ELSEVIER

Journal of Marine Systems 36 (2002) 29–49

JOURNAL OF MARINE SYSTEMS

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Particulate matter and plankton dynamics in the Ross Sea Polynya of Terra Nova Bay during the Austral Summer 1997/98

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Received 13 July 2001; accepted 20 March 2002

Abstract

The structure and variability of the plankton community and the distribution and composition of suspended particulate matter, were investigated in the polynya of Terra Nova Bay (western Ross Sea) during the austral summer 1997/1998, with the ultimate objective of understanding the trophic control of carbon export from the upper water column. Sampling was conducted along a transect parallel to the shore, near the retreating ice edge at the beginning of December, closer to the coast at the beginning of February, and more offshore in late February. Hydrological casts and water sampling were performed at several depths to measure total particulate matter (TPM), particulate organic carbon (POC), biogenic silica (BSi), chlorophyll *a* (Chl *a*) and phaeopigment (Phaeo) concentrations. Subsamples were taken for counting autotrophic and heterotrophic pico- and nanoplankton and to assess the abundance and composition of microphyto- and microzooplankton. Statistical analysis identified two major groups of samples: the first included the most coastal surface samples of early December, characterized by the prevalence of autotrophic nanoplankton biomass; the second included all the remaining samples and was dominated by microphytoplankton. With regard to the relation of the plankton community composition to the biogenic suspended and sinking material, we identified the succession of three distinct periods. In early December *Phaeocystis* dominated the plankton assemblage in the well-mixed water column, while at the retreating ice-edge a bloom of small diatoms (ND) was developing in the lens of superficial diluted water. Concentrations of biogenic particulates were generally low and confined to the uppermost layer. The very low downward fluxes, the near absence of faecal pellets and the high Chl *a*/Phaeo ratios suggested that the herbivorous food web was not established yet or, at least, was not working efficiently. In early February the superficial pycnocline and the increased water column stability favoured the development of the most intense bloom of the season, essentially sustained by micro-sized diatoms (MD). The shift of the autotrophic community toward this size component produced major changes in the composition of particulate matter and determined its export to depth. The particulate organic carbon (POC)/chlorophyll *a* (Chl *a*) and Chl *a*/Phaeo ratios more than halved, biogenic silica (BSi)/POC and BSi/Chl *a* strongly increased. Downward fluxes were greatly enhanced (reaching the yearly maximum) and essentially occurred via faecal pellets, underscoring the high efficiency of the herbivorous food web. In late February the deepening of the pycnocline, together with the decrease in light intensity, contributed to halting the diatom bloom. The biomass of small heterotrophs (HNF and MCZ) significantly increased relative to the previous period, favouring the shift toward a mistivorous food web (sensu [Ophelia 41 (1995) 153]) and resulting in the retention of biogenic matter in the superficial layer. Only in early February, with the increase in

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PII: S0924-7963(02)00133-1

the size of primary producers (essentially represented by micro-sized diatoms), did the grazing food web become efficient [S. Afr. J. Mar. Sci. 12 (1992) 477], fuelling the long-lived carbon pool and enhancing export to depth (and hence carbon sequestration) via the sinking of large diatoms and high amounts of faecal pellets. The conditions predominating in the Terra Nova Bay polynya in mid-summer probably increased the efficiency of the CO_2 pump, possibly causing the Bay to act as a carbon sink.

Keywords: Particulate matter; Plankton dynamics; Carbon export; Terra Nova Bay (Ross Sea) polynya; Austral summer

1. Introduction

The Southern Ocean is considered a crucial area in the contemporary global cycle of matter (Sullivan et al., 1993). The flux of biogenic carbon towards large metazoans (i.e. renewable resources) and into deep waters (i.e. carbon sequestration), plays a pivotal role in regulating the concentration of atmospheric CO_2 and is nowadays a matter of great interest (see Legendre and Michaud, 1998; Hanson et al., 2000; Tréguer et al., in press). Volk and Hoffert (1985) identified three types of mechanisms, the so-called "pumps" that can drive CO_2 from the atmosphere into the deep ocean. The solubility (physical) pump is particularly active in areas of deep-water formation, resulting from the increase in water density produced by a temperature decrease (e.g. at high latitudes) and/or by a salinity increase (e.g. in latent-heat polynyas, such as Terra Nova Bay). The other two types of pump are of biological nature. The carbonate pump depends on the sedimentation to depth of organisms with calcareous tests. The soft-tissue pump (the so-called CO_2 biological pump) is activated by the photosynthetic incorporation of inorganic carbon into organic molecules by microscopic algae followed by the export of phytodetritus to deep waters. Legendre and LeFèvre (1992) proposed to classify the pools of biogenic carbon in the ocean on the basis of their turnover times (i.e. the time elapsed between the photosynthetic uptake of carbon and its return as CO_2 to the atmosphere) and defined three main compartments: short-lived organic carbon ($<10^{-2}$ years), long-lived organic carbon (10^{-2}–10^{2} years) and sequestered biogenic carbon ($>10^{2}$ years). Short-lived organic carbon consists of organisms with high turnover rates and labile dissolved organic carbon, and is transported essentially through the microbial food web (small phytoplankton–heterotrophic bacteria–protozoa). Long-lived organic carbon includes renewable marine resources and transits through the grazing food chain (Azam, 1998). Sequestered biogenic carbon comprises a variety of forms, such as organic remains buried in sediments, inorganic deposits of biogenic origin, refractory dissolved organic matter and dissolved CO_2 in deep waters resulting from deep respiration (Legendre, 1996). Primary production may be respired within the euphotic layer, or can be channeled by vertical export of sinking materials and/or through the biomass of larger consumers. The size of photosynthetic products, i.e. large (>2–5 μm) or small (<2–5 μm) phytoplankton, and the nature of dissolved organic carbon (labile or refractory) can strongly influence the incorporation of biogenic carbon into the short-lived, long-lived or sequestered pools.

Polynyas are areas of increased phytoplankton production, which can be considered as "hot spots" of biological productivity in ice-covered seas. Despite their limited overall surface area, these zones are known to greatly contribute to the primary production of polar seas. In polynyas, both bacteria and microzooplankton can be tightly coupled to phytoplankton development (e.g., Deibel et al., 2000; Bjornsen and Nielsen, 2000; Nielsen et al., 2000) influencing the fate of primary production and consequently the fuelling of the grazing or detritus food webs. This can yield important consequences for the whole system, driving its behavior in terms of utilisation or export of biogenic matter, and has also implications for carbon and nitrogen cycling. In ice-edge zones, the melting of sea ice releases ice organisms into the water column and hence can play a significant role in seeding the phytoplankton spring bloom (Spindler and Dieckmann, 1994). Algae within the sea ice, mostly pennate diatoms (Horner et al., 1992), are responsible for a large proportion of

the total annual primary production of the Southern Ocean (>20%, Legendre, 1996). The total production associated with sea ice (i.e. within the ice, in the under-ice water column and at ice edges) accounts for >80% of the total production of the Southern Ocean (Legendre et al., 1992). In the western Ross Sea, blooms exceeding 20 mg Chl *a* m^{-3} have been observed to extend several hundred kilometers eastward of the retreating ice edge (Smith and Nelson, 1985; Nelson and Treguer, 1992; Arrigo and McClain, 1994). In this area, where overwintering krill seems to be absent or scarce, surface waters are seeded by ice diatoms and *Phaeocystis* at the time of ice melting, and intense blooms dominated by these taxa develop (Legendre, 1996).

This study focuses on the area of the Terra Nova Bay polynya, which was investigated in the austral summer 1997/1998, during the XIII Italian Expedition. Terra Nova Bay is the site of a coastal, annually recurring polynya in the western Ross Sea that was first described by Bromwich and Kurtz (1984) and more recently described in terms of water masses distribution and thermohaline variability by Budillon and Spezie (2000). Previous studies in this area (Innamorati et al., 1991, 1999) have shown the presence of a high chlorophyll maximum in late December, followed by a temporary decrease in phytoplankton biomass and then by another maximum in February. The first bloom is dominated by microphytoplankton, while the second is characterized by an increasing percentage of nanoplankton (Innamorati et al., 1992; Nuccio et al., 1992). The water column stability has been observed to play an important role in enhancing and maintaining the bloom over the polynya (Catalano et al., 1997). A very large (16,000 km^2) and persistent *Phaeocystis* bloom, with average pigment concentration exceeding 10 mg m^{-3}, has been detected in this area from the middle to the end of January (Arrigo and McClain, 1994). Equal proportions of *Phaeocystis* and diatoms were observed in the early stage of the spring bloom (20–21 December), while afterwards (4–5 January) the community composition shifted towards a diatom-dominated assemblage, in response to the shoaling of the mixed layer (Arrigo et al., 1999). Picophytoplankton (<2 μm) is generally negligible (Vanucci and Bruni, 1998), and nanoplankton is characterized by the dominance of 3–5-μm-size cells (Vanucci and Bruni, 1999). The microzooplankton community distribution appears strongly influenced by shifts in the nano-/microphytoplankton alternating dominance, with the highest abundances being related to the highest occurrence of small autotrophs (Fonda Umani et al., 1998; Monti and Fonda Umani, 1999). This study describes the changes in suspended particulate matter composition and the evolution of the plankton assemblage throughout the austral summer 1997/1998. The ultimate objective is to understand the trophic control of carbon export in the Terra Nova Bay polynya water column, from late spring to summer.

2. Methods

The results reported here are part of an interdisciplinary study conducted in the framework of the CLIMA Project (Climatic Long-term Interactions of the Mass balance in Antarctica), under the umbrella of the Italian National Program for Antarctic Research (PNRA). The oceanographic cruise was conducted aboard the R/V Italica from November 1997 to March 1998. Terra Nova Bay was sampled during three periods: early December 1997 (first period, also referred to as "late spring"); early February 1998 (second period, or "mid-summer"); late February 1998 (third period, or "late summer"). During the first period, samples were taken along a S–N transect parallel to the coast (Sts. 4, 2, 11, and 9) between 164° and 165°E, and 75°15′ and 74°45′ S (Fig. 1). In December 1997, the polynya was limited to a smaller area than in previous years, due to the absence of katabatic winds. At the time of our sampling, the ice-free area was spreading northward, so that the northernmost station of the transect (St. 9) was in proximity of the receding ice-edge. During the second leg (early February), the sampling area was wider (from 163°40′ to 166°20′ E, and from 75°20′ to 74°40′ S) (Fig. 1) and patches of frazil and grease ice started to appear. The stations sampled in early February included a nearshore transect (Sts. 135, 133, and 132 from S to N) and an offshore site (St. 148). The stations visited in late February included an offshore transect from the edge of the Drygalski Ice Tongue to Cape Washington (Sts.

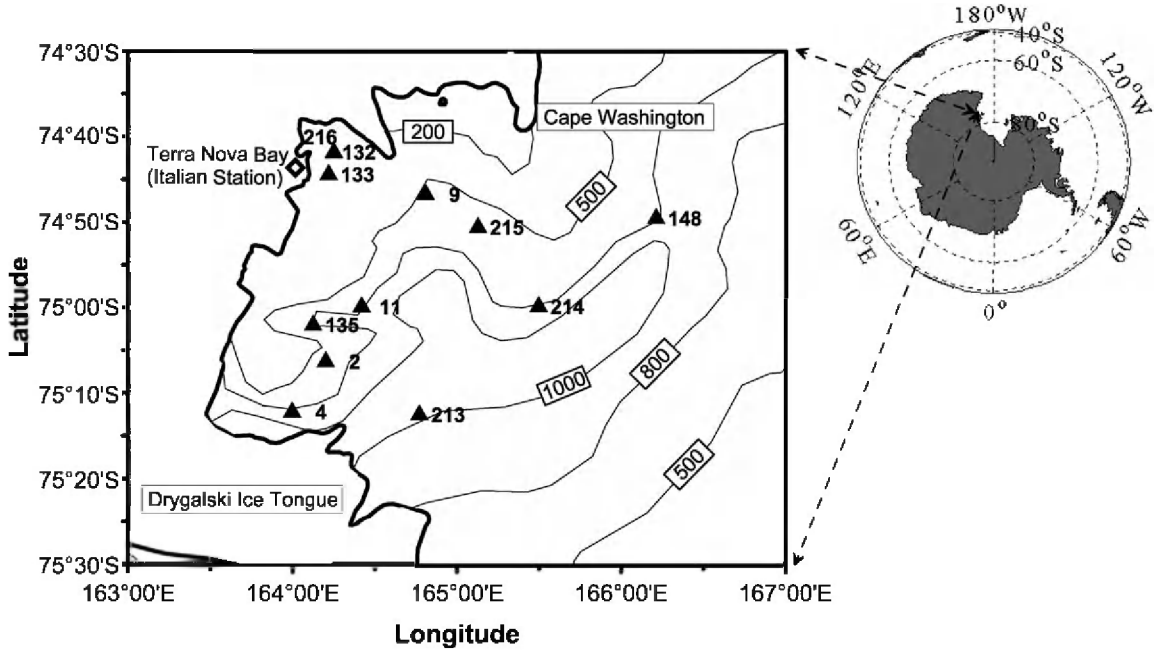


Fig. 1. Study area and sampling stations.

