell densities obtained with the same equation.

Cell volumes (Table 2) were computed from linear dimensions, equating shapes to standard geometric figures, or were taken from the literature (Hasle 1969). Biomass ($\mu g\,l^{-1}$ of carbon) was computed from the equation of Strathmann (1967).

Results

The summer evolution of the phytoplankton assemblages (Figs. 2, 3), followed in the north-western waters of Terra Nova Bay (station BTN, MRG, SMN; Fig. 1b), showed the main peak of the bloom between December and January. Biomass and cell densities followed similar trends (Figs. 2a, 3c,d, 4), up to $10\,mg\,m^{-3}$ of Chl and 9.8×10^6 cells l^{-1}, slowly decreasing with their maxima in deeper waters until the end of January and with a tendency to increase again in February.

The phytoplankton assemblages had the same composition down to the depth of 25 m (Fig. 2b), with a contribution of diatoms that was never lower than 80%. *Fragilariopsis* cf. *curta*, up to 7.6 $\times 10^6$ cells l^{-1}, overwhelmed all other diatoms (on average, 83% of the class), and was followed by *Pseudonitzschia* spp. and *Nitzschia* sp. 1 that did not exceed an average of 10%. Only these pennate diatoms reached high densities; the centric species (*Proboscia alata*, *Rhizosolenia truncata*, *Thalassiosira* sp. 43 µm) showed only very scarce abundances. Dinoflagellates represented, on average, 5% of the total density, and increased in mid January up to 2.15×10^5 cells l^{-1}, mainly with naked forms. In the deeper layers (Fig. 2c,d) *Phaeocystis* sp. appeared, and dinoflagellates became relatively more important.

In the surface waters of st. BTN, where it was possible to take samples for a longer period of time, the early phase of the bloom (Fig. 3c,d) was evident from mid-December, when more species showed a growth phase (*Naviculacea* sp., *Fragilariopsis* sp. 1). *Fragilariopsis* cf. *curta* reached its highest contribution in the peak of the bloom. Afterwards, the bloom declined, mainly due to the
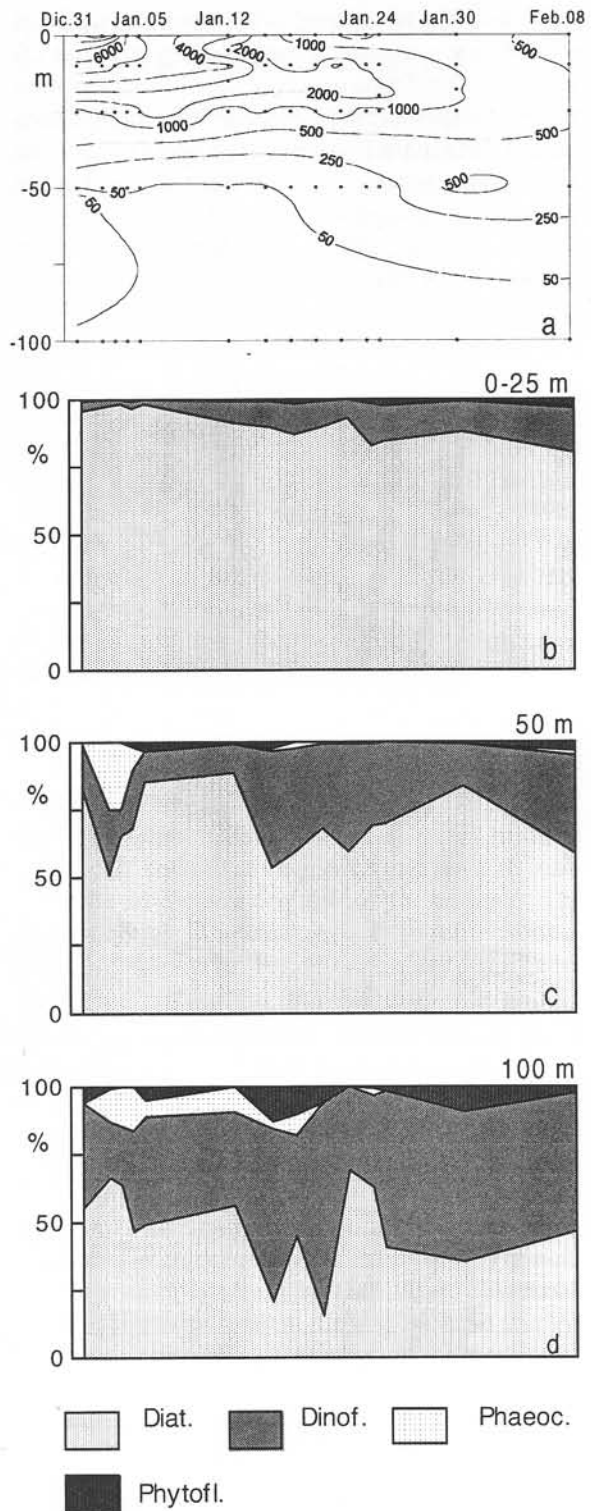

Fig. 2a–d. Vertical distribution of phytoplankton densities (10^3 cells l^{-1}) (a), and percentage composition of phytoplankton classes: 0–25 m (b); 50 m (c); 100 m (d), at st. SMN (Jan.–Feb. 1990)

decrease of the latter species. The increasing trend in February was again due to *Fragilariopsis* cf. *curta* and *Naviculacea* sp., and *Phaeocystis* was present in this period (Fig. 3a). Phytoflagellates showed their main increase at the beginning of the bloom, and a more or less constant decrease until February. Dinoflagellates showed little variability in their density, with a shift towards a greater number of thecate dinoflagellates (*Prorocentrum*

