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# Abundance and distribution of phototrophic and heterotrophic nano- and microplankton in the southern Ross Sea

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**Abstract**

Phototrophic and heterotrophic nanoplankton (PNAN, HNAN; 2–20 μm protists) and microplankton (PMIC, HMIC; 20–200 μm protists and micrometazoa) are major taxa involved in partitioning carbon and energy within the pelagic food web. In the Ross Sea, Antarctica, plankton biomass appears to be controlled by the seasonal recession of the sea ice and the formation of the Ross Sea polynya during the short austral spring-summer period. During four cruises in 1996–1997 within the southern Ross Sea as part of the US JGOFS program, we determined the abundances and biomasses of phototrophic and heterotrophic nanoplankton and microplankton primarily along a transect at 76°30′S. The colonial prymnesiophyte *Phaeocystis antarctica* (excluding mucus carbon) contributed significantly to community structure during both non-bloom and bloom periods (~25% and 90%, respectively, of microbial biomass). However, shifts occurred both seasonally and spatially between a diatom/heterotrophic dinoflagellate and a colonial *P. antarctica*-dominated assemblage. While nanoplankton biomass varied <50% during any particular cruise, PNAN and HNAN biomass ranged more than three orders of magnitude among the four cruises (0.1–359 and 1.5–268 mmol C $m^{-2}$, respectively). Cruise averages of PMIC biomass ranged from 2.5 to 530 mmol C $m^{-2}$, and a maximum biomass of 1530 mmol C $m^{-2}$ was observed during the bloom of colonial *P. antarctica* in summer. Average heterotrophic biomass was <30% of the total microbial biomass (excluding bacteria) from early austral spring through summer. This value rose to ≈87% in autumn following the decline and disappearance of *P. antarctica*. The contribution of total nano- and microplankton biomass to POC in the upper 60 m over the three sampled seasons varied from 7% to 52.4% with an overall average of 21.8% for all four cruises which is comparable to contributions of these assemblages in other oceans even with the strong seasonal dominance of *P. antarctica*. 

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## 1. Introduction

Massive phytoplankton blooms are regular, seasonal occurrences in the Ross Sea, Antarctica (e.g., Smith and Nelson, 1985; Arrigo and McClain, 1994; Arrigo et al., 1998; Smith et al., 2000b). Indeed, the magnitude of the seasonal phytoplankton maximum is among the largest observed anywhere in the ocean, with particulate organic carbon concentrations at times exceeding $120\,\mu mol\,l^{-1}$ (Smith et al., 1996) and biogenic silica concentrations exceeding $60\,\mu mol\,l^{-1}$ (Smith and Nelson, 1985). Satellite imagery and on-site water sampling indicate that microalgal growth is initiated by at least early November, with the biomass maximum occurring by late December or early January (Smith et al., 2000b). The bloom appears to be related spatially and temporally to the appearance of the Ross Sea polynya, which greatly expands in spring.

Recent studies have shown that two phytoplankton taxa dominate the phytoplankton assemblages of the region: diatoms, which often occur in the western and eastern portions of the southern Ross Sea (Leventer and Dunbar, 1996; Sweeney et al., 2000), and prymnesiophytes, which generally are found in the south central region (DiTullio and Smith, 1996; Arrigo et al., 1999). Locations dominated by cryptophytes also have been observed, but these are largely restricted to waters near the coast influenced by glacial run-off (Arrigo et al., 1999).

Diatom assemblages in the western region of the Ross Sea have been shown to be dominated frequently by the pennate diatom *Fragilariopsis curta* (Smith and Nelson, 1985), although other forms (e.g., *Fragilariopsis* sp., *Thalassiosira* sp.) also contribute substantially both to total abundance and biomass (El-Sayed et al., 1983; Leventer and Dunbar, 1996). Prymnesiophytes in the south central region are dominated by the species *P. antarctica* which, like other species within the genus *Phaeocystis*, has a pleomorphic life history (Lancelot et al., 1998). In all regions where *P. antarctica* blooms develop, it is the colonial form that dominates, although solitary cells are also present as well (Mathot et al., 2000). Colonies of *P. antarctica* are generally spherical and can reach up to 600 μm in diameter, and upon a reduction in growth, age or senescence become distorted into cylinders or other, non-spherical shapes. The colonies are hollow, and cells are housed in an organic mucus matrix (Hamm et al., 1999). During periods of rapid growth, the matrix constitutes a small part (ca. 15%) of the total organic matter of colonies, but this increases to maximal contributions near 35% by mid-summer in the Ross Sea (Mathot et al., 2000).