213, 214, 215 from S to N), and a coastal site (St. 216).

Hydrological casts and water sampling were carried out using an SBE 9/11 Plus CTD, with double temperature and conductivity sensors, coupled with an SBE 32 Carousel sampler, carrying 24 bottles of 12 l each. Calibration of temperature sensors was performed at the SACLANT CENTRE of La Spezia (Italy), before and after the cruise. During the cruise, CTD temperature was controlled by means of two SIS RTM 4200 digital reversing platinum thermometers. At every station, several replicate samples were collected at all depths and analyzed on board by means of an Autosal Guidline Salinometer.

Samples, 1.5 to 5 l, were collected for particulate matter and plankton analyses at several depths in the upper 200 m (down to 350 m at St. 2), selected on the basis of the physical (temperature and salinity) and optical (fluorescence profile) characteristics. Samples were vacuum-filtered through preweighed 0.45-μm Millipore filters for total particulate matter (TPM) determination. Nuclepore filters, 0.6 μm, were used for biogenic particulate silica (BSi) and precombusted (450 °C for 4 h) Whatman GF/F filters for particulate organic carbon (POC) analyses. Filters were then dried at 60 °C and stored in covered Petri dishes until analysis in the laboratory. Water (100 ml) from each depth was analysed by means of a Coulter Counter, equipped with 30- and 140-μm capillaries, to assess the numerical abundance (NP) and size (in the 0.6–91 μm range) of particles (Krank and Milligan, 1978).

TPM concentration was determined gravimetrically with a precision electronic balance (± 10 μg), POC was analysed by means of a LECO CS 125 analyser, after acidification with 2N H_3PO_4 and 1 N HCl (UNESCO, 1994). BSi was extracted by a time-series dissolution experiment in a 0.5M NaOH solution at 85 °C for 5 h. An aliquot of each sample was taken for analysis after every hour and the relative silica data were extrapolated back to time zero to correct for the silica originating from coexisting clay minerals (DeMaster, 1991). Prior to extraction, the material was pretreated with 10% hydrogen peroxide and 1 N HCl, to remove organic particle coatings (Mortlock and Froelich, 1989). Dissolved silica was analysed by spectrophotometric assay, and values

were calculated according to Mortlock and Froelich (1989).

For chlorophyll *a* (Chl *a*) and phaeopigment (Phaeo) analyses, three replicates were fractionated by filtration of 2 l of seawater, according to the following sets: 10-μm Nucleopore → GF/F; 2-μm Nucleopore → GF/F; GF/F. Filters were immediately frozen and stored at −20 °C. Pigment analyses were performed on an LS50B Perkin Elmer spectrofluorometer, according to Lorenzen and Jeffrey (1980), within 5 months from sampling.

For bacteria (BAC) determination, 100 ml of water was preserved with formalin (2% final concentration) and stained with DAPI (4,6-diamidino-2 phenyl indole) (Porter and Feig, 1980). For nanoplankton (<10 μm) analysis, 250 ml was preserved with glutaraldehyde (1% final concentration) and stained with DAPI and Primulin (Caron, 1983; Martinussen and Thingstad, 1991). Bacteria and nanoplankton counts were made using an Olympus BX60-FL microscope equipped with epifluorescent light (100-W HBO mercury lamp) and a 100× oil immersion objective.

For phytoplankton identification, samples (500 ml) were preserved with buffered formalin (4% final concentration) and stored in dark glass bottles. Species composition and abundance were determined on 50-ml aliquots with an inverted microscope, according to Utermöhl (1958) method as described by Zingone et al. (1990). The main taxonomic references used for species identification were Priddle and Fryxell (1985), Medlin and Priddle (1990), Throndsen (1993), Hasle and Syvertsen (1996), and Steindinger (1996).

For microzooplankton (>10 μm) (MCZ) analyses, two types of samples were taken. An aliquot of 5 l was gently reverse-flow concentrated with a 10-μm mesh, to obtain samples of 250 ml, which were then fixed with 4% buffered formaldehyde. Subsamples from this aliquot (50 ml) were examined in a settling chamber (Utermöhl, 1958). Another 100-ml aliquot was preserved with glutaraldehyde (1% final concentration), stained with DAPI (5 μg ml^{-1} final concentration, Porter and Feig, 1980) and filtered onto 2-μm blackened polycarbonate filters. Analyses were performed using a Leitz Diaplan epifluorescence microscope, at 400× magnification. Heterotrophic dinoflagellates were identified according to Balech (1976). Loricate ciliates were classified according to Brandt (1906, 1907), Laackmann (1910), and Kofoid and Campbell (1929, 1939); aloricate ciliates were grouped into separate taxa on the basis of size, shape, visible ciliature, and morphology (Hamburger and Buddenbrock, 1911; Corliss, 1979; Lynn and Montagnes, 1988a,b).

Biomass was estimated by measuring the linear dimensions and equating shapes to standard geometric figures; the resulting volumes were transformed into organic carbon values by using the following conversion factors: picoplankton: fg C = $\mu m^3 \times 20$ (Carlson et al., 1998); nanoplankton: fg C = $\mu m^3 \times 0.14$ (Edler, 1979); diatoms: pg C = $\mu m^3 \times 0.11$ (Strathmann, 1967); ciliates other than tintinnids: pg C = $\mu m^3 \times 0.14$ (Putt and Stoecker, 1989); all the other groups: pg C = $\mu m^3 \times 0.008$ (Beers and Stewart, 1970).

Cluster analysis, based on the complete linkage method, was computed using Matedit (Burba et al., 1992), after calculating the correlation coefficient of parameters and the similarity ratio of stations. Correspondence analysis (Fabbris, 1997) was then employed to identify the structure of inner dependency of data matrices through a graphical representation. For each pair of related parameters the correlation coefficient was obtained by linear regression.

3. Results

3.1. Hydrology

In early December, open water extended over a relatively small area in Terra Nova Bay and sea-ice was retreating in a northward direction. Hydrographic features were spatially diversified along the study section: although the transect was completely ice-free, the northern part was still influenced by late ice melting. At St. 9, the water column was relatively stratified and characterized by a lens of superficial fresher water, which produced a weak pycnocline at 25–30 m depth (Fig. 2a). Conversely, southward, the top 150–200 m was well mixed and characterized by a mean salinity exceeding 34.7. The fluorescence profile exhibited surface (0 m) and subsurface (5–10 m) peaks (not shown).

In early February, the pycnocline became stronger and well established at 25–60 m along the transect

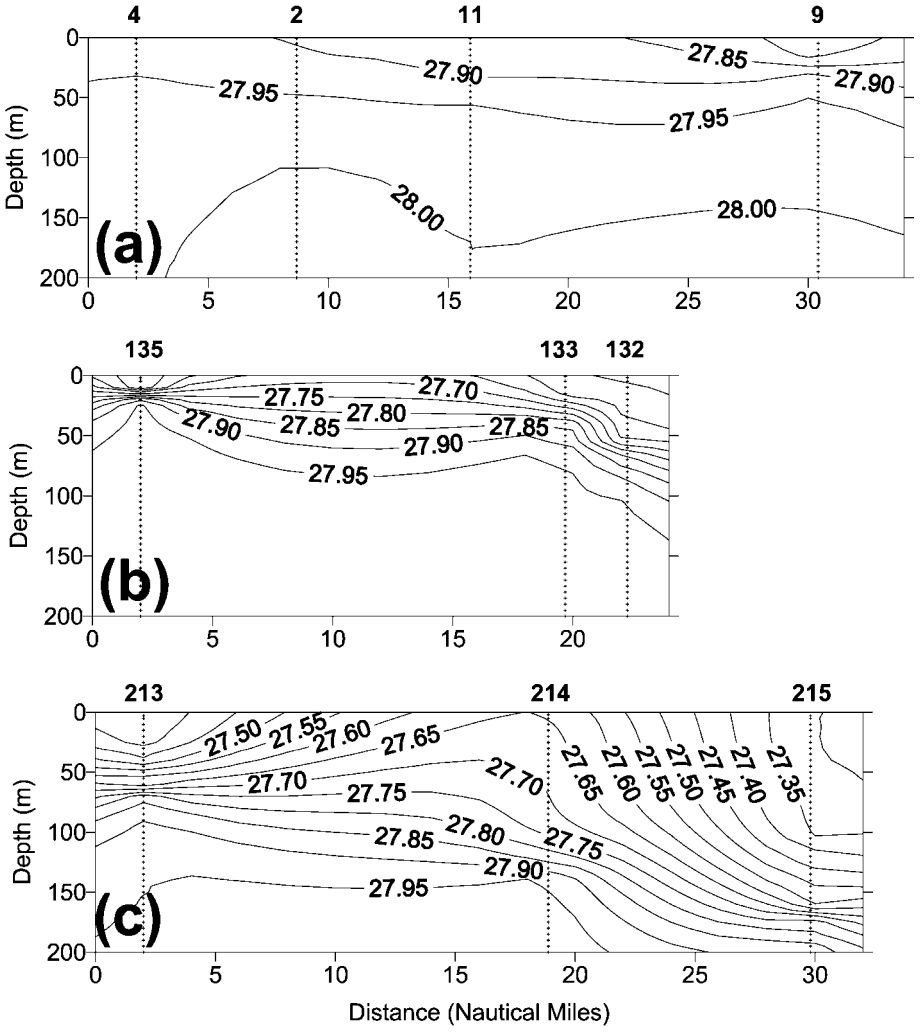


Fig. 2. Potential density (kg m^{-3}) along the transect in early December (a), early February (b), and late February (c).

(Fig. 2b), while fluorescence maxima typically appeared at about 60 m below the surface, but did not correspond to Chl *a* maxima.

In late February, the pycnocline deepened further to 70–150 m (Fig. 2c) and the fluorescence profile was similar to that observed in early December.

In terms of stability (calculated according to the Hesselberg–Sverdrup method, UNESCO, 1991), during the first period the southern stations (Sts. 4 and 2) exhibited homogeneous low levels along the water column, while the northern sector (Sts. 11 and 9) showed higher stability, particularly in correspondence of the pycnocline (Fig. 3a). In February, stability increased throughout the transect, with high values observed down to 100 m depth at the beginning of the month (Fig. 3b), and extending later to deeper water by late February (Fig. 3c).

3.2. Particulate matter

In late spring TPM ranged from 120 μg l^{-1} (St. 9, 80 m) to 462 μg l^{-1} (St. 11, 0 m) (Table 1) and was more concentrated in the uppermost layer (0–20 m). POC and BSi showed the highest concentrations at the surface (0 m), while Chl *a* displayed subsurface maxima (30–50 m) at both ends of the transect.