cf. *antarcticum*, *Protoperidinium antarcticum*, *P. applanatum*, *P. defectum*). Not all the 1994–95 samples were analyzed but, although a temporal shift of maxima, the same trend (Fig. 3b,d) and a new increase in February, up to 9.0×10^6 cells l^{-1}, due to *Fragilariopsis*, *Naviculacea* and *Pseudonitzschia*, appeared. It should be noted that the phytoflagellates (Fig. 3d) dominated during December, when they reached 70% of the total
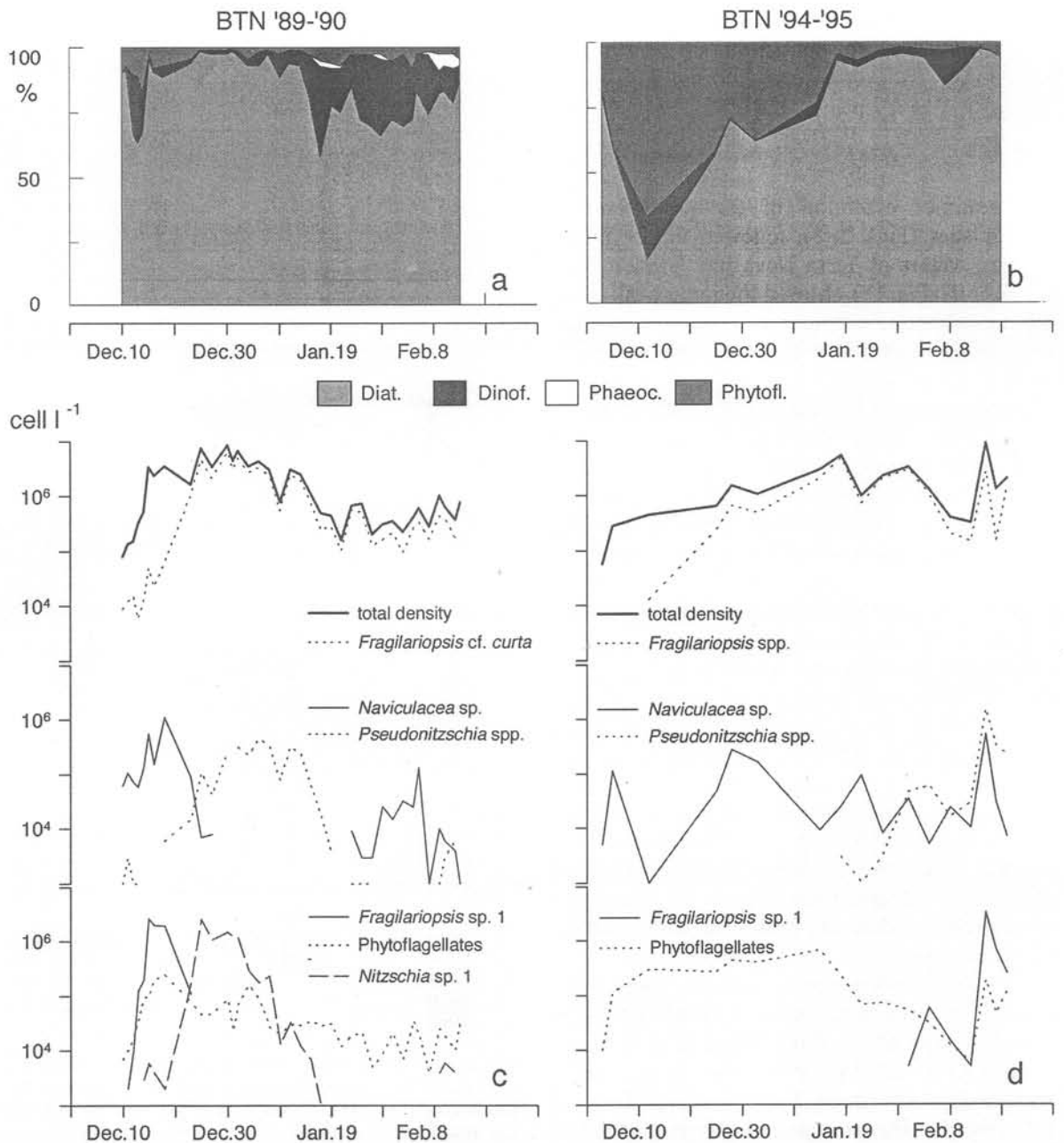

Fig. 3a–d. Surface percentage composition of phytoplankton classes and cell densities (cells l^{-1}) at station BTN during summer 1989–90 (a, c) and 1994–95 (b, d)

density, with forms <10 μm; their increase during the second half of February was due to a bloom of *Dictyocha speculum* with healthy cells forming chains. The greater variety of the February assemblages is reflected by the specific diversity ($\bar{H}$): more than 2 in this case, and not more than 1.8 bits cell^{-1} during the first bloom.

The phytoplankton biomass confirmed this temporal evolution (Fig. 4), and an opposite trend between Chl concentrations and phaeopigment/Chl ratios appeared. The highest values of the ratio were in the declining phase of the first bloom, with ratios up to 0.7, while the lowest ones were evident in the early phases, at the beginning and at the end of the period. Furthermore, the dominant role of *Fragilariopsis* cf. *curta* and a few other diatoms in the bloom was evident not only from cell numbers (always the highest percentages of total phytoplankton densities) but also in terms of biomass (Table 2). During the temporal evolution at station SMN (Table 2), the diatoms of greater size were present with very low densities and their contribution, as cell volume or carbon concentration, mainly in the period of bloom, was

of at least one order of magnitude less than the one of the smallest dominant diatoms.

During the 1989-90 summer, at the same time as the temporal sampling in Terra Nova Bay, a much larger area of the Ross Sea (moving southwards from 20 Dec. to 7 Jan. and northwards in the first fortnight of January) was investigated. Between 70° and 75°S (Fig. 1c), low phytoplankton densities (Fig. 5a) generally less than 10^5 cells l^{-1} were found. The surface composition (Fig. 5b) was different from the other layers (Fig. 5c), because of the scarce presence of *Phaeocystis* sp. as far as the Ross Sea slope (stations 15-18), where there was evidence of the Circumpolar Deep Water upwelling (Jacobs et al. 1970; Artegiani and Paschini 1992) and a nutrient depletion (Catalano 1992). A slight increase, up to 3.0×10^5 cells l^{-1}, of *Phaeocystis* sp. and other flagellates (Fig. 5b) occurred here. The other characteristics were (Fig. 5b,c,d) a very low percentage of diatoms (*Fragilariopsis* cf. *curta*, *Nitzschia* sp. 1, unidentified pennates) and a general dominance of flagellates (naked dinoflagellates, unidentified phytoflagellates, cryptophyceans). Along 75°S quite a different situation (Fig. 6) was found. Moving westward, densities became very high, up to 4.0×10^6 cells l^{-1} at station 23 and over 10^6 cells l^{-1} on the whole western side of the transect. The phytoplankton assemblages had the same composition down to 25 m (Fig. 6b), with the dominance of *Phaeocystis* sp. on the eastern side and of diatoms in the western one, where densities increased. Mainly *Nitzschia* sp. 1 dominated at station 22, and then decreased westward, while *Fragilariopsis* cf. *curta* reached the highest densities towards the coast. *Phaeocystis* sp. increased its relative importance in the deeper layers (Fig. 6c), just as did dinoflagellates, mainly Gymnodiniaceae and *Prorocentrum* cf. *antarcticum* (Fig. 6d).