Surveys of Ross Sea phytoplankton based on pigments have indicated that the distributions of diatoms and *P. antarctica* are largely but not completely distinct. DiTullio and Smith (1996) found that areas with the largest 19′-hexanoyloxyfucoxanthin concentration (19-hex, a proxy for *P. antarctica*) had less than $0.4\,\mu g\,l^{-1}$ fucoxanthin (a diatom pigment). Conversely, when fucoxanthin exceeded $2.8\,\mu g\,l^{-1}$, 19-hex concentrations were reported to be less than $0.3\,\mu g\,l^{-1}$. This observation indicates that while one group was clearly dominant, the other still reached detectable concentrations. Arrigo et al. (1999) and Smith and Asper (2001) confirmed this finding.

Analyses of phytoplankton biomass in the Ross Sea have been restricted largely to chemical pigment analyses, and few data are available on the contribution of these taxa to total plankton biomass or to standing stocks of particulate organic carbon. Although numerically dominant in some areas, single cells of *P. antarctica* are small (generally about 4 μm in diameter), whereas diatoms can be significantly larger (15–60 μm). Thus, diatoms often contribute more to carbon biomass relative to solitatary *P. antarctica* than indicated by abundance estimates. Furthermore, diatoms and *P. antarctica* may play different ecological and biogeochemical roles in these waters.

Diatoms may be grazed heavily by micro- and mesozooplankton (DiTullio and Smith, 1996), whereas *P. antarctica* in the Ross Sea is ingested at very low rates by microzooplankton (Caron et al., 2000). Diatoms contribute substantially to vertical flux to the benthos on an annual basis, whereas *P. antarctica* is more completely remineralized within the water column (Smith and Dunbar, 1998) although *P. antarctica* does form large aggregates that sink rapidly and episodically to the sea floor (DiTullio et al., 2000).

Relative to phytoplankton distributions and abundances, little is known about nano- (2–20 μm) and micro- (20–200 μm) zooplankton in the Ross Sea. Diverse assemblages of heterotrophic protistan species inhabit these waters, including substantial populations of ciliated protozoa, heterotrophic dinoflagellates and choanoflagellates (Marchant, 1985; Garrison and Gowing, 1993; Marchant and Murphy, 1994; Garrison et al., 1996). However, seasonal abundances and biomasses of these assemblages are very poorly characterized. Nevertheless, these assemblages may play fundamental roles in the consumption of bacterial and microalgal biomass in the Ross Sea, and may serve as an important food source for mesozooplankton (Caron et al., 1999; Caron et al., 2000; Lonsdale et al., 2000).

In this study, we report results from a series of cruises to the southern Ross Sea in 1996–1997 as part of the US JGOFS (AESOPS) program. The overall goals of the project were to assess the time-varying fluxes among the various pools of carbon in the Ross Sea, and to investigate the controls on these fluxes (Smith et al., 2000a). Here we attempt to quantify the contributions of phototrophic and heterotrophic nanoplankton and microplankton to the carbon budget of the surface waters of the region in order to elucidate the variations (and their causes) in the biomass of the major taxonomic groups.

## 2. Material and methods

Samples were collected for nanoplankton (2–20 μm) and microplankton (20–200 μm) on all four of the US JGOFS Ross Sea cruises aboard the R.V.I.B. *Nathanial B. Palmer* (Table 1). Principal sampling stations were located 2° apart between 169°E and 178°W along 76°30′S latitude (Fig. 1). Stations along this line were visited at least once during each cruise. Reoccupation during a single cruise depended on ice conditions. Additional stations were also occupied occasionally as time permitted (i.e. a full transect was not performed). These additional stations included Ice Shelf located near the Ross Ice Shelf, Sei in the northern Ross Sea, and Cooper between Stations A and E along the main transect (Fig. 1). Nine, five, five and seven additional occupations of stations along 76°30′S were conducted during the early spring, summer, autumn and late spring cruises, respectively. These latter data were excluded from the abundance and biomass data in Figs. 2–8 to facilitate comparisons of transects. However, information from the additional stations was included in the overall summary (Table 1) and in an examination of the seasonal contribution of heterotrophic biomass to total nano- and microplankton biomass.