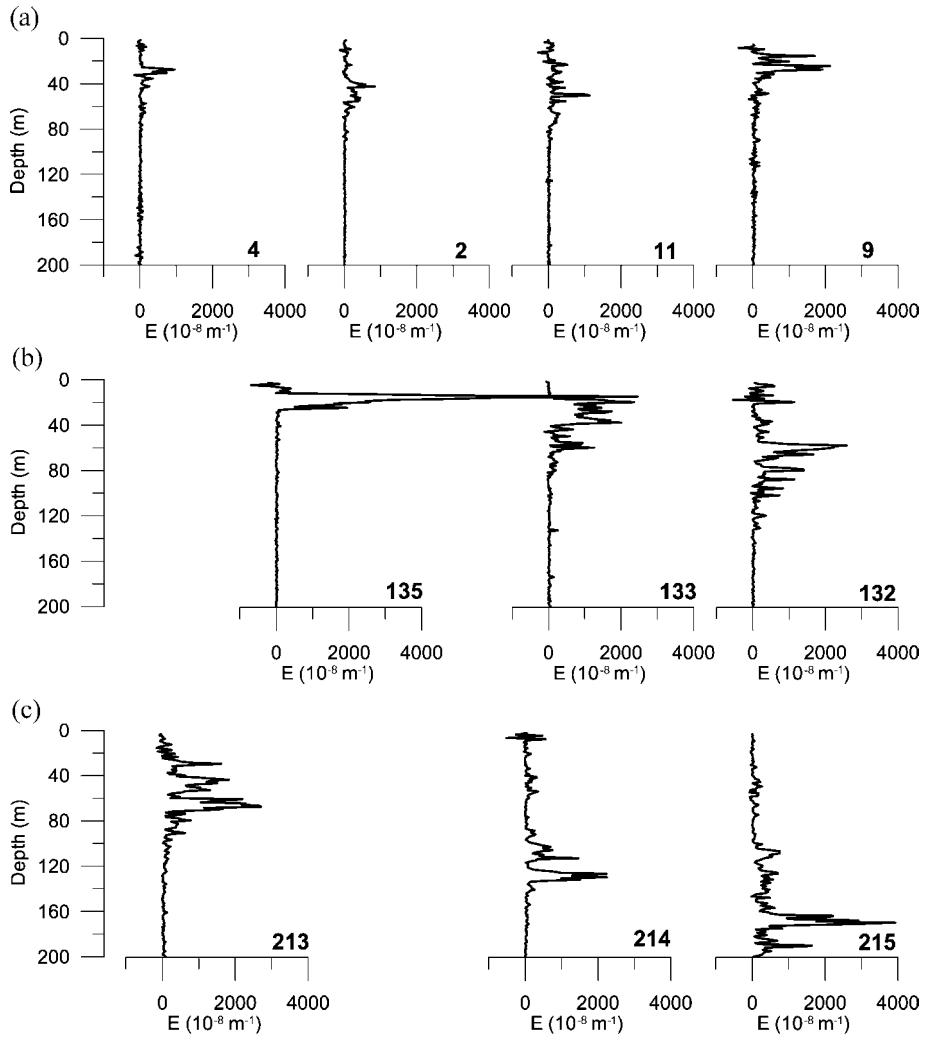


Fig. 3. Water column stability (10^{-8} m^{-1}) at the sampling stations in early December (a), early February (b), and late February (c).

POC and Chl *a* surface values decreased along the transect from the southernmost station (St. 4, POC: 260.0 μg l^{-1}, Chl *a*: 2.22 μg l^{-1}) towards the receding ice-edge (St. 9, POC: 170.9 μg l^{-1}, Chl *a*: 0.44 μg l^{-1}). BSi surface concentrations did not show such a gradient and ranged from 42.3 μg l^{-1} at St. 2 to 91.8 μg l^{-1} at St. 4. In general, in early December particulate matter was more concentrated in the central part of the transect: values integrated over the upper 100 m water column were higher at St. 2 than at the other stations for TPM and POC and at St. 11 for BSi (Fig. 4).

In February, all parameters increased in concentration and were distributed more homogeneously in the upper 100 m but, contrary to the previous period, the central part of the study area was now the poorest in particulate matter (Fig. 4). From late December to early February, the 0–100 m integrated POC and BSi displayed a 7-fold and 10-fold increase, respectively, all over the study area, except in the central part (i.e., St. 135 in the second period and St. 214 in the third) (Fig. 4). Both parameters remained steady or increased slightly until the end of the month. In terms of contribution to total suspended matter, POC and

Table 1
Range of values of physical, chemical and biological parameters along the study transect during the three sampling periods

Terra Nova Bay polynya	December 1997			early February 1998			late February 1998		
	min	max	mean ± SD	min	max	mean ± SD	min	max	mean ± SD
T	− 1.9182	− 1.4325	− 1.7773 ± 0.1796	− 1.9606	− 0.8814	− 1.5505 ± 0.422	− 1.9499	− 1.20588	− 1.6371 ± 0.3377
S	34.4989	34.8159	34.7243 ± 0.0868	33.8561	34.7615	34.4667 ± 0.3184	33.9409	34.7575	34.3774 ± 0.3565
NP	11032	336000	64860 ± 84846	6301	53275	25458 ± 14567	3555	49059	23370 ± 15528
mode	15.22	73.83	34.30 ± 17.56	21.66	101.1	60.19 ± 22.14	32.11	77.29	56.47 ± 17.04
TPM µg/l	120.00	462.00	279.55 ± 130.40	123.33	2500.00	1131.87 ± 619.19	551.67	2030	1098.81 ± 517.82
POC µgC/l	25.50	260.00	104.33 ± 79.33	16.58	427.60	191.93 ± 122.45	83.1	278.53	165.80 ± 66.35
BSi µg/l	4.21	91.80	41.66 ± 32.31	15.67	313.07	222.69 ± 110.20	127.23	480.92	252.64 ± 124.09
BSi/POC	0.11	0.52	0.34 ± 0.15	0.61	1.99	1.24 ± 0.49	0.98	1.73	1.50 ± 0.25
BSi/Chl *a*	26.79	220.00	87.41 ± 64.02	79.20	304.67	154.07 ± 69.07	90.23	287.48	158.29 ± 83.88
POC/Chl *a*	103.98	458.32	265.11 ± 127.65	74.09	202.18	130.76 ± 45.31	58.93	176.86	105.97 ± 50.37
Chl *a* tot µg/l	0.06	2.22	0.74 ± 0.66	0.17	2.69	1.72 ± 0.76	0.75	3.56	2.31 ± 1.03
Chl>10 µg/l	0.02	1.33	0.37 ± 0.37	0.03	1.61	0.71 ± 0.69	0.01	2.94	1.2 ± 1.04
Chl 2–10 µg/l	0	1.33	0.30 ± 0.38	0	1.76	0.34 ± 0.70	0	2.49	0.66 ± 0.76
Chl<2 µg/l	0	0.77	0.10 ± 0.17	0.04	0.48	0.19 ± 0.16	0.05	1.54	0.46 ± 0.44
Phaeo µg/l	0.02	1.67	0.57 ± 0.55	0.35	3.75	2.26 ± 1.03	0.73	4.89	2.63 ± 1.26
Chl/Phaeo	0.87	3.47	1.7 ± 0.79	0.49	1.36	0.77 ± 0.26	0.67	1.19	0.92 ± 0.14
BAC									
10^5 cells/ml	0.3	4.1	2.2 ± 1.0	1.3	12	5.6 ± 3.5	0.4	9.5	4.6 ± 2.7
µgC/l	0.7	8.1	4.5 ± 2.1	2.6	24	11.1 ± 7.0	0.9	19	9.2 ± 5.5
tot Nanopl.									
cells/ml	701	5284	2236.3 ± 1514.2	1092	2802	1829.7 ± 638.1	1185	3374	2274 ± 853
µgC/l	1.6	30.2	10.7 ± 8.6	1.6	17.7	7.3 ± 5.5	3.1	25	10 ± 9.2
PNF									
cells/ml	330	2631	1132.8 ± 785.4	458	1302	917.4 ± 271.3	254	2311	995.5 ± 706.3
µgC/l	0.3	2.1	0.9 ± 0.6	0.4	1.1	0.7 ± 0.2	0.2	1.8	0.8 ± 0.6
ND									
cells/ml	115	2803	959.3 ± 802.7	79	1674	626.6 ± 538.0	174	2438	881.1 ± 936.1
µgC/l	1.2	20	9.7 ± 8.1	0.8	16.9	6.3 ± 5.4	1.8	24.5	8.9 ± 9.4
tot Microphyto.									
10^5 cells/l	0.014	16.12	4.228 ± 5.577	0.124	5800	4.926 ± 2.489	0.0296	10.46	6.039 ± 3.241
µgC/l	0.12642	195.9948	27.5808 ± 49.601	1.15733	80.5	40.096 ± 22.788	0.6722	81.923	42.183 ± 24.232
MD									
10^5 cells/l	0	4.585	0.533 ± 1.218	0.084	5800	4.131 ± 2.909	0.016	9.843	5.522 ± 2.862
µgC/l	0	161.5274	19.39 ± 43.53	0.5793	77.787	26.168 ± 24.102	0.5281	70.3456	29.214 ± 19.705
MCZ									
ind./l	0	178.2	40.71 ± 50.39	6.48	960.48	315.74 ± 346.57	4.64	765.6	230.91 ± 261.67
µgC/l	0	2.17	0.43 ± 0.68	0.04	3.73	1.54 ± 1.36	0.08	6.58	2.22 ± 2.51

BSi showed opposite trends: on average POC represented 40% of the total particulate standing stock throughout the study area in early December, and decreased to 15% in late February. Over the same period, BSi increased from 13% to 23% of TPM.

Mean Chl *a* concentration doubled from the first to the second period, and doubled again from early to late February, when it reached a maximum of 3.6 μg l^{-1} at St. 213 (Table 1).

The average POC/Chl *a* ratio decreased strongly from December to February, but remained fairly steady until late summer (Table 1). The mean Chl *a*/Phaeo ratio was 1.7 in late spring, and decreased significantly in February. The BSi/POC and BSi/Chl *a* ratios exhibited an opposite trend, increasing significantly from late spring to the summer and keeping then relatively constant values throughout February (Table 1).