Only samples from surface layers were collected in the same area on the way back, so that the spatial variation of surface phytoplankton assemblages (Fig. 7) during two consecutive periods, December and January, could be compared. Going southwards (Fig. 7a,c), from about 70°S to Terra Nova Bay (TNB), the surface phytoplankton densities showed the variations just mentioned in relation to the transects (Figs. 5a, 6a). At the beginning of the northward route (Fig. 7b,d), the bloom of *Fragilariopsis* in Terra Nova Bay was still evident. Afterwards, in the Ross Sea open waters, previously poor and dominated by flagellates, *Nitzschia* sp. 1 and *Phaeocystis* sp. produced the
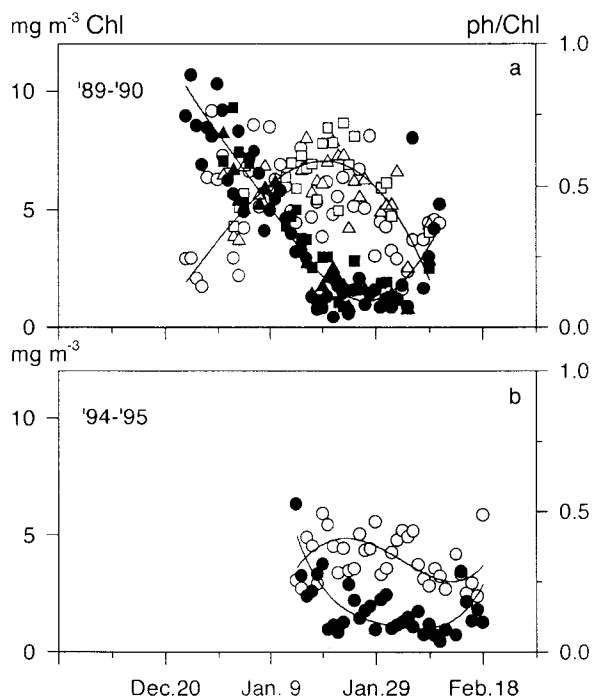

Fig. 4a,b. Temporal evolution of Chl concentrations (*closed symbols*) and phaeopigments/Chl (ph/Chl) ratios (*open symbols*) in the layer 0-25 m of station MRG (*square*) and station SMN (*triangle*), and surface of station BTN (*circles*) 1989-90 (a); surface samples of station BTN 1995 (b)
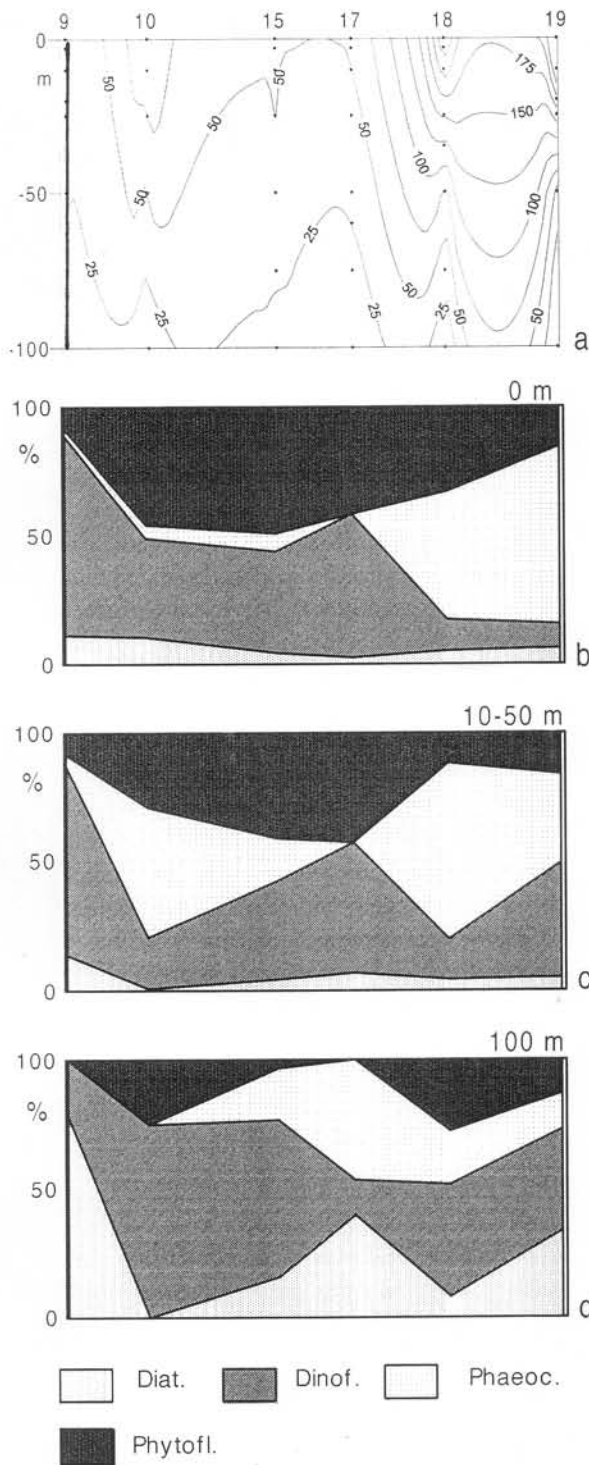
Fig. 5a–d. Vertical distribution of phytoplankton densities (10^3 cells l^{-1}) (a), and percentage composition of phytoplankton classes: 0 m (b), 10–50 m (c), 100 m (d), between 70° and 75°S (stations 9–19)
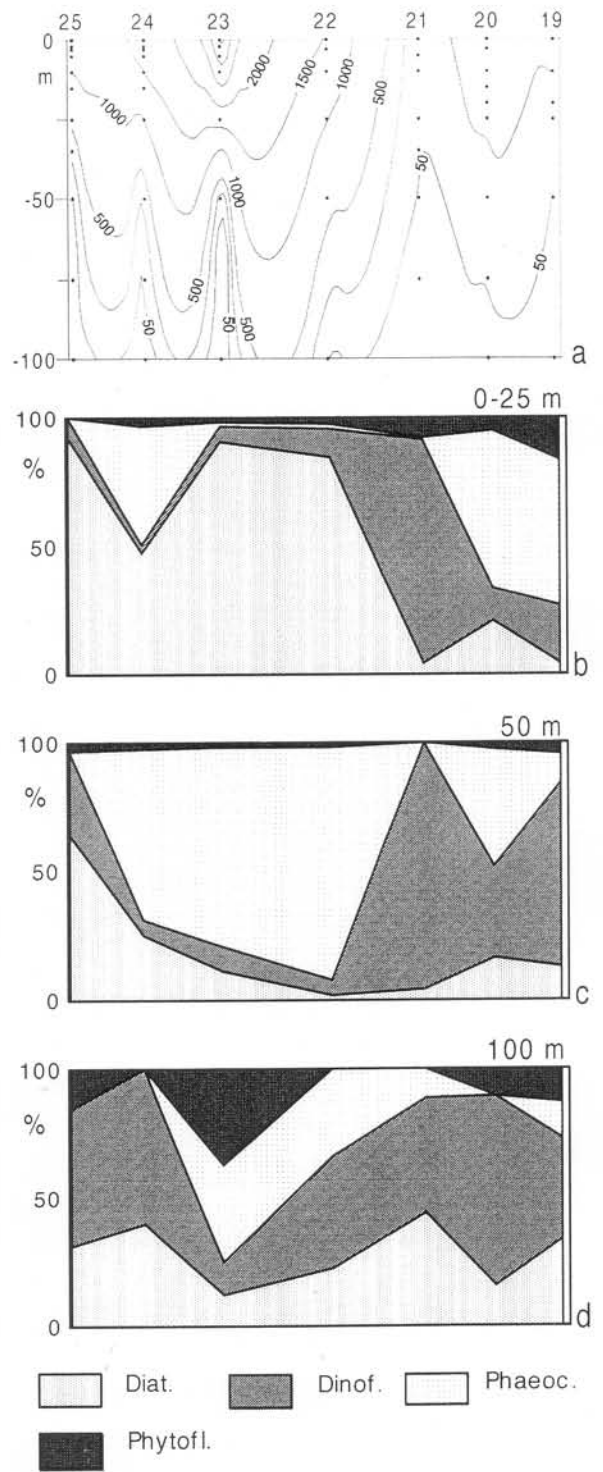
Fig. 6a–d. Vertical distribution of phytoplankton densities (10^3 cells l^{-1}) (a), and percentage composition of phytoplankton classes: 0–25 m (b), 50 m (c), 100 m (d), in the transect along 75°S (stations 19–25)
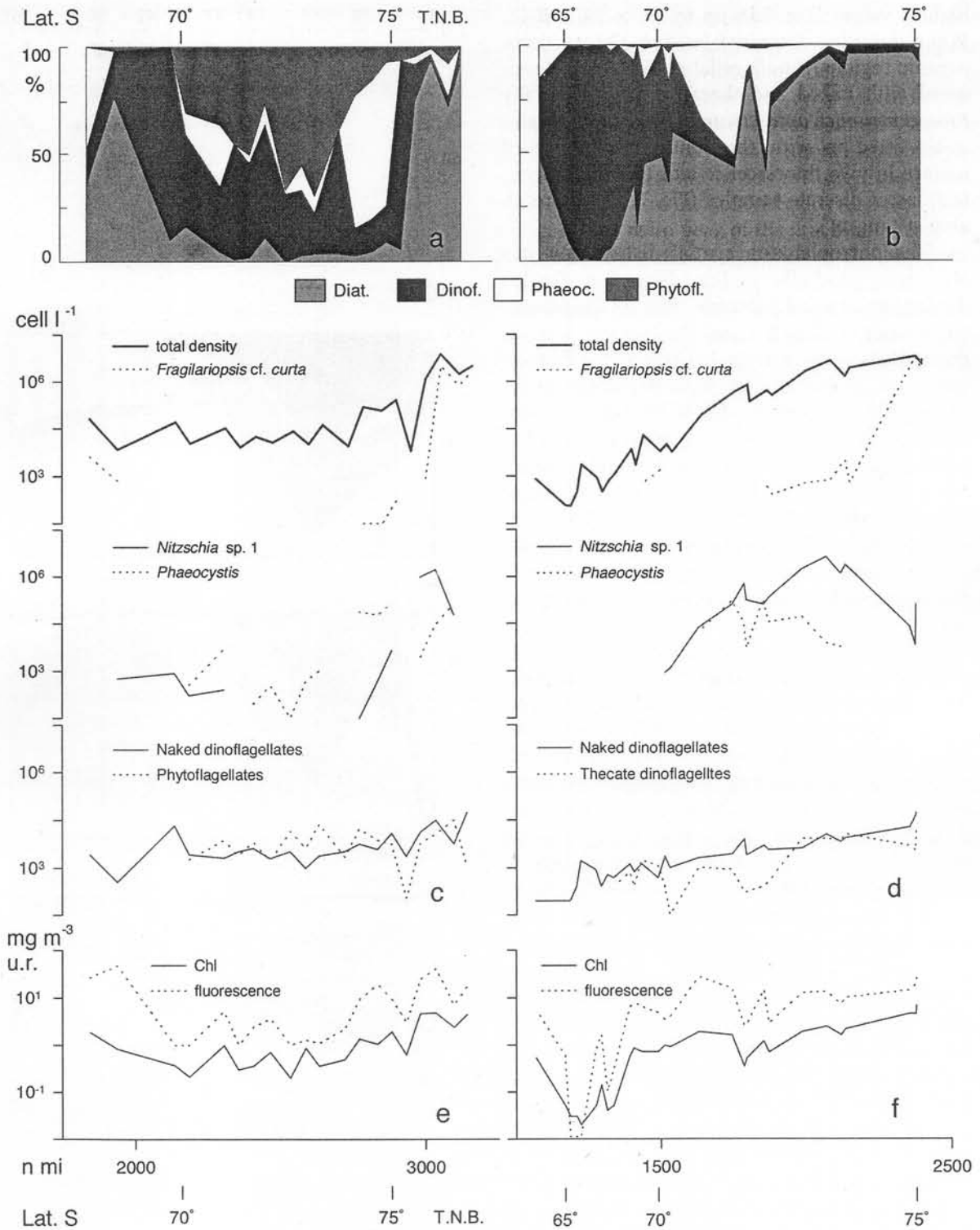
Fig. 7a–f. Surface percentage composition of phytoplankton classes, cell densities (cells l^{-1}), in vivo fluorescence continuous measurements and Chl concentrations from discrete samples along the southwards (a, c, e) and northwards (b, d, f) routes during the Cariboo cruise (Dec. 1989–Jan. 1990)