Water from the upper 100 m was collected using Niskin or Go-Flo bottles on a rossette sampler. Depths sampled for nano- and microplankton counts varied depending upon water column characteristics (e.g. depth of the chlorophyll maximum or the 1% isolume). Up to five depths were routinely sampled from each vertical profile. Chlorophyll concentrations, mixed-layer depths and

Table 1
Mean, minimum, and maximum values for nano- and microplankton integrated (0–60 m) abundance and carbon biomass during 1996 and 1997. [# stations] is the number of stations used for the analysis of each cruise

| | | Abundance $\times 10^4$ cells $l^{-1}$ | | | | Biomass mmol C $m^{-2}$ | | | |
|---|---|---|---|---|---|---|---|---|---|
| Dates/cruise | | PNAN | HNAN | PMIC | HMIC | PNAN | HNAN | PMIC | HMIC |
| *Early spring* | Mean (13 stations) | 23.1 | 2.66 | 22.2 | 0.13 | 6.6 | 3.5 | 17 | 6.3 |
| 10/2/96–11/8/96 | Min | 5.72 | 0.82 | 0.02 | 0.04 | 2.6 | 1.5 | 0.1 | 0.4 |
| NBP96-4A | Max | 55.5 | 4.14 | 100 | 0.24 | 12 | 6.7 | 70 | 55 |
| *Spring* | Mean (22 stations) | 146 | 84.5 | 514 | 0.89 | 39 | 33 | 241 | 43 |
| 11/5/97–12/13/97 | Min | 15.3 | 25.1 | 5.82 | 0.17 | 7.7 | 2.6 | 11 | 6.2 |
| NBP97-8 | Max | 567 | 135 | 1990 | 1.39 | 103 | 66 | 1400 | 178 |
| *Mid-summer* | Mean (20 stations) | 326 | 190 | 657 | 0.63 | 109 | 89 | 530 | 193 |
| 1/13/97–2/11/97 | Min | 13.1 | 38.9 | 160 | 0.08 | 28 | 16 | 132 | 0.6 |
| NBP97-1 | Max | 1140 | 603 | 2170 | 2.14 | 359 | 268 | 1530 | 1090 |
| *Autumn* | Mean (12 stations) | 1.24 | 23.1 | 2.41 | 0.19 | 0.3 | 13 | 2.5 | 3.8 |
| 4/4/97–5/12/97 | Min | 0.20 | 17.5 | 1.16 | 0.05 | 0.1 | 7.9 | 1.2 | 0.4 |
| NBP97-3 | Max | 2.30 | 30.8 | 4.72 | 0.58 | 0.7 | 20 | 6.2 | 14 |

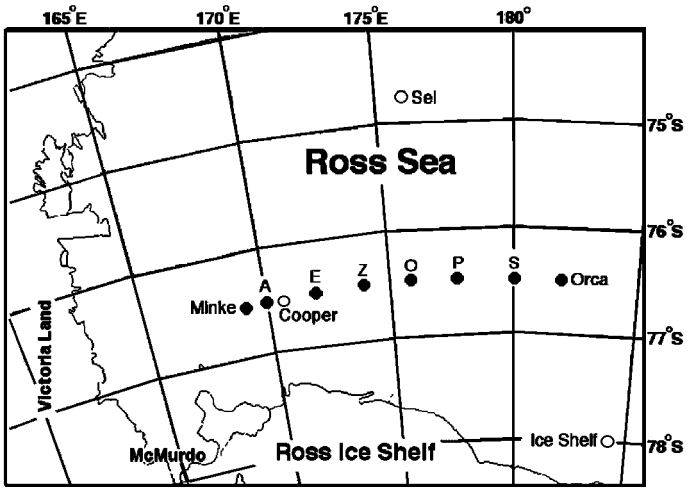


Fig. 1. Principal sampling stations (solid circles). Each station along 76°30′S is separated by approximately 2° of longitude. Additional stations (open circles) occupied as time permitted.

the depth of the 1% light levels for each station were determined fluorometrically, from density profiles, and from continuous measurements of irradiance within the water column.