3.3. The phototrophic communities

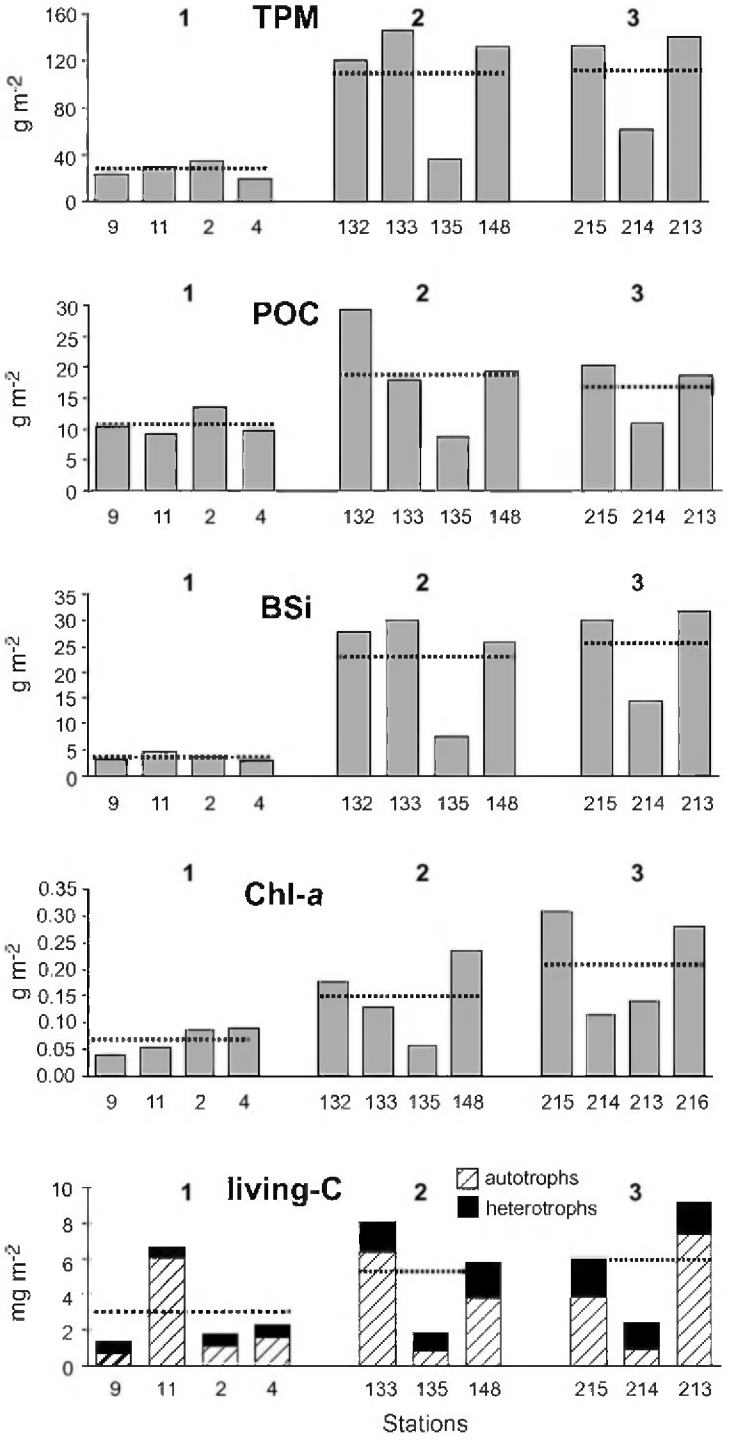
In early December, both nano- (2–10 μm) and micro- (10–200 μm) sized fractions contributed substantially to the total Chl *a* amount, except at St. 2 where only nanoplanktonic algae appeared abundant. Phototrophic nanoplankton (PNAN) showed the highest abundance in the upper 30 m (max. at St. 11, 5 m depth) and was mainly constituted of nanoflagellates (PNF) and small diatoms (ND). These latter belonged mostly to a single species, 4–5 μm long and 1–1.5 μm large, which could be ascribed to the genus *Fragilariopsis*. Carbon content (CC) of PNAN varied between 1.5 and 22.1 μg C l^{-1} along the transect, with the contribution of ND almost always exceeding 80%. Surface/subsurface maximum abundances were in the range $0.33–2.63 \times 10^6$ and $1.15–2.8 \times 10^6$ cells l^{-1} for PNF and ND, respectively. In the southern part of the transect (Sts. 4 and 2), microphytoplankton (MP) was the most abundant size category and was overwhelmingly constituted by *Phaeocystis* cfr. *antarctica*, which was present in colonies as well as individual cells. Micro-sized diatoms (MD) (e.g., *Thalassiosira decipiens*) and autotrophic flagellates other than *Phaeocystis* clearly prevailed in the northern part of the study area (Sts. 11 and 9). Microphytoplankton CC ranged from 0.13 at depth to 195.99 μg C l^{-1} at the surface (Table 1), with maxima due to the MD fraction, namely to *Thalassiosira* spp.

In early February, total PNAN ranged between 0.5 and 2.98×10^6 cells l^{-1}, showing a slight decrease in both PNF and ND abundances. The carbon content was almost entirely due to ND, and reached a maximum of 18 μg C l^{-1}. Microphytoplankton was dominated by MD (e.g., *Fragilariopsis curta*, *F. kerguelensis*, *Pseudonitzschia pseudodelicatissima*) and reached a maximum abundance of 0.6×10^6 cells l^{-1}. Maxima of microphytoplankton CC varied between 30 and 80 μg C l^{-1}, except at St. 135 (where grease ice was present), where it reached an unusually high value of 32.4 mg C l^{-1}, in correspondence of a dense bloom of *F. curta* (up to 5.5×10^8 cells l^{-1}) and *P pseudodelicatissima* (up to 0.3×10^8 cells l^{-1}). Such high densities were detected in the thin newly formed ice and remained concentrated close to the water surface (Table 1).

In late February, the 10–200-μm fraction provided the largest contribution to total Chl *a*. The autotrophic picoplankton increased as well, compared to the previous December period and to early February. This component was however never detected in significant abundances in our samples. It was partially constituted of very small diatoms, <2 μm in diameter. Total PNAN ranged between 0.43 and 4.7×10^6 cells l^{-1}. Except for a peak at the surface at St. 213 (24.8 μg C l^{-1}), PNAN carbon was always lower than 7.5 μg C l^{-1}. Microphytoplankton was clearly dominated by diatoms (e.g., *F. curta*, *F. kerguelensis*, *P pseudodelicatissima*), but in the nearshore site (St. 216) flagellates were also abundant. Total MP reached a maximum density of 1.05×10^6 cells l^{-1} (Table 1) and its CC ranged from 20 to 82 μg C l^{-1} at the surface, decreasing with depth.

Notes to Table 1:

Temperature (*T*, °C), salinity (*S*), number of particles per liter (NP l^{-1}), total particulate matter (TPM, μg l^{-1}), particulate organic carbon (POC, μg C l^{-1}), biogenic silica (BSi, μg l^{-1}), chlorophyll a (Chl *a*, μg l^{-1}), Phaeopigments (Phaeo, μg l^{-1}), Chl/Phaeo ratio, densities and biomasses of bacteria (BAC, 10^{-5} cells ml^{-1}, μg C l^{-1}) total nanoplankton (tot Nanopl., cells ml^{-1}, μg C l^{-1}), phototrophic nanoflagellates (PNAN, cells ml^{-1}, μg l^{-1}), nanoplanktonic diatoms (ND, cells ml^{-1}, μg C l^{-1}), total microphytoplankton (tot Microphyto. 10^{-5} cells l^{-1}, μg C l^{-1}), microplanktonic diatoms (MD, 10^{-5} cells l^{-1}, μg C l^{-1}) and total microzooplankton (MCZ, cells l^{-1}, μg C l^{-1}).


TPM
POC
BSi
Chl-a
living-C
1
2
3
g m-2
mg m-2
autotrophs
heterotrophs
9 11 2 4 132 133 135 148 215 214 213
9 11 2 4 132 133 135 148 215 214 213 216
133 135 148
Stations

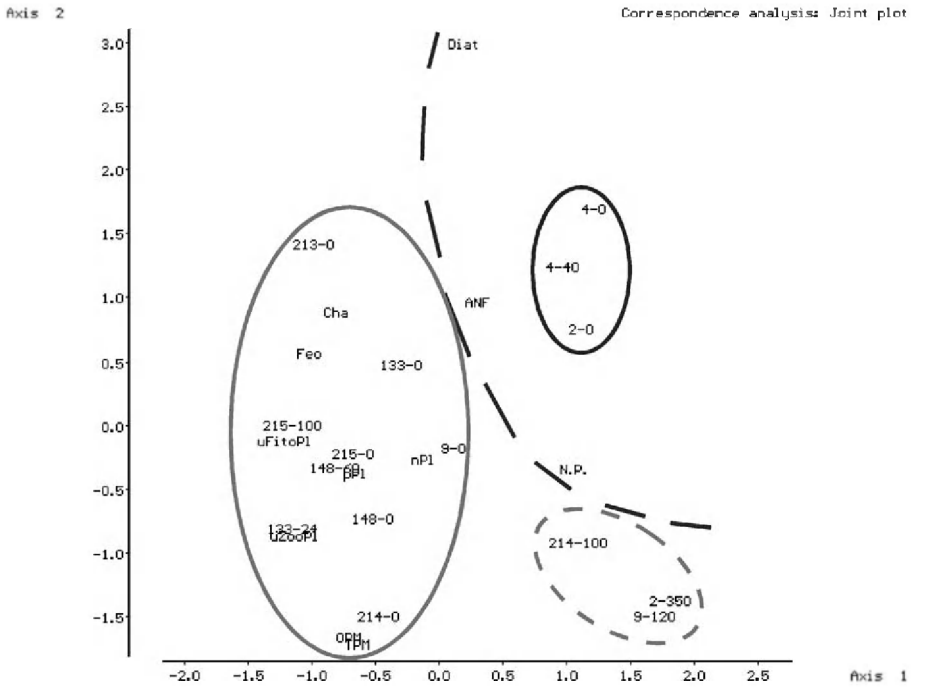


Fig. 5. Joint plot of correspondence analysis: the three ellipses include subcluster B2 (left), cluster A (right, top), and subcluster B1 (right, bottom).

3.4. Heterotrophic bacteria, heterotrophic nanoplankton and microzooplankton

During the first period, heterotrophic bacteria (BAC) concentration ranged between 2.3 and 4×10^5 cells ml^{-1} in the upper 50 m, clearly decreasing with depth. Bacterial carbon varied between 0.7 and 8.1 μg C l^{-1} (Table 1). Heterotrophic nanoplankton (HNAN: 2–10 μm) was relatively scarce, with CC ranging from 0.1 to 0.5 μg C l^{-1}. Heterotrophic microplankton (MCZ) was scarce as well (max. 178 ind. l^{-1} at St. 9 at the surface), and mainly due to heterodinoflagellates (*Protoperidinium* sp.). Maxima were always detected at the surface, where CC varied between 0.7 and 2.2 μg C l^{-1}, and abundances increased towards the edge of the retreating ice. The highest contribution to MCZ carbon was generally due to heterodinoflagellates, even though at Sts. 4 and 11 (0 m) tintinnids contributed >50% and 30% of the total, respectively (Table 1).

In early February, BAC abundance generally increased by one order of magnitude, with surface maxima up to 1×10^6 cells ml^{-1} and deep minima never below 1×10^5 cells ml^{-1}. Consequently, bacterial carbon increased, varying between 2.6 and 24 μg C l^{-1}. HNAN abundances were in the same range as in the previous period and CC showed almost homogeneous values (~ 0.4 μg C l^{-1}) throughout the water column. MCZ increased sharply (up to 960 ind. l^{-1} at 50 m at St. 133), with surface/subsurface maxima >390 ind. l^{-1}). The MCZ assemblage was more diversified as compared to that observed in late spring, changing from the almost monospecific *Protoperidium*-dominated community of early December to a community richer in heterodinoflagellates species

Fig. 4. Standing stock of total particulate matter (TPM), particulate organic carbon (POC), biogenic silica (BSi), chlorophyll *a* (Chl *a*), and living carbon (living-C, separated into two categories according to its autotrophic or heterotrophic origin) integrated over the upper 100 m of the water column. Dotted lines represent the average of all stations. Numbers above bars indicate different sampling periods: early December (1), early February (2), and late February (3).

(e.g., *P. defectum*, *P. pseudoantarcticum*, *P. applanatum*, *Protoperidinium* sp., *Gyrodinium* sp.) and tintinnids (e.g., *Codonellopsis gaussi*, *C. glacialis*, *Laackmanniella prolongata*). MCZ carbon increased throughout the water column and exhibited surface maxima between 2.5 and 3.7 μg C l^{-1}. Tintinnids became more important than in late spring, particularly at St. 135, were they exceeded the heterodinoflagellate CC at the surface (Table 1).

In late February, BAC decreased, never exceeding 9.5×10^5 cells ml^{-1}, and CC showed values from 0.9 to 19 μg C l^{-1}. HNAN ranged between 113 and 683 cells ml^{-1}, thus showing a slight increase compared to mid-summer. HNAN carbon was generally around 0.4 μg C l^{-1} and reached maxima of 0.8 μg C l^{-1} in the subsurface layer at St. 213. MCZ abundance was still high, but lower than in early February, with surface maxima >700 ind. l^{-1}. Species richness increased, particularly that of tintinnids, with *Cymatocylis drygalskii*, *C. vanhöffeni*, *L. naviculaefera*, *Salpingella* sp. enriching the community. MCZ carbon showed surface maxima of 5 to 6.6 μg C l^{-1}, with the relative contribution of tintinnids becoming even higher than during the previous period (Table 1).