highest values (Fig. 7d), up to 2.6×10^6 cell l^{-1}. When densities decreased towards the northern oceanic regions, dinoflagellates (Fig. 7b,d) dominated with naked and thecate forms, especially *Prorocentrum* cf. *antarcticum*. This spatial distribution fitted in with the continuous record of surface in vivo fluorescence and the Chl concentrations of discrete samples (Fig. 7e,f) that reach almost $4 \, mg \, m^{-3}$.

The phytoplankton spatial distribution was also investigated all over Terra Nova Bay (Fig. 1a) during January and February 1988. As a representative situation, Fig. 8 shows the transect towards the offshore waters (Fig. 1a) where the highest values of phytoplankton biomass, about 18 mg m^{-3} of Chl, and density, 5.5×10^6 cells l^{-1}, were found. After the nearshore rich waters sampled at the beginning of January (stations 10, 11; Fig. 8a), a larger area (stations 12–16) had low densities of $<2.5 \times 10^5$ cells l^{-1} at the end of January. The richest zone (stations 17–51) was observed during the first fortnight of February, with characteristics of a senescent assemblage for the high percentage of phaeopigments (up to 60% of Chl). In the 0–25 m layer, the phytoplankton assemblage (Fig. 8b) was dominated by *Phaeocystis* sp., up to 2.5×10^6 cells l^{-1}, and diatoms (*Nitzschia* sp. 1 and *Fragilariopsis* cf. *curta*) in the richest zone, dinoflagellates and other flagellates in the poorest one, *Fragilariopsis* cf. *curta* and *Nitzschia* sp. 1 in nearshore waters. From 25 to 50 m (Fig. 8c), *Phaeocystis* sp. increased its densities in this latter zone, while diatoms in the richest part and diatoms and flagellates in the other part of the transect were still dominant. *Phaeocystis* sp. generally increased from 25 to 50 m (Fig. 8d), as already assessed in the Ross Sea (El-Sayed et al. 1983; Smith et al. 1990; Nuccio et al. 1992), and showed a widespread distribution all over Terra Nova Bay (Fig. 9), in assemblages with less mature characteristics, as phaeopigments/ Chl ratios and specific diversity, than the surface diatom ones (Nuccio et al. 1992).