Samples for the enumeration of phototrophic (i.e. chloroplast-bearing) and heterotrophic (apochlorotic) nanoplankton (PNAN, HNAN, 2–20 μm algae and protozoa, respectively) were preserved with 1% formalin or 0.5% glutaraldehyde (from 10% stock solutions prepared with filtered natural seawater) and refrigerated until processed for epifluorescence microscopy (within 24 h of collection). Aliquots were stained with DAPI at 50 μg $ml^{-1}$ final stain concentration, filtered onto black 0.8-μm polycarbonate filters, sealed with paraffin onto microscope slides and

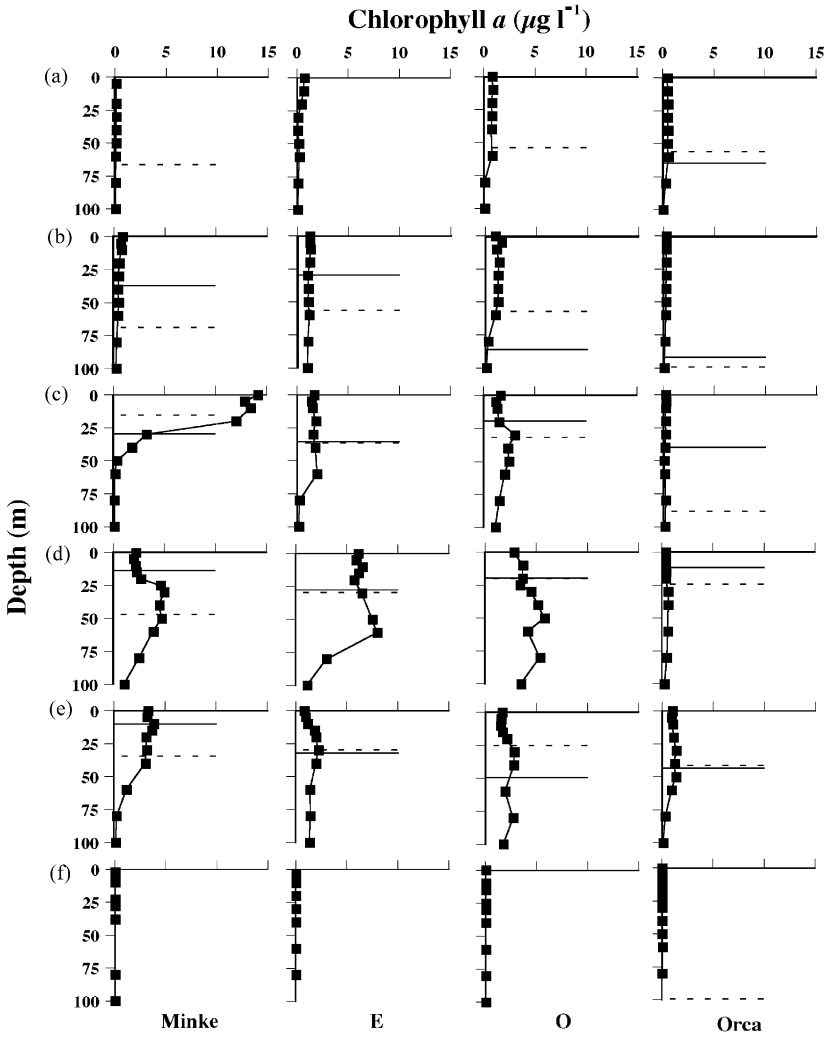


Fig. 2. Vertical profiles of chlorophyll *a* (squares), mixed layer depth (defined by a change in $\sigma_T$ of 0.02 from the surface value, solid line), and the 1% light penetration depth (dashed line) from four stations (Minke, E, O, Orca) along 76°30′S during October/November 1996 (a), the first transect in November 1997 (b), the final transect of the line in December 1997 (c), the first transect of the line in mid-January 1997 (d), the final transect in late January 1997 (e), and April/May 1997 (f). Mixed layer depth and 1% light depths greater than 100 m are not shown. No mixed layer or 1% light depths were available for early spring, Station E.

stored at –20°C (Sherr et al., 1993; Sherr and Sherr, 1993). Slides were returned frozen to the laboratory for counting. Nanoplankton were visualized by DAPI fluorescence, and PNAN were distinguished from HNAN by the autoflouresence of chlorophyll *a* using blue light excitation. Although individual *Phaeocystis antarctica* cells are in the nanoplankton size range (2–20 μm), colonies generally fall in the range of microplankton (20–200 μm) or larger. Thus from these filters, flagellated, single cells of *P. antarctica* were enumerated as nanoplankton, and non-motile cells associated with colonies were included in the counts of microplankton.