3.5. Statistical analyses

Cluster and correspondence analyses identified two major groups of samples (Fig. 5): the first (cluster A) included only Sts. 2 and 4 (first period) down to 40 m depth, while the second (cluster B) included samples from all remaining stations (the remaining of the first leg and all depths of the second and third legs). In the second cluster two subgroups were highlighted, of which the first (subcluster B1) was constituted of deep samples of Sts. 2 and 9 (first period) and 214 (third period), characterized by very low values for all the parameters used in the statistical analysis. The last subgroup (subcluster B2) included all the other samples collected during the second and third legs, as well

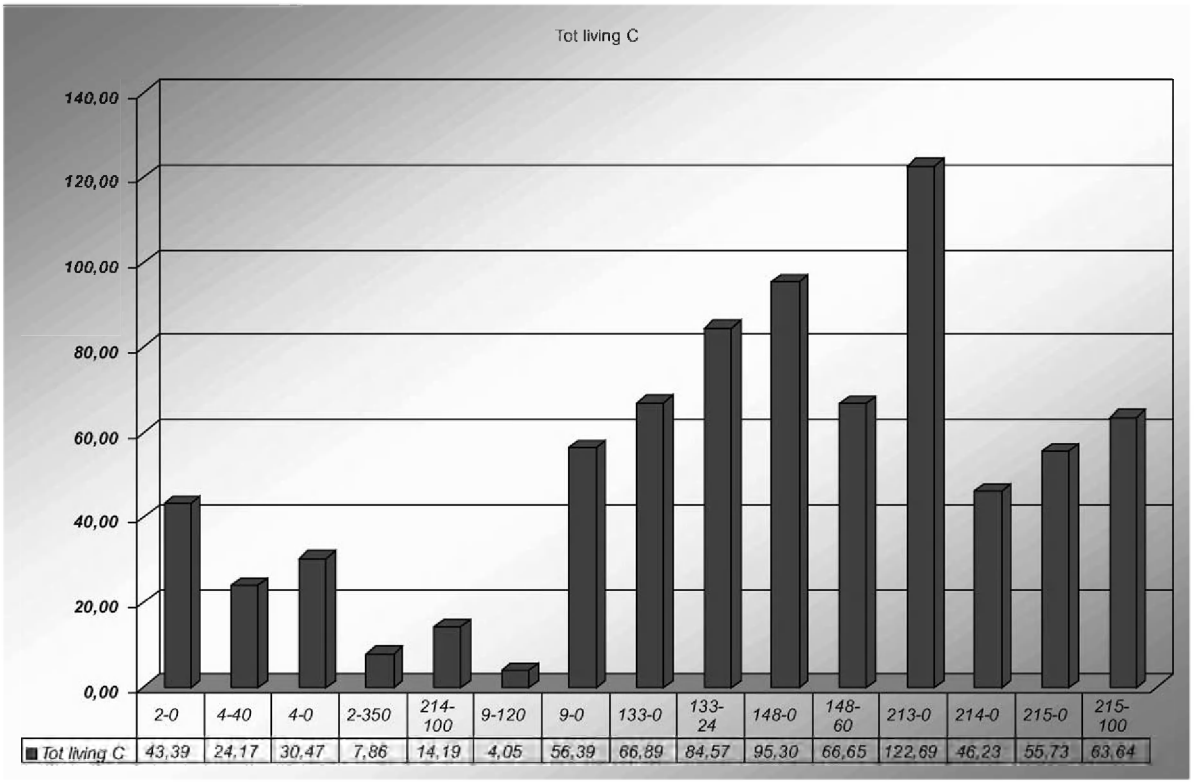


Fig. 6. Total living carbon at the various stations and depths used in the statistical analysis.

as the surface sample of St. 9 (first leg). The distribution pattern of the total living carbon (Fig. 6) matched very well the separation into groups obtained with the cluster analysis, highlighting a group of stations with intermediate values (corresponding to cluster A), a second group of stations characterized by very scarce biomass (corresponding to subcluster B1) and a group constituted by all the other samples (corresponding to subcluster B2), in which biomass almost doubled.

Following the separation obtained with cluster analysis we calculated the mean relative contribution to total living carbon of the autotrophic and heterotrophic constituents (Fig. 7). In cluster A, 50% of the community CC was constituted of ND, 20% of BAC and 6% of PNAN, namely *Phaeocystis*. In cluster B, MP (mostly large diatoms) constituted 55% of the living CC and the heterotrophic fraction increased its contribution up to 29% of the total content. The most relevant differences between the two groups were a decrease in the PNAN component, and an increase in MCZ and BAC in the second group.

4. Discussion

4.1. Phytoplankton and particulate matter dynamics

In late spring, the spatially diversified hydrographic features corresponded to different phytoplankton assemblages along the transect. A *Phaeocystis* bloom was detected in the southern part of the polynya (which had been ice-free for a long time), shifting to a diatomaceous community closer to the ice edge. *Phaeocystis* blooms are a common event during late spring/early summer in polynya areas of the Ross Sea (El-Sayed et al., 1983; Putt et al., 1994; Smith and Gordon, 1997; Carlson et al., 1998; Saggiomo et al., 1998; Innamorati et al., 1999; Nuccio et al., 1999; Arrigo et al., 2000; Marino et al., in preparation).

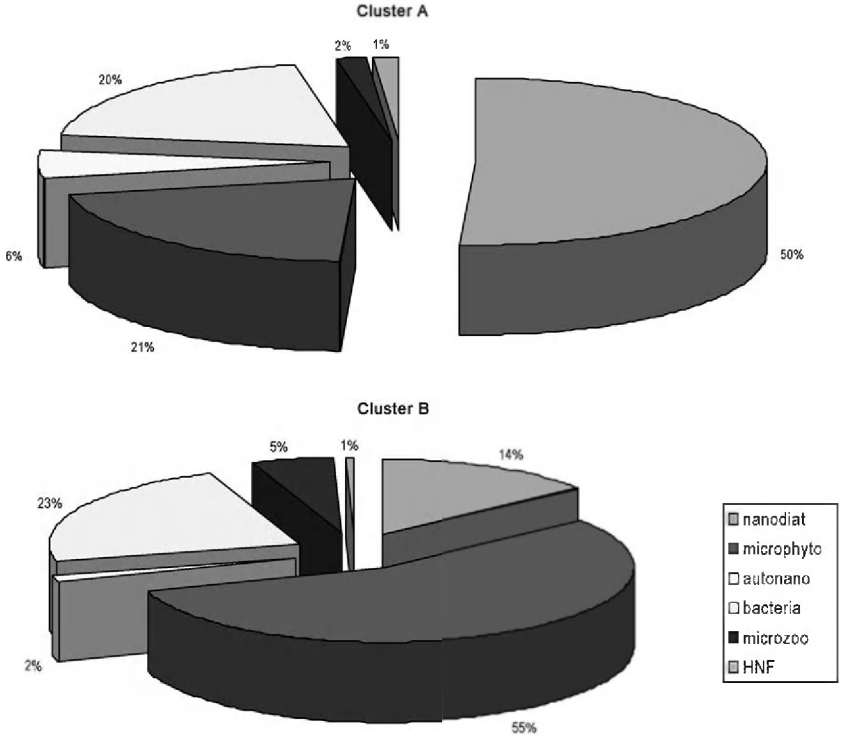


Fig. 7. Mean relative contribution of bacteria (BAC), nanoplanktonic diatoms (ND), autotrophic nanoplankton other than diatoms (PNAN), heterotrophic nanoflagellates (HNAN), microphyto- (MP), and microzooplankton (MCZ) to total living carbon in the two groups identified by cluster analysis.

Despite the earlier disappearance of sea ice in the southern part of the transect, strong winds and the weak stratification of the water column (Fig. 2a) may have hindered the development of diatom blooms, favoring the growth of *Phaeocystis* over that of diatoms. Similar dynamics were already observed in Terra Nova Bay in early December (Arrigo et al., 2000), suggesting that this could possibly represent a recurring feature of this area in late spring. Sedwick et al. (2000) explained a similar trend observed in shelf waters as resulting from the supply of iron from melting sea ice that enhanced diatom blooms. We do not have any evidence of this effect, but we think that the higher stability and stratification of the upper water column (Figs. 2a and 3a) could have played a role in favoring diatom growth in the northern part of the transect (see Catalano et al., 1997; Arrigo et al., 2000; Goffart et al., 2000).

The predominance of diatoms near the edge of the retreating ice in early December is consistent with previous observations of intense diatom blooms generally occurring in Terra Nova Bay, and in the western Ross Sea, in late December/early January (Smith and Nelson, 1985; Innamorati et al., 1992; Nuccio et al., 1992; Arrigo and McClain, 1994; Innamorati et al., 1999; Nuccio et al, 1999; Arrigo et al., 2000). These diatoms, predominantly *Thalassiosira* spp., could possibly originate from phytoplankton populations released from the melting sea-ice into the water column.

In February, the more homogeneous hydrographic conditions, together with the stronger stratification of the water column, allowed the development of a diatom bloom throughout the transect (see Sunda and Huntsman, 1997). The polynya area experienced a moderate but widely extended diatom bloom in early February, which lasted and increased throughout the month, attaining the highest intensity in late February. The bloom was sustained by a different diatom community as compared to that observed in December, and was dominated by equal proportions of *F. curta*, *F. kerguelensis* and *P. pseudodelicatissima*. The late February bloom was also recorded in previous years (Innamorati et al., 1999; Nuccio et al., 1999) and hence may be a recurring event in Terra Nova Bay. In the Terra Nova Bay polynya primary production peaks substantially later after the occurrence of the bloom in the Ross Sea polynya, despite the fact that the former polynya forms first. Although the temporal relationship between phytoplankton bloom and sea ice dynamics in Terra Nova Bay is still to be clarified, the different timing of the bloom in the two polynyas is probably a consequence of the different meteorological conditions predominating in the two systems, namely of the fact that wind stress in Terra Nova Bay is much higher and does not allow water column stratification as early in the season as in the Ross Sea polynya (Arrigo et al., 1998).

Throughout the sampling period, Chl *a* concentrations in the polynya of Terra Nova Bay (Table 1) were in the lower range of those measured both directly (Smith and Gordon, 1997; Caron et al., 2000) and by remote sensing (Arrigo and McClain, 1994) in the Ross Sea polynya in December (max: 11 $\mu g\ l^{-1}$), and were more similar to concentrations reported for November (max: 3 $\mu g\ l^{-1}$, Smith and Gordon, 1997; Caron et al., 2000) or late January (max: 2 $\mu g\ l^{-1}$, Smith et al., 1996). However, concentrations were very similar to those measured in the Ross Sea polynya from early spring 1996 to late summer 1997 (0.04 to 3.6 $\mu g\ l^{-1}$, Caron et al., 2000). It is worth noting that, during the whole summer, 10% to 12% of the total autotrophic biomass was represented by the pico-sized fraction (see Table 1), although we never visually counted significant numbers of picoplanktonic autotrophs. This is an unusually high percentage for Antarctic waters. Conversely, high and relatively constant abundances of nanodiatoms were always observed in our study, confirming previous records in Antarctic waters (Kang and Lee, 1995; Villafane et al., 1995), where *Fragilariospis pseudonana* was identified as the dominant species. This diatom is only few micrometers large and approximately 8–10 μm long. A similar species, ascribable to the same genus and with identical dimensions, was observed in the investigated area. The small size of this diatom, particularly of its width, could have led to its inclusion in the pico-sized fraction. This could possibly explain why, despite the very low abundances of autotrophic picoplankton, the picoplanktonic contribution to total Chl *a* was not negligible in our study. We hypothesize that the Chl *a* pico-sized fraction was probably also biased by the presence of *F. pseudonana*, which could be held responsible for the relatively high concentrations of pico-Chl *a*.