As regards the taxonomic composition of phytoplankton, identification work is still in progress. Table 1 provides a list in which many adopted denominations (Gymnodiniaceae, naked or thecate dinoflagellates, phytoflagellates, etc.) consist of five to six different forms that have not yet been identified. Among the diatoms, only a few pennates (*Fragilariopsis*, *Nitzschia*, *Pseudonitzschia* and *Naviculacea*) dominated the blooms. Dinoflagellates were present mainly with nanoplanktonic naked forms, probably belonging
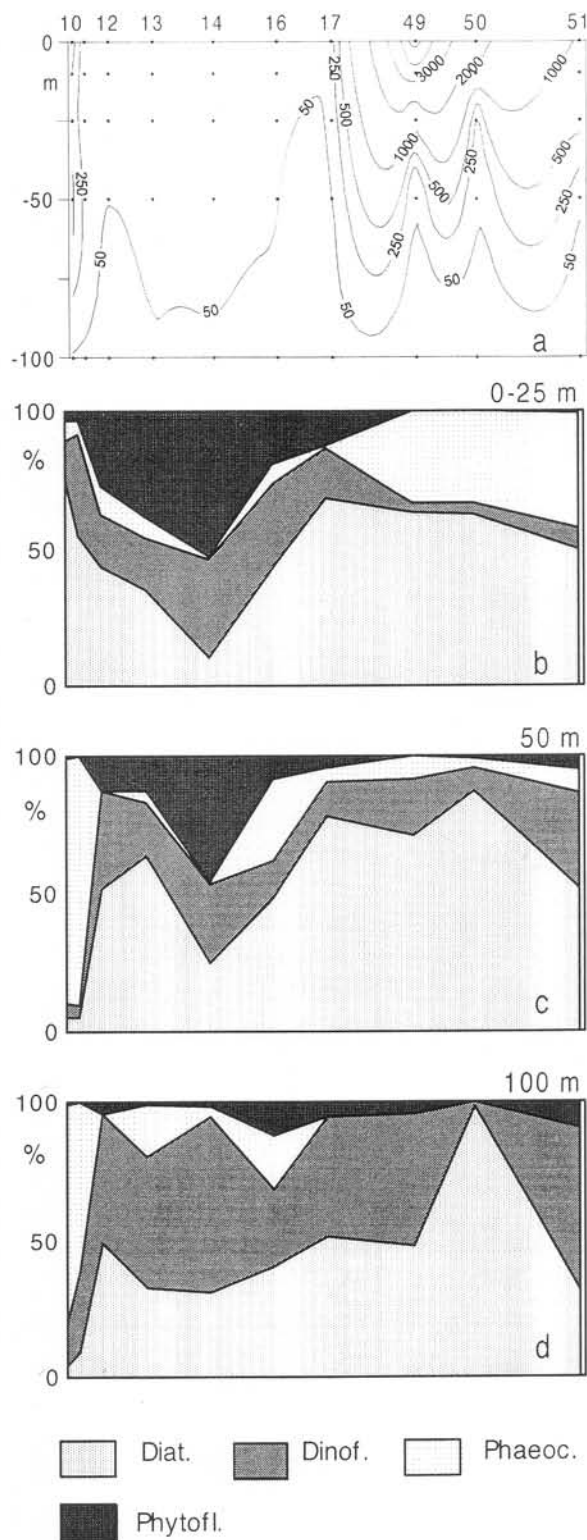

Fig. 8a–d. Vertical distribution of phytoplankton densities (10^3 cells l^{-1}) (a), and percentage composition of phytoplankton classes: 0–25 m (b), 50 m (c), 100 m (d), in the transect sampled during summer 1987–88 (stations 10–51)
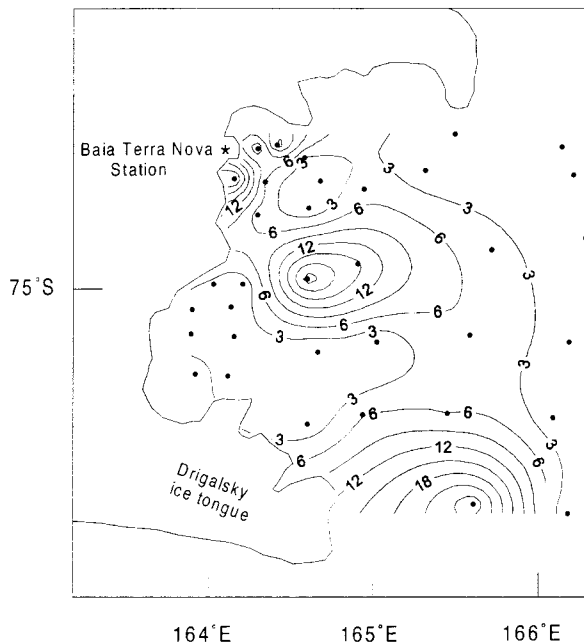
Fig. 9. Horizontal distribution of integrated (0–100 m) densities (10^9 cells m^{-2}) of *Phaeocystis* sp. in Terra Nova Bay

to the *Amphidinium*, *Gymnodinium*, *Gyrodinium* genera. Among thecate dinoflagellates, only *Protoperidinium* was present with many species (Table 1), and represented a consistent fraction of the heterotrophic biomass in Terra Nova Bay (Fonda Umani et al. 1998). The "phytoflagellates" listed in Table 1 probably consist of Prasinophyceans, with many small forms ≤5 μm with one or two flagella and some other tetraflagellates which had a remarkable presence at stations BTN (Fig. 3). In the open waters from 70° to 75°S (Fig. 7), forms with an asymmetric flagellar insertion, therefore assigned to Cryptophyceans, prevailed.

Discussion

In recent years, it has been estimated, mainly from satellite images (Sullivan et al. 1993; Arrigo and McClain 1994), that the western Ross Sea is one of the most productive regions of the Southern Ocean, with intense blooms extending both in space and time, as recognized from our first findings (Innamorati et al. 1990c; 1992a). The bloom develops (Arrigo and McClain 1994) from the second half of December, over the large areas of the pack ice retreating from south to north and from open to coastal waters (Innamorati et al., this Vol.). During January the bloom declines, also if

high pigment concentrations can cover large areas in Terra Nova Bay in late summer. Our data appear to be in agreement with this pattern.

Despite differences in cycle periods and amplitudes during the three summer seasons (probably related to the interannual variability of irradiance and time of ice melting), the phytoplankton cycle in the northwestern Ross Sea shows (Fig. 10) the main peak of the first bloom from the second fortnight of December to the beginning of January, when the daily irradiance reaches its maximum (Innamorati et al., this Vol.). The bloom of *Fragilariopsis* cf. *curta* develops over a large area (Fig. 6a) in the water column of the ice-edge zone (Fig. 11a,d) that is stabilized by the high irradiance and the lowered surface salinity due to the ice melting, with surface maxima in the upper mixed layer that causes a very shallow euphotic zone.

During the 1987–88 summer, only the declining phase of the *Fragilariopsis* bloom was detected (Fig. 10). The most common vertical structure of the phytoplankton assemblages shows (Figs. 8, 11g) the surface dominance of the senescent *Fragilariopsis* bloom and the underlying prevalence of *Phaeocystis* sp. in an early stage in a water column in which the thermal stratification replaced the haline one (Fig. 11l).

The subsequent decrease in the phytoplankton during January (Fig. 10) appears to be related to the change in environmental conditions: in the area of the bloom (Fig. 6a), nutrients were depleted [NO_3 8.4 μM; $Si(OH)_4$ 17.8 μM; PO_4 0.18 μM, Catalano 1992; NO_3 4.2 μM; PO_4 0.03 μM at SMN, Innamorati et al. 1991] and phosphorus in particular may have played a limiting role (N/P >>16; Innamorati et al., this Vol.). This consumption and the characteristics of these assemblages (Lazzara and Nuccio 1994): high phaeopigment/Chl and phaeopigment/particles ratios, average size of the particles and specific diversity, show that the bloom was in senescence.

The large area (Fig. 5) sampled about 2 weeks after ice melt (Hecq et al. 1992) is characterized (Fig. 11b,e) by a deep mixing layer, a deep euphotic zone and a flagellate assemblage in a growing phase (low phaeopigment/Chl ratios, small particles size, low specific diversity; Lazzara and Nuccio 1994) in which *Phaeocystis* sp. is increasing in the surface waters (Figs. 5, 6). The higher concentrations of pheophorbides (Hecq et al. 1992) in these waters and the numerous krill swarms observed along the Ross Sea slope during the Cariboo cruise
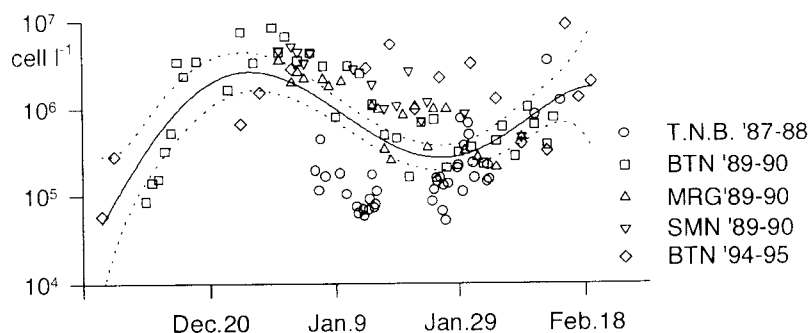
Fig. 10. Temporal evolution of surface (station BTN 1989–90 and 1994–95) and 0–25 m (Terra Nova Bay 1987–88; SMN and MRG 1989–90) phytoplankton densities (cells l⁻¹) in Terra Nova Bay during the three expeditions. Polinomial fitted curve 5th order ($P \leq 0.05$)

(Azzali et al. 1992) lead us to hypothesize, in agreement with other research from the Southern Ocean (Kopczynska 1992), that the phytoflagellate assemblages represent a stage following an initial diatom bloom that had occurred at the ice edge and had been grazed by zooplankton. In fact, some stations (stations 5, 6; Fig. 1c) sampled during the early days of December, in an area of just-broken pack ice, showed a much higher biomass, up to 6 mg m⁻³ of Chl.

In Terra Nova Bay, flagellate assemblages with very low densities prevail towards the end of January (Figs. 8, 11h,m) after the diatom bloom and, at the same time, Phaeocystis sp. reaches its highest densities in the centre of the bay (Fig. 9), where the microzooplankton fraction, probably feeding on nanoplankton, reaches its maximum abundance (Fonda Umani et al. 1998). Afterwards, the late summer increase, in February 1988 and 1990 occurs as in 1995 (Fig. 10); therefore, it does not appear as an episodical trend.

Offshore, in the waters that had been free of ice longer (Fig. 11c,f), Nitzschia sp. 1 and Phaeocystis sp. were growing up to the bloom detected later in the same area in the first half of January (Fig. 7). Furthermore, the high phytoplankton biomass (stations 49–51; Fig. 8a) that developed in the surface mixed layer (Fig. 11i,n) of waters affected by ice melting and depleted nutrients (NO₃ 10.2 μM; PO₄ 0.29 μM; SiO₂ 26 μM, Catalano and Benedetti 1990) in February 1988, had a composition similar (Nitzschia sp. 1, Phaeocystis sp.) to the one blooming in January 1990 (Fig. 7b,d). It could therefore be its later senescent phase.

The waters in which the seasonal cycle was followed (Fig. 1b) appear to have a more stable phytoplankton composition (Figs. 2, 3) during time than the open waters (Figs. 5, 6, 8). It is possible that these waters are restricted by the cyclonic circulation in the Bay (Jacobs et al. 1970; Boldrin and Stocchino 1990) and affected mainly

by surface thermal processes (Boldrin and Stocchino 1990) that support environmental conditions more stable during time than offshore.

The massive bloom of Fragilariopsis cf. curta confirms previous studies on the importance of this species in western Ross Sea ice-edge blooms (Wilson et al. 1986; Carbonell-Moore 1994) and as revealed from sediment traps (Leventer and Dunbar 1996). In February, more species (Nitzschia sp. 1, Naviculacea sp., Fragilariopsis sp. 1, Pseudonitzschia spp., Phaeocystis sp., Dictyocha speculum), together with Fragilariopsis increase. Also Phaeocystis shows an intense diffusion in the subeuphotic layers of stratified waters during the first period of the season (Figs. 2, 11c,g), but also up to the surface in deep mixed waters or later in the season (Figs. 3, 5, 8, 11b,i).