Because of this, we do believe that our data are not in contrast with previous observations underscoring that picophytoplankton biomass is generally scarce in Antarctic waters (Robineau et al., 1994; Kang and Lee, 1995; Karl et al., 1996; Vanucci and Bruni, 1998, 1999). Total Chl *a* concentrations, integrated in the upper 100 m (Fig. 5), were consistent with the typical summer values observed within the southernmost Ross Sea polynya (range: 19.9–165.0 mg m^{-2}, Smith and Dunbar, 1998). POC concentrations (Table 1) were in the range of those measured in polynya areas of the Ross Sea from December through February (97.2–646.8 μg l^{-1}: Smith and Gordon, 1997; 93.2–362.9 μg l^{-1}: Povero et al., 1999) and were generally higher than in spring (from mid-November to mid-December, 27.5–221.9 μg l^{-1}: Fabiano et al., 1999b). POC, Chl *a*, and BSi standing stocks increased with the progressing of the season, suggesting the likely accumulation of biogenic material in the upper water column. The temporal changes in the plankton assemblage deeply affected the overall composition of particulate matter. POC was significantly correlated with the autotrophic components throughout the summer, but particularly with Chl *a* in early December ($n=24$, $r=0.94$, $p<0.001$), and with BSi in late February ($n=26$, $r=0.96$, $p<0.001$), as a consequence of the increasing contribution of diatoms to the phytoplankton assemblage through the summer. The correlation of BSi with microphytoplankton biomass ($n=20$, $r=0.64$, $p<0.01$) was generally much stronger than with nanodiatoms ($n=18$, $r=0.56$, $p<0.05$), indicating the greater importance of large size diatoms in determining the build up of the BSi stock with the progressing of the season. BSi and Chl *a* were not related in late spring, owing to the predominance of *Phaeocystis* in the southern part of the polynya, and become correlated afterwards, with increasing strength in late February ($n=23$, $r=0.90$, $p<0.01$). Over the whole sampling period the sum of auto- and heterotrophic living carbon was significantly related to POC ($n=47$, $r=0.72$, $p<0.01$), underscoring the biogenic origin of the latter, in agreement with previous observations carried out in Terra Nova Bay during the summer (Fabiano et al., 1996). The temporal evolution of the BSi/POC and BSi/Chl *a* ratios clearly showed the increase in the diatom biomass over the phytoplankton assemblage from late spring to the summer. In February the BSi/POC ratio exhibited values typical of diatom-dominated blooms in the marginal ice zone (Quéguiner et al., 1997). The patterns of the Chl *a*/Phaeo and BSi/POC ratios (Table 1) also suggested the progressive increase in the detrital autotrophic fraction, overwhelmingly represented by microdiatoms, from early December to late February. The deepening of the pycnocline determined a more homogeneous vertical distribution of detrital particulate matter. The quantitative dominance of microparticulate matter containing a high fraction of organic detritus was already highlighted in Terra Nova Bay in mid-summer (Fabiano et al., 1999a), with the detrital fraction increasing when large particles were dominant.

4.2. Processes affecting the planktonic system through the summer

Cluster analysis, performed excluding any taxonomical information, clearly separated two groups of samples (Fig. 5). Cluster A only included samples from the southern area of the polynya (Sts. 2 and 4) down to 40-m depth, spatially corresponding to the late spring *Phaeocystis* bloom, which remained confined to a relatively small area. In the conditions corresponding to this cluster the planktonic biomass was dominated by nano-sized diatoms, which represented 50% of the total living carbon (i.e. autotrophic+heterotrophic) and up to 65% of the autotrophic biomass (Fig. 7). POC/Chl *a* ratios characterizing cluster A ranged from 116.8 to 240.7, BSi/Chl *a* from 41.3 to 49.2, BSi/POC from 0.20 to 0.35, and Chl *a*/Phaeo from 0.87 to 1.41. Heterotrophic biomass was largely dominated by bacteria, which accounted for 20% of the total living carbon.

Cluster B was characterized by a completely different autotrophic assemblage, overwhelmingly dominated by micro-sized diatoms, and by the greater importance of the heterotrophic community. POC/Chl *a* ratios of samples included in cluster B ranged from 58.9 to 202.2, BSi/Chl *a* from 79.2 to 304.7, BSi/POC from 0.61 to 2.0, and Chl *a*/Phaeo from 0.49 to 1.36. Cluster B, and particularly subcluster B2, largely corresponded to February conditions, when species richness increased and plankton included greater abundances of consumers, particularly microzooplankton, resulting in a better structured commun-

ity at the end of the summer. This is consistent with previous observations in this area (Stoecker et al., 1995; Fonda Umani et al., 1998; Monti and Fonda Umani, 1999). The consumer community increased in both biomass and complexity over the summer. The biomass of heterotrophic nano- and microplankton was in the higher range of values (or even higher) of summer records from the Indian sector of the Southern Ocean (Becquevort et al., 2000). Microzooplankton concentrations were similar, but generally in the lower range, to values reported for the Ross Sea polynya from early spring to late summer (Caron et al., 2000). Bacterial biomass varied over a wider range of values in our study, but was of the same order of magnitude of those reported by Becquevort et al. (2000). Bacterial abundances in the euphotic zone were similar to those observed in the polynya of the Ross Sea from mid-January to early February (Ducklow et al., 2000).

Microzooplankton biomass was always positively related to bacteria ($n=32$, $r=0.68$, $p<0.001$) and heterotrophic nanoflagellates ($n=32$, $r=0.42$, $p<0.05$), but not significantly related to nanodiatoms. Microzooplankton generally represents the major grazer of total nanoplankton, including both hetero- and autotrophic forms (Froneman and Perissinotto, 1996). The lack of a direct correlation with nanodiatoms probably suggests that, when available, larger diatoms were preferred as food, particularly by heterodinoflagellates (Jacobson and Anderson, 1986; Hansen, 1992; Hansen and Nielsen, 1997). Microzooplankton is considered as an efficient consumer of bacteria (Sherr et al., 1987, 1989; Vaqué et al., 1994), even if heterotrophic nanoflagellates are known to be their most active predators (Fenchel, 1982; Rassoulzadegan and Sheldon, 1986; Vaqué et al., 1994). The coupling between bacteria and microzooplankton increases is likely to result from an indirect control of bacterial biomass through grazing of microzooplankton on heteronanoflagellates (Thingstad and Rassoulzadegan, 1995).

Throughout the sampling period sedimentation rates were measured in the polynya of Terra Nova Bay by a time-series sediment trap moored at 180 m depth at 75°06′ S, 164°13′ E, in close proximity to Sts. 2 and 135. (Accornero et al., submitted for publication). The sinking of biogenic materials from the upper water column was very low in December 1997 (3.02 mg m^{-2} day^{-1}) and included very small amounts of faecal pellets. The downward flux peaked 1–2 weeks after our early February sampling, attaining 144.6 mg m^{-2} day^{-1}. At this time the flux mostly consisted of diatomaceous detritus and large amounts of faecal pellets. The micro-sized diatoms, which predominated in the water column in early February, are known to be largely grazed upon by copepods and krill and can enhance sedimentation rates directly after dead or indirectly through large faecal pellets production (Legendre and LeFèvre, 1992). In the study area, the microzooplankton biomass had substantially increased and the Chl *a*/Phaeo ratio had strongly decreased from December to February, possibly suggesting an increase in the grazing activity. In late February/early March, the downward flux significantly decreased (35.6 mg m^{-2} day^{-1}) and the faecal pellet component reduced to a third. In the overlying water column, the microphyto- and microzooplankton biomasses had maintained relatively constant values over February and the Chl *a*/Phaeo ratio had increased. Although we cannot exclude that sedimentation in late February was hindered by hydrodynamic conditions (see Accornero et al., 1999), it is also reasonable to hypothesize that an efficient microbial food web, exploiting the DOC released during the blooming season, could play a significant role in retaining biogenic materials in the upper water column. This hypothesis is supported by the significant increase of bacterial biomass observed in the water column from late spring to summer (Table 1). Microbial populations are known to respond efficiently to phytoplankton blooms in the Ross Sea (Fabiano et al., 1999b) and other polar waters (Sullivan et al., 1990; Deibel et al., 2000), by utilizing and mineralizing a large part of the available organic matter.

5. Synthesis and conclusion

Conceptual models have highlighted the importance of the planktonic community structure and dynamics in determining the fate of biogenic carbon (Legendre and Rassoulzadegan, 1996; Legendre and Michaud, 1998; Boyd and Newton, 1999). As a result of these dynamics, biogenic materials can either accumulate or be recycled within the upper

water column, where they ultimately reintegrate the dissolved inorganic carbon pool, and hence hinder the CO_2 uptake from the atmosphere, or be exported to depth, leading to the sequestration of carbon and consequent enhancement of the CO_2 pump.

Our study confirms the results of previous investigations of the evolution of phytoplankton size and succession in the polynya of Terra Nova Bay throughout the summer (Arrigo et al., 1999). The novelty of this work is the interdisciplinary approach of relating the dynamics of the whole plankton community to the biogenic suspended and sinking materials (with special consideration of the hydrodynamic control), with the main objective of understanding how the composition and trophic dynamics of the plankton community can affect the ultimate fate of the autotrophically produced carbon. With this approach we identified the succession of three distinct periods. In early December *Phaeocystis* dominated the plankton assemblage in the well-mixed water column, while at the retreating ice-edge a bloom of small diatoms (ND) was developing in the lens of superficial diluted water. Concentrations of biogenic particulates were generally low and confined to the uppermost layer. The very low downward fluxes, the near absence of faecal pellets, and the high Chl *a*/Phaeo ratios suggest that the herbivorous food web is not established yet or, at least, is not working efficiently. In early February, the superficial pycnocline and the increase in water column stability favored the development of the most intense bloom of the season, essentially sustained by micro-sized diatoms (MD). The shift of the autotrophic community towards this size component produced major changes in the composition of particulate matter and determined its export to depth. The POC/Chl *a* and Chl *a*/Phaeo ratios more than halved, BSi/POC and BSi/Chl *a* strongly increased. Downward fluxes were greatly enhanced (reaching the maximum of the whole year) and essentially occurred via faecal pellets, underscoring the high efficiency of the herbivorous food web. In late February the deepening of the pycnocline, together with the decrease in light intensity, contributed to halting the diatom bloom. The biomass of small heterotrophs (HNF and MCZ) significantly increased relative to the previous period, favoring the shift toward a mistivorous food web (*sensu* Legendre and Rassoulzadegan, 1995) and resulting in the retention of biogenic matter in the superficial layer.

From the above considerations we can conclude that processes occurring in the uppermost layer essentially fuel the microbial food web in late spring, as a result of the small size (ND) and specific composition (large contribution of *Phaeocystis*) of primary producers. This is due to two main reasons: (i) small phytoplanktons are essentially consumed by microheterotrophs (Legendre and LeFèvre, 1992), which produce buoyant faecal pellets with low carbon content, that remain in suspension for long periods (Nöthig and von Bodungen, 1989; Elbrächter, 1991; Longhurst, 1991; González, 1992); (ii) *Phaeocystis* is not grazed upon by mesozooplanktons (Smith et al., 1998), which are responsible for the production of fast sinking faeces. In late spring the upper layer processes supply biogenic carbon to the short-lived carbon pool and virtually hinder export, hampering the transfer of CO_2 from the atmosphere.

Only with the increase in the size of primary producers (MD) can the grazing food web become efficient (Legendre and LeFèvre, 1992), fuelling the long-lived carbon pool and enhancing export to depth (and hence carbon sequestration) via the sinking of large diatoms and numerous faecal pellets. The conditions predominating in the pelagic system of the Terra Nova Bay polynya in mid-summer are thus likely to actively increase the efficiency of the CO_2 pump, possibly causing Terra Nova Bay to act as a carbon sink.

Acknowledgements

We thank two anonymous reviewers for their helpful comments and valuable suggestions. We are grateful to Dr. S. Greco, for helping with the sample collection, and to all the physical oceanographers of the CLIMA group, for supplying CTD data. Special thanks are due to the crew of the R/V Italica, who helped us in overcoming all logistical problems. This research was supported by the Italian National Programme for Antarctic Research (PNRA)–CLIMA Project.