Summarizing the major findings, we can conclude that: the early summer bloom of Fragilariopsis cf. curta develops when conditions of irradiance and temperature are not limiting and the melting of pack ice and the warming of surface layers lead to water column stability that allows phytoplankton growth; this bloom extends over large areas of the retreating ice edge and its decline can be related to nutrient depletion, zooplankton grazing and to the loss of water stability mainly due to meteorological perturbations; after this bloom, flagellates dominate the phytoplankton assemblage in conditions of a mixed column water and a bloom of Phaeocystis spreads in Terra Nova Bay; another bloom, with phytoplankton composition different from the first one, develops when availability of new nutrients and conditions of water stability occur.
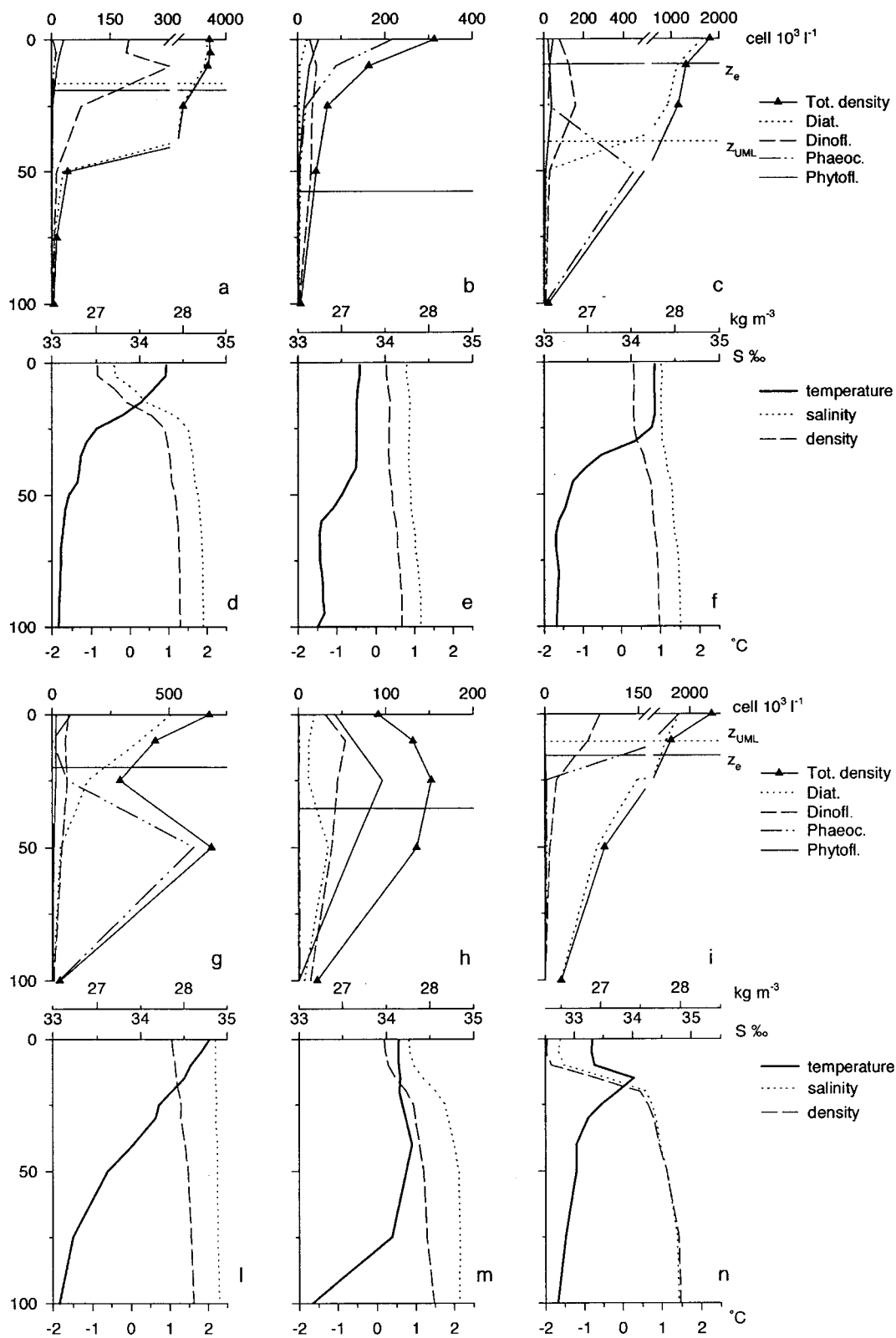
Fig. 11a–n. Representative profiles of phytoplankton classes and total densities (a, b, c, g, h, i) and corresponding profiles (d, e, f, l, m, n) of temperature, salinity and density. Station 26, Jan. 1990 (a, d); station 19, Dec. 1989 (b, e); station 22, Jan. 1990 (c, f); station 10, Jan. 1988 (g, l); station 14, Jan. 1988 (h, m); station 50, Feb. 1988 (i, n). The depths of upper mixed layer (z_{UML}) and euphotic zone (z_e) are indicated

References

Andreoli C, Tolomio C, Moro I, Radice M, Moschin E, Bellato S (1995) Diatoms and dinoflagellates in Terra Nova Bay (Ross Sea-Antarctica) during austral summer 1990. Polar Biol 15: 465–475

Arrigo KR, McClain CR (1994) Spring phytoplankton production in the Western Ross Sea. Science 266: 261–263

Arrigo KR, Weiss AM (1996) Interannual variation in pigment concentration and primary production in the Western Ross Sea as seen by the Nimbus 7 Coastal Zone Color Scanner. EOS Trans AGU, 76 (3): 137

Artegiani A, Paschini E (1992) Condizioni oceanografiche nel settore neozelandese dell'Oceano Antartico durante l'estate australe 1989–90. In: Gallardo VA, Ferretti O, Moyano HI (eds) Oceanografía en Antártica. ENEA-PNRA-EULA, Concepción, Chile, pp 33–38

Artegiani A, Azzolini R, Paschini E, Creazzo S (1992) Physical oceanographic conditions in the Southern Pacific Ocean and in the Western Ross Sea. In: National Scientific Commission for Antarctica (ed) Oceanographic Campaign 1989/90, Data Rep Part II, Genova, pp 5–62

Azzali M, Kalinowski J, Castagnani R (1992) Biomass of krill in the Ross Sea (Pacific sector) in relation to BIOMASS FIBEX/SIBEX results. In: Gallardo VA, Ferretti O, Moyano HI (eds) Oceanografía en Antártica. ENEA-PNRA-EULA, Concepción, Chile, pp 331–338

Balech E (1976) Clave ilustrada de Dinoflagelados Antarticos. Publ Inst Antart Argent 11: 1–99

Boldrin A, Stocchino C (1990) On the hydrological characteristics of Terra Nova Bay. In: National Scientific Commission for Antarctica (ed) Oceanographic Campaign 1987–88, Data Rep Part I, Genova, pp 11–57

Carbonell-Moore MC (1994) Phytoplankton of an ice-edge bloom in the Ross Sea, with special reference to the elemental composition of antarctic diatoms. EOS Trans AGU, 75 (3): 201

Catalano G (1992) L'attività del gruppo di oceanografia chimica nell'ambito delle Campagne Oceanografiche Italiane in Antartide. In: Gallardo VA, Ferretti O, Moyano HI (eds) Oceanografía en Antártica. ENEA-PNRA-EULA, Concepción, Chile, pp 59–70

Catalano G, Benedetti F (1990) Distribution of nutrients in the Terra Nova Bay and in the Ross Sea. In: National Scientific Commission for Antarctica (ed) Oceanographic Campaign 1987/88, Data Rep Part I, Genova, pp 59–83

El-Sayed S, Biggs DC, Holm-Hansen O (1983) Phytoplankton standing crop, primary productivity, and near-surface nitrogenous nutrient fields in the Ross Sea, Antarctica. Deep Sea Res 30 8A: 871–886

Fonda Umani S, Monti M, Nuccio C (1998) Microzooplankton biomass distribution in Terra Nova Bay, Ross Sea (Antarctica). J Mar Syst 17: 289–303

Garrison DL, Mathot S, Gowing MM, Kunze H (1996) Phytoplankton and microzooplankton community structure in the Ross Sea polynya: November-December, 1994. EOS Trans AGU, 76 (3): 137

Hasle GR (1964) Nitzschia and Fragilariopsis species studied in the light and electron microscopes. I. Some marine species of Nitzschiella and Lanceolatae. Skr Nor Vidensk Akad Oslo Mat Naturvidents Kl NS 16: 1–48

Hasle GR (1965a) Nitzschia and Fragilariopsis species studied in the light and electron microscopes. II. The group Pseudonitzschia. Skr Nor Vidensk Akad Oslo Mat Naturvidents Kl NS 18: 1–45

Hasle GR (1965b) Nitzschia and Fragilariopsis species studied in the light and electron microscopes. III. The genus Fragilariopsis. Skr Nor Vidensk Akad Oslo Mat Naturvideusts Kl NS 21: 1–49

Hasle GR (1969) An analysis of the phytoplankton of the Pacific Southern Ocean: abundance, composition, and distribution during the Brattegg expedition, 1947–1948. Hvalradets Skr 52: 1–168

Hecq JH, Magazzù G, Goffart A, Catalano G, Vanucci S, Guglielmo L (1992) Distribution of planktonic components related to structure of water masses in the Ross Sea during the Vth ITALIANTARTIDE expedition. Atti IX Congr Ass Ital Oceanogr Limnol, Lang, Genova, pp 665–678

Hendey NI (1937) The plankton diatoms of the southern seas. Disc Rep 16: 151–364, VI–XIII

Innamorati M, Mori G, Lazzara L, Nuccio C, Lici M, Vanucci S (1990a) Ecology of Phytoplankton. In: National Scientific Commission for Antarctica (ed), Oceanographic Campaign 1987–88, Data Rep Part I, Genova, pp 161–238

Innamorati M, Mori G, Lazzara L, Nuccio C, Lici M, Catalano G, Benedetti F (1990b) Phytoplankton Ecology in the Ross Sea. In: National Scientific Commission for Antarctica (ed), Oceanographic Campaign 1987/88, Data Rep Part II, Genova, pp 9–63

Innamorati M, Mori G, Lazzara L, Vanucci S (1990c) Eutrofia ed oligotrofia nell'Oceano Antartico. Oebalia XVI-1: 153–162

Innamorati M, Lazzara L, Mori G, Nuccio C, Saggiomo V (1991) Phytoplankton ecology. In: National Scientific Commission for Antarctica (ed) Oceanographic Campaign 1989/90, Data Rep Part I, Genova, pp 141–252

Innamorati M, Lazzara L, Massi L, Mori G, Nuccio C, Saggiomo V (1992) Indagine sulla biomassa fitoplanctonica nel Mare di Ross in relazione ai fattori ambientali. In: Gallardo VA, Ferretti O, Moyano HI (eds) Oceanografía en Antártica. ENEA-PNRA-EULA, Concepción, Chile, pp 235–252

Innamorati M, Lazzara L, Massi L, Mori G, Nuccio C, Saggiomo V, Cartei P, Franchini L, Gamba C (1994) Phytoplankton ecology: particles, gilvin, fluorescence spectra, irradiance and phytoplankton specie density in the Ross Sea. Ocean Camp 1989–90. In: National Scientific Commission for Antarctica (ed) 1989–90, Data Rep Part III, Genova, pp 101–178

Jacobs SS, Amos AF, Bruchhausen PM (1970) Ross Sea oceanography and Antarctic bottom water formation. Deep Sea Res 17: 935–962

Knox GA (1994) The biology of the Southern Ocean. Cambridge University Press, Cambridge

Kopczynska EE (1992) Dominance of microflagellates over diatoms in the Antarctic areas of deep vertical mixing and krill concentration. J Plankton Res 14 (8): 1031–1054

Lazzara L, Nuccio C (1994) Relazioni tra particellato, biomassa e popolamenti fitoplanctonici nel Mare di Ross durante la fioritura estiva. Atti X Congr Ass Ital Oceanogr Liminol. Lang, Genova, pp 655–665

Leventer A, Dunbar RB (1996) Factors influencing the distribution of diatoms and other algae in the Ross Sea. J Geophysical Res 101 (C8): 18489–18500

Lorenzen CJ (1967) Determination of chlorophyll and phaeophytin spectrophotometric equations. Limnol Oceanogr 12: 343–346

Manguin E (1960) Les diatomées de la Terre Adélie. Campagne du Commandant Charcot 1949–1950. Ann Sci Nat (Bot) 12 (1): 223–363

Medlin LK, Priddle J (1990) Polar marine diatoms. British Antarctic Survey, Cambridge

Nuccio C, Innamorati M, Lazzara L, Mori G (1992) Popolamenti fitoplanctonici nella Baia di Terra Nova, Mare di Ross. In: Gallardo VA, Ferretti O, Moyano HI (eds) Oceanografí a en Antártica. ENEA-PNRA-EULA, Concepción, Chile, pp 253–262

Nuccio C, Innamorati M, Mori G, Lazzara L, Nizzi Grifi G (1994) Phytoplankton ecology: species density in the Ross Sea. Oceanographic Campaign 1987–88. In: National Scientific Commission for Antarctica (ed) Oceanographic Campaign 1987–88. Data Rep Part III, Genova, pp 5–48

Priddle J, Fryxell G (1985) Handbook of the common plankton diatoms of the Southern Ocean: centrales except the genus *Thalassiosira*. British Antarctic Survey, Cambridge

Riemann B (1978) Carotenoid interference in the spectrophotometric determination of chlorophyll degradation products from natural populations. Limnol Oceanogr 23 (5): 1059–1066

Smith WO Jr, Kelly HP, Rich JH (1990) Chlorophyll distribution and primary productivity in the Ross Sea, austral summer 1990. Antarct J US 25 (5): 179–182

Sournia A, Grall JR, Jacques G (1979) Diatomées et dinoflagellés planctoniques d'une coupe méridienne dans le sud de l'océan Indien (campagne Antiprod I du Marion-Dufresne, mars 1977). Bot Mar 22: 183–198

Strathmann RR (1967) Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnol Oceanogr 12: 411–418

Sullivan CW, Arrigo KR, McClain CR, Comiso JC, Firestone J (1993) Distributions of phytoplankton blooms in the Southern Ocean. Science 262: 1832–1837

Wilson DL, Smith OW Jr, Nelson DM (1986) Phytoplankton bloom dynamics of the Western Ross Sea ice edge. I. Primary productivity and species-specific production. Deep Sea Res 33 (10): 1375–1387