References

Accornero, A., Bergamasco, A., Monaco, A., Tucci, S., 1999. Particle fluxes at the edge of the Ross Ice Shelf: the role of physical forc-

ing. In: Spezie, G., Manzella, G.M.R. (Eds.), Oceanography of the Ross Sea (Antarctica). Springer-Verlag, Milano, pp. 165–173.
Accornero, A., Manno, C., Martini, A., Tucci, S., submitted for publication. The vertical flux of biogenic and lithogenic material in a coastal polynya of the western Ross Sea. Antarct. Sci.
Arrigo, K.R., McClain, C.R., 1994. Spring phytoplankton production in the western Ross Sea. Science 266, 261–263.
Arrigo, K.A., Weiss, A.M., Smith Jr., W.O. 1998. Physical forcing of phytoplankton dynamics in the southwestern Ross Sea. J. Geophys. Res. 103, 1007–1021.
Arrigo, K.R., Robinson, D.H., Worthen, D.L., Dunbar, R.B., DiTullio, G.R., VanWoert, M., Lizotte, M.P., 1999. Phytoplankton community structure and the drawdown of nutrients and CO_2 in the Southern Ocean. Science 283, 365–367.
Arrigo, K.A., DiTullio, G.R., Dunbar, R.B., Robinson, D.H., VanWoert, M., Worthen, D.L., Lizotte, M.P., 2000. Phytoplankton taxonomic variability in nutrient utilization and primary production in the Ross Sea. J. Geophys. Res. 105, 8827–8846.
Azam, F., 1998. Microbial control of oceanic carbon flux: the plot thickness. Science 280, 694–696.
Balech, E., 1976. Clave ilustrada de Dinoflagelados antarticos. Inst. Antart. Argent. 11, 1–100.
Becquevort, S., Menon, P., Lancelot, C., 2000. Differences of the protozoan biomass and grazing during spring and summer in the Indian sector of the Southern Ocean. Polar Biol. 23, 309–320.
Beers, J.R., Stewart, G.L., 1970. Numerical abundance and estimated biomass of microzooplankton. In: Strickland, J.D.H. (Ed.), The Ecology of the Plankton off La Jolla, California, in the Period April Through September 1967. University of California Press, Berkeley, pp. 67–87.
Bjornsen, P., Nielsen, T., 2000. Microbial plankton ecology studies in two Arctic polynyas. ASLO Aquatic Sciences Meeting "Research Across Boundaries", Copenhagen, Denmark, 5–9 June, SS02–SS13 Abstract book.
Boyd, P.W., Newton, P.P., 1999. Does planktonic community structure determine downward particulate organic carbon flux in different oceanic provinces. Deep-Sea Res., Part 1, Oceanogr. Res. Pap. 46, 63–91.
Brandt, K., 1906. Die Tintinnodeen der Plankton-Expedition. Tefelerklarungen nebts kurzer Diagnose der neuen Arten. Ergebn. Atlant. Ozean Planktonexped. Humboldt-Stift 3, 1–33.
Brandt, K., 1907. Die Tintinnodeen der Plankton-Expedition. Sistematischer Teil. Ergebn. Atlant. Ozean Planktonexped. Humboldt-Stift 3, 1–488.
Bromwich, D.H., Kurtz, D.D., 1984. Katabatic wind forcing of the Terra Nova Bay polynya. J. Geophys. Res. 89, 3561–3572.
Budillon, G., Spezie, G., 2000. Thermohaline Structure and variability in the Terra Nova Bay Polynya (Ross Sea) between 1995–98. Antarctic Science 12 (4), 501–516.
Burba, N., Feoli, E., Malaroda, M., Zuccarello, V., 1992. Un sistema informativo per la vegetazione. Software per l'archiviazione della vegetazione italiana e per l'elaborazione di tabelle. Manuale di utilizzo dei programmi. Quad. CETA 2, 78.
Carlson, C.A., Ducklow, H.W., Hansell, D.A., Smith Jr., W.O. 1998. Organic carbon partitioning during spring phytoplankton blooms in the Ross Sea polynya and the Sargasso Sea. Limnol. Oceanogr. 43, 375–386.
Caron, D.A., 1983. Technique for enumeration of heterotrophic and phototrophic nanoplankton, using epifluorescence microscopy, and comparison with other procedures. Appl. Environ. Microbiol. 46, 491–498.
Caron, D.A., Dennett, M.R., Lonsdale, D.J., Moran, D.M., Shalapyonok, L., 2000. Microzooplankton herbivory in the Microzooplankton herbivory in the Ross Sea, Antarctica. Deep-Sea Res., Part 2, Top. Stud. Oceanogr. 47, 3249–3272.
Catalano, G., Povero, P., Fabiano, M., Benedetti, F., Goffart, A., 1997. Nutrient utilisation and particulate organic matter changes during summer in the upper mixed layer (Ross Sea, Antarctica). Deep-Sea Res. 44, 97–112.
Corliss, J.O., 1979. The Ciliated Protozoa. Pergamon, London, p. 455.
Deibel, D., Saunders, P., Rivkin, R., Pakulski, J., Anderson, M., Acuna, J., Bussey, H., 2000. Trophic coupling of the microbial and metazoan food webs in the North Water Polynya (NOW). ASLO Aquatic Sciences Meeting "Research Across Boundaries", Copenhagen, Denmark, 5–9 June, SS07–SS38 Abstract book.
DeMaster, D.J., 1991. Measuring biogenic silica in marine sediments and suspended matter. In: Marine Particles: Analysis and Characterization. Geophysical Monograph, vol. 63 AGU, Washington, DC, pp. 363–367.
Ducklow, H.W, Dickson, M.L., Kirchman, D.L., Steward, G., Orchardo, J., Marra, J., Azam, F., 2000. Constraining bacterial production, conversion efficiency and respiration in the Ross Sea, Antarctica, January–February 1997. Deep-Sea Res., Part 2, Top. Stud. Oceanogr. 47, 3227–3247.
Edler, L., 1979. Recommendations on methods for marine biological studies in the Baltic Sea. Phytoplankton and chlorophyll. Balt. Mar. Biol. Publ. 5, 1–37.
Elbrächter, M., 1991. Faeces production by dinoflagellates and other small flagellates. Mar. Microb. Food Webs 5, 189–204.
El-Sayed, S.E., Biggs, D.C., Holm-Hansen, O., 1983. Phytoplankton standing crop, primary productivity, and near-surface nitrogenous nutrient fields in the Ross Sea, Antarctica. Deep-Sea Res. 30, 871–886.
Fabbris, L., 1997. Statistica multivariata—Analisi esplorativa dei dati. McGraw-Hill Libri Italia srl, Milan, Italy, p. 437, ISBN 883860765-6.
Fabiano, M., Povero, P., Danovaro, R., 1996. Particulate organic matter composition in Terra Nova Bay (Ross Sea, Antarctica) during summer 1990. Antartic Science 8, 7–13.
Fabiano, M., Danovaro, R., Povero, P., 1999a. Vertical distribution and biochemical composition of pico- and microparticulate organic matter in the Ross Sea (Antarctica). In: Spezie, G., Manzella, G.M.R. (Eds.), Oceanography of the Ross Sea (Antarctica). Springer-Verlag, Berlin, pp. 233–246.
Fabiano, M., Povero, P., Misic, C., 1999b. Spatial and temporal distribution of particulate organic matter in the Ross Sea. In: Faranda, F.M., Guglielmo, L., Ianora, A. (Eds.), Ross Sea Ecology. Springer-Verlag, Berlin, pp. 135–149.
Fenchel, T., 1982. Ecology of heterotrophic microflagellates. II. Bioenergetics and growth. Mar. Ecol., Prog. Ser. 8, 225–231.
Fonda Umani, S., Monti, M., Nuccio, C., 1998. Microzooplankton biomass distribution in photic and aphotic layers in the Ross Sea. J. Mar. Syst. 17, 287–302.

Froneman, P.W., Perissinotto, R., 1996. Structure and grazing of the microzooplankton communities of the Subtropical Convergence and a warm-core eddy in the Atlantic sector of the Southern Ocean. Mar. Ecol., Prog. Ser. 135, 237–245.

Goffart, A., Catalano, G., Hecq, J.H., 2000. Factors controlling the distribution of diatoms and *Phaeocystis* in the Ross Sea. J. Mar. Syst. 27, 161–175.

González, H.E., 1992. Distribution and abundance of minipellets around the Antarctic Peninsula: implications for protistan feeding behaviour. Mar. Ecol., Prog. Ser. 90, 223–236.

Hamburger, C., Buddenbrock, H., 1911. Nordisches ciliata mit ausschluss der Titinnoidea. Nordisches Plankton Zoologischer Teil VII Protozoa. Neudruck A. Asher & Co., Amsterdam, pp. 1–152.

Hansen, P.J., 1992. Prey selection, feeding rates and growth dynamics of heterotrophic dinoflagellates with special emphasis on *Gyrodinium spirale*. Mar. Biol. 114, 327–334.

Hansen, P.J., Nielsen, T.G., 1997. Mixotrophic feeding of *Fragilidium subglobosum* (Dinophyceae) on three species of *Ceratium*: effects of prey concentration, prey species and light intensity. Mar. Ecol., Prog. Ser. 147, 187–196.

Hanson, R.B., Ducklow, H.W., Field, J.G., 2000. . The Changing Ocean Carbon Cycle. A Midterm Synthesis of the Joint Global Ocean Flux Study. Cambridge Univ. Press, Cambridge, p. 514.

Hasle, G.R., Syvertsen, E., 1996. Marine diatoms. In: Tomas, C.R. (Ed.), Identifying Marine Diatoms and Dinoflagellates. Academic Press, San Diego, pp. 1–385.

Horner, R., Ackley, S.F., Dieckmann, G.S., Gulliksen, B., Hoshial, T., Melnikov, I.A., Reeburgh, W.S., Spindler, M., Sullivan, C.W., 1992. Ecology of sea ice biota: 1. Habitat and terminology. Polar Biol. 12, 417–427.

Innamorati, M., Lazzara, L., Mori, C., Nuccio, C., Saggiomo, V., 1991. Phytoplankton ecology. Nat. Sc. Com. Ant. Ocean. Camp. 1989–90. Data Rep. 1, 141–252.

Innamorati, M., Lazzara, L., Massi, L., Mori, C., Nuccio, C., Saggiomo, V., 1992. Indagine sulla biomassa fitoplanctonica nel Mare di Ross in relazione ai fattori ambientali. Atti Seminario Internazionale Oceanografia in Antartide. ENEA-Progetto Antartide Italia, Conception, Chile, pp. 235–252.

Innamorati, M., Mori, C., Massi, L., Lazzara, L., Nuccio, C., 1999. Phytoplankton biomass related to environmental factors in the Ross Sea. In: Faranda, F.M., Guglielmo, L., Ianora, A. (Eds.), Ross Sea Ecology. Springer-Verlag, Berlin, pp. 217–230.

Jacobson, D.M., Anderson, D.M., 1986. Thecate heterotrophic dinoflagellates: feeding behavior and mechanism. J. Phycol. 22, 249–258.

Kang, S.H., Lee, S.H., 1995. Antarctic phytoplankton assemblages in the western Bransfield Strait region. February 1993. Composition, biomass, and mesoscale distribution. Mar. Ecol., Prog. Ser. 129, 253–267.

Karl, D.M., Christian, J.R., Dore, J.E., Letelier, R.M., 1996. Microbiological oceanography in the region west of the Antarctica Peninsula: microbial dynamics, nitrogen cycle and carbon flux. In: Foundations for Ecological Research in the Region West of the Antarctica Peninsula. Antarctic Res. Ser. 70, 303–332.

Kofoid, C.A., Campbell, A.S., 1929. A conspectus of the marine and fresh-water Ciliata belonging to the suborder Tintinnoinea with descriptions of new species principally from the Agassiz Expedition to the eastern tropical Pacific, 1904–1905. Univ. Calif. Publ. Zool. 34, 1–403.

Kofoid, C.A., Campbell, A.S., 1939. Reports on the scientific results of the expedition to the Eastern Tropical Pacific. The Ciliata: the Tintinnoinea. Bull. Mus. Comp. Zool. 84, 1–473.

Krank, K., Milligan, T., 1978. The use of the Coulter Counter in studies of particle size distribution. Aquatic Environment Report Series BI-R.79. Bedford Institute of Oceanography, Dartmouth, Canada.

Laackmann, H., 1910. Die Tintinnodeen der Deutschen Südpolar-Expedition 1901–1903. Dtsch. Südpolar-Exped. 1901–1903 11, 341–496.

Legendre, L., 1996. The biological CO_2 pump in seasonally ice-covered waters. Proc. NIPR Symp. Polar Biol. 9, 61–74.

Legendre, L., LeFèvre, J., 1992. Interactions between hydrodynamics and pelagic ecosystems: relevance to resource exploitation and climate change. S. Afr. J. Mar. Sci. 12, 477–486.

Legendre, L., Michaud, J., 1998. Flux of biogenic carbon in oceans: size-dependent regulation by pelagic food webs. Mar. Ecol., Prog. Ser. 164, 1–11.

Legendre, L., Rassoulzadegan, F., 1995. Plankton and nutrient dynamics in marine waters. Ophelia 41, 153–172.

Legendre, L., Rassoulzadegan, F., 1996. Food web mediated export of biogenic carbon in oceans: hydrodynamic control. Mar. Ecol., Prog. Ser. 145, 179–193.

Legendre, L., Ackley, S.F., Dieckmann, G.S., Gulliksen, B., Horner, R., Hoshiai, T., Melnikov, I.A., Reeburgh, W.S., Spindler, M., Sullivan, C.W., 1992. Ecology of sea ice biota: 2. Global significance. Polar Biol. 12, 429–444.

Longhurst, A.R., 1991. Role of the marine biosphere in the global carbon cycle. Limnol. Oceanogr. 36, 1507–1526.

Lorenzen, C.J., Jeffrey, S., 1980. Determination of chlorophyll in seawater. SCOR UNESCO, Tech. Pap. Mar. Sci. 35, 1–20.

Lynn, D.H., Montagnes, D.J.S., 1988a. Taxonomic descriptions of some conspicuous species of Strobilidiine ciliates (Ciliophora: Choreotrichida) from the Isles of Shols, Gulf of Maine. J. Mar. Biol. Assoc. U.K. 68, 639–658.

Lynn, D.H., Montagnes, D.J.S., 1988b. Taxonomic descriptions of some conspicuous species of Strombidiidae (Ciliophora: Oligotrichida) from the Isles of Shols, Gulf of Maine. J. Mar. Biol. Assoc. U.K. 68, 259–266.

Marino, D., Cabrini, M., Cataletto, B., in preparation. Phytoplankton structure and dynamics in the Ross Sea during austral spring.

Martinussen, I., Thingstad, T.F., 1991. A simple double staining technique for simultaneous quantification of auto- and heterotrophic nano- and picoplankton. Mar. Microb. Food Webs 5, 5–11.

Medlin, L.K., Priddle, J., 1990. Polar marine diatoms. British Antarctic Survey. Natural Environment Research Council. Cambridge Univ. Press, Cambridge, p. 214.

Monti, M., Fonda Umani, S., 1999. Distribution of the main microzooplankton taxa in the Ross Sea (Antarctica): austral summer 1994. In: Faranda, F.M., Guglielmo, L., Ianora, A. (Eds.), Ross Sea Ecology. Springer-Verlag, Berlin, pp. 275–289.

Mortlock, R.A., Froelich, P.N., 1989. A simple method for the determination of biogenic opal in pelagic marine sediments. Deep-Sea Res. 36, 1415–1426.

Nelson, D.M., Treguer, P., 1992. Role of silicon as a limiting nutrient to Antarctic diatoms: evidence from kinetic studies in the Ross Sea ice-edge zone. Mar. Ecol., Prog. Ser. 80, 255–264.

Nielsen, T., Thomsen, H., Hansen, B., Levinsen, H., Madsen, S., 2000. Annual dynamics of primary and bacterial production in the Disko Bay, western Greenland. ASLO Aquatic Sciences Meeting "Research across boundaries", Copenhagen, Denmark, 5–9 June, SS06–SS38 Abstract book.

Nöthig, E.-M., von Bodungen, B., 1989. Occurrence and vertical flux of faecal pellets of probably protozoan origin in the southeastern Weddell Sea (Antarctica). Mar. Ecol., Prog. Ser. 56, 281–289.

Nuccio, C., Innamorati, M., Lazzara, L., Mori, G., 1992. Popolamenti fitoplanctonici nella Baia di Terranova, Mare di Ross. Atti Seminario Internazionale Oceanografia in Antartide. ENEA Progetto Antartide Italia, Conception, Chile, pp. 253–262.

Nuccio, C., Innamorati, M., Lazzara, L., Mori, G., Massi, L., 1999. Spatial and temporal distribution of phytoplankton assemblages in the Ross Sea. In: Faranda, F.M., Guglielmo, L., Ianora, A. (Eds.), Ross Sea Ecology. Springer-Verlag, Berlin, pp. 231–245.

Porter, K., Feig, Y.S., 1980. The use of DAPI for identify and counting aquatic microflora. Limnol. Oceanogr. 25, 943–948.

Povero, P., Fabiano, M., Catalano, G., 1999. Particulate organic matter and nutrient utilization in the mixed layer of the Ross Sea. In: Faranda, F.M., Guglielmo, L., Ianora, A. (Eds.), Ross Sea Ecology. Springer-Verlag, Berlin, pp. 121–134.

Priddle, J., Fryxell, G., 1985. Handbook of the common plankton diatoms of the Southern Ocean: Centrales except the genus *Thalassiosira*. British Antarctic Survey. Natural Environment Research Council. Cambridge Univ. Press, Cambridge, p. 159.

Putt, M., Stoecker, D.K., 1989. An experimentally determined carbon: volume ratio for marine "oligotrichous" ciliates from estuarine and coastal waters. Limnol. Oceanogr. 34, 1097–1107.

Putt, M., Miceli, G., Stoecker, D.K., 1994. Association of bacteria with *Phaeocystis* sp. in McMurdo Sound, Antarctica. Mar. Ecol., Prog. Ser. 105, 179–189.

Quéguiner, B., Tréguer, P., Peeken, I., Scharek, R., 1997. Biogeochemical dynamics and the silicon cycle in the Atlantic sector of the Southern Ocean during austral spring 1992. Deep-Sea Res., Part 2, Top. Stud. Oceanogr. 44, 69–89.

Rassoulzadegan, F., Sheldon, R.W., 1986. Predator–prey interactions of nanozooplankton and bacteria in an oligotrophic marine environment. Limnol. Oceanogr. 31, 1010–1021.

Robineau, B., Legendre, L., Therriault, J.C., Fortier, L., Rosenberg, G., Demers, S., 1994. Ultra-algae (< 5 μm) in the ice, at the ice–water interface and in the under-ice water column (southeastern Hudson Bay Canada). Mar. Ecol., Prog. Ser. 115, 169–180.

Saggiomo, V., Carrada, G.C., Mangoni, O., Ribera d'Alcalà, M., Russo, A., 1998. Spatial and temporal variability of size fractionated biomass and primary production in the Ross Sea (Antarctica) during the austral spring and summer. J. Mar. Syst. 17, 115–127.

Sedwick, P.N., DiTullio, G.R., Mackey, D.J., 2000. Iron and manganese in the Ross Sea, Antarctica: seasonal iron limitation in Antarctic shelf waters. J. Geophys. Res. 105, 11321–11336.

Sherr, B.F., Sherr, E.B., Fallon, R.D., 1987. Use of monodispersed, fluorescently labeled bacteria to estimate in situ protozoan bacterivory. Appl. Environ. Microbiol. 53, 958–965.

Sherr, B.F., Sherr, E.B., Pedro-Alto, C., 1989. Simultaneous measurement of bacterioplankton production and protozoan bacterivory in estuarine water. Mar. Ecol., Prog. Ser. 54, 209–219.

Smith Jr., W.O., Dunbar, R.B. 1998. The relationship between new production and vertical flux on the Ross Sea continental shelf. J. Mar. Syst. 17, 445–457.

Smith Jr., W.O., Gordon, L.J. 1997. Hyperproductivity of the Ross Sea (Antarctica) polynya during austral spring. Geophys. Res. Lett. 24, 233–236.

Smith Jr., W.O., Nelson, D.M. 1985. Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with the density field. Science 227, 163–166.

Smith Jr., W.O., Nelson, D.M., DiTullio, G.R., Leventer, A.R. 1996. Temporal and spatial patterns in the Ross Sea: phytoplankton biomass, elemental composition, productivity and growth rates. J. Geophys. Res. 101, 18467–18478.

Smith Jr., W.O., Carlson, C.A., Ducklow, H.W., Hansell, D.A. 1998. Growth dynamics of *Phaeocystis antarctica*-dominated plankton assemblages from the Ross Sea. Mar. Ecol., Prog. Ser. 168, 229–244.

Spindler, M., Dieckmann, G., 1994. Ecological significance of the sea ice biota. In: Hempel, G. (Ed.), Antarctic Science. Springer-Verlag, Berlin, pp. 60–68.

Steindinger, K.A., 1996. Dinoflagellates. In: Tomas, C.R. (Ed.), Identifying Marine Diatoms and Dinoflagellates. Academic Press, San Diego, pp. 387–598.

Stoecker, D.K., Putt, M., Moisan, T., 1995. Nano- and microplankton dynamics during the spring *Phaeocystis* sp. bloom in McMurdo sound, Antarctica. J. Mar. Biol. Assoc. U.K. 75, 815–832.

Strathmann, R.R., 1967. Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnol. Oceanogr. 12, 411–418.

Sullivan, W.C., Cota, G.F., Krempin, D.W., Smith Jr., W.O., 1990. Distribution and activity of bacterioplankton in the marginal ice zone of the Weddel-Scotia Sea during austral spring. Mar. Ecol., Prog. Ser. 63, 239–252.

Sullivan, C.W., Arrigo, K.R., McClain, C.R., Comiso, J.C., Firestone, J., 1993. Distributions of phytoplankton blooms in the Southern Ocean. Science 262, 1832–1837.

Sunda, W.G., Huntsman, S.A., 1997. Interrelated influence of iron, light and cell size on marine phytoplankton growth. Nature 390, 389–392.

Thingstad, T.F., Rassoulzadegan, F., 1995. Nutrient limitation, microbial food webs, and biological "C-pumps", suggested interactions in P-limited Mediterranean. Mar. Ecol., Prog. Ser. 117, 299–306.

Throndsen, J., 1993. The planktonic marine flagellates. In: Tomas, C.R. (Ed.), Marine Phytoplankton: A Guide to Naked Flagellates and Coccolithophorids. Academic Press, San Diego, pp. 7–145.

Tréguer, P., Pondaven, P., Boyd, P.W., Anderson, R.F., Nelson, D.M., in press. Climatic changes and the cycle of carbon in the Southern Ocean. Deep-Sea Res., Part 2, Top. Stud. Oceanogr.

UNESCO, 1991. Processing of Oceanographic Station Data, 138 Paris.

UNESCO, 1994. Protocols for the Joint Global Ocean Flux Study (JGOFS) Core Measurements. UNESCO, Paris, p. 170.

Utermöhl, H., 1958. Zur Vervolkommung der quantitativen Phytoplankton-Methodik. Mitt. Int. Ver. Theor. Angew. Limnol. 9, 1–38.

Vanucci, S., Bruni, V., 1998. Presence or absence of picophytoplankton in the western Ross Sea during spring 1994: a matter of size definition? Polar Biol. 20, 9–13.

Vanucci, S., Bruni, V., 1999. Ultraphytoplanktonic community structure in the Ross Sea during the austral spring 1994. In: Faranda, F.M., Guglielmo, L., Ianora, A. (Eds.), Ross Sea Ecology. Springer-Verlag, Berlin, pp. 181–193.

Vaqué, D., Gasol, J.M., Marras, C., 1994. Grazing rates on bacteria: the significance of methodology and ecological factors. Mar. Ecol., Prog. Ser. 109, 263–274.

Villafane, V.E., Hebling, E.W., Holm-Hansen, O., 1995. Spatial and temporal variability of phytoplankton biomass and taxonomic composition around Elephant Island, Antarctica, during the summers 1990–1992. Mar. Biol. 123, 677–686.

Volk, T., Hoffert, M.I., 1985. Ocean carbon pumps: analysis of relative strenghts and efficiencies in ocean-driven atmospheric CO_2 changes. In: Sundquist, E.T., Broecker, W.S. (Eds.), The Carbon Cycle and Atmospheric CO_2: Natural Variations Archean to Present. Am. Geophys. Union, Washington, DC, pp. 99–110 (AGU monograph 32).

Zingone, A., Honsell, G., Marino, D., Montresor, M., Socal, G., 1990. Fitoplancton. In: Innamorati, M., Ferrari, I., Marino, D., Ribera D'Alcalà, M. (Eds.), Metodi nell'ecologia del plancton marino. Nova Thalassia, vol. 11, pp. 183–198 (suppl.).