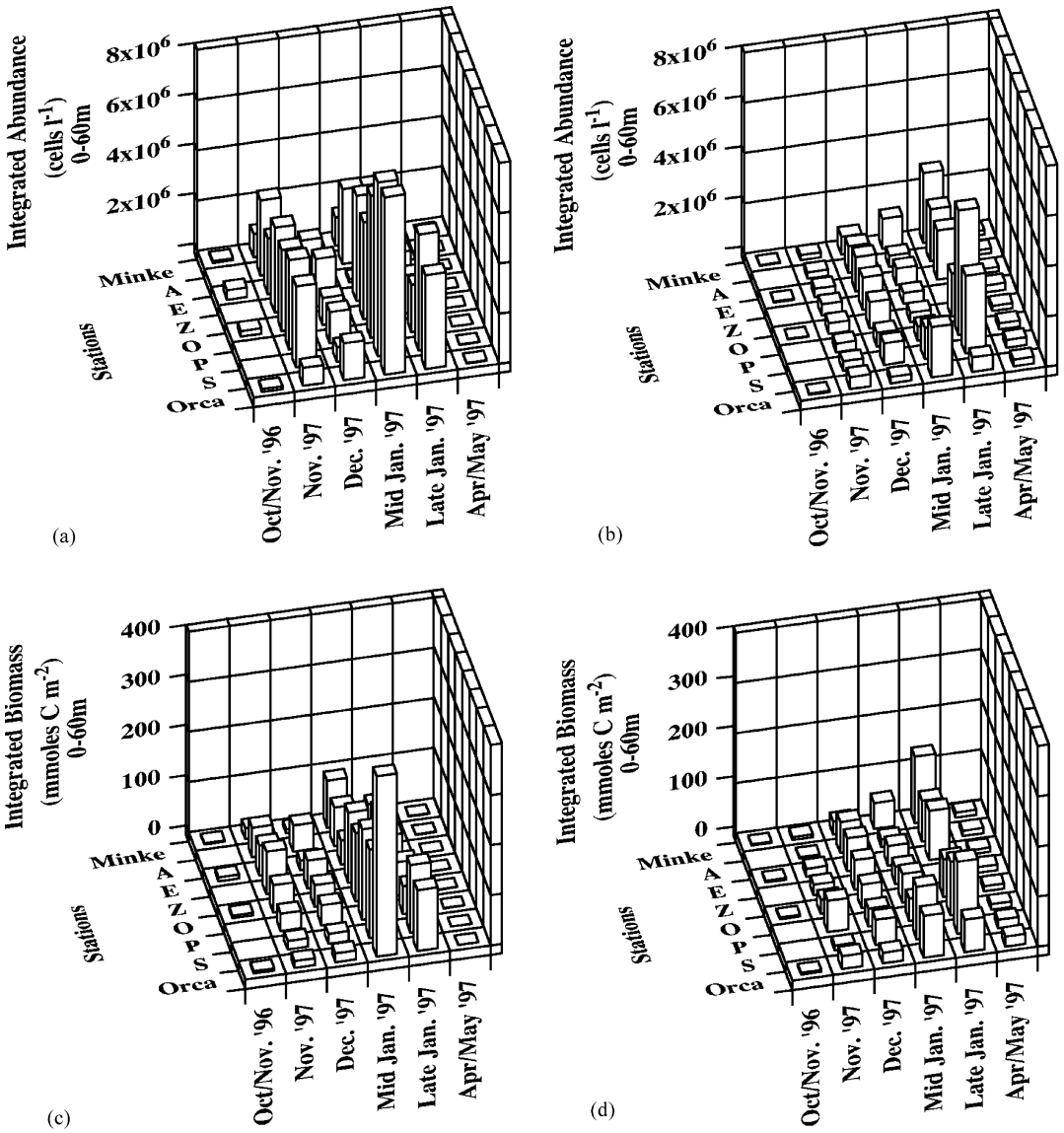


Fig. 3. Average depth integrated (0–60 m) cell abundance and biomass of phototrophic (PNAN) and heterotrophic (HNAN) nanoplankton at stations along 76°30′S from early spring (October–November) to late autumn (April–May). Plots a and b are depth integrated cell abundances of PNAN and HNAN and plots c and d are of PNAN and HNAN integrated carbon biomass, respectively.

Samples for the enumeration of phototrophic and heterotrophic microplankton (PMIC, HMIC, 20–200 μm algae and protozoa, respectively) were preserved in amber glass bottles with acid Lugols and/or glutaraldehyde-Lugols solution (35%, v/v) at a final concentration of 1% or 10% (Rousseau et al., 1990), and stored in the dark (Stoecker et al., 1994a). Settling volumes varied between 50 and 400 ml depending upon microplankton abundance. Samples with low

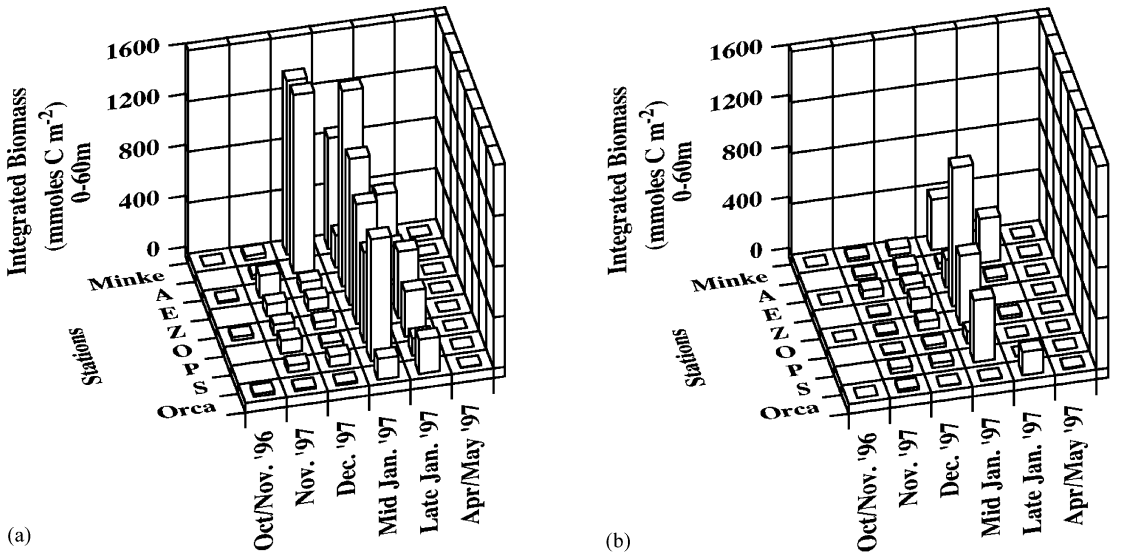


Fig. 4. Integrated (0–60 m) biomass of (a) phototrophic (PMIC) and (b) heterotrophic (HMIC) microplankton at stations along 76°30′S from early spring (October–November) to late autumn (April–May).

abundance of microplankton (primarily from the early spring and autumn) were concentrated 10-fold before finally settling the samples into counting chambers for the enumeration of 20–200 μm organisms using an inverted microscope (Utermöhl, 1958). A minimum of 50–100 microplankton observed within 10–20 fields of view (160X magnification) were grouped by major taxa (diatoms, dinoflagellates, non-loricate ciliates, tintinnid ciliates). The high concentration of Lugols solution used to minimize losses of ciliated protozoa, and the storage of these samples for extended periods before examination, precluded distinguishing phototrophs from heterotrophs in settled samples. Therefore, phototrophic and heterotrophic microplankton were distinguished using epifluoresence microscopy and formalin-preserved samples filtered onto black 0.8-μm polycarbonate filters.

Biovolume estimates were determined for nanoplankton from microscopical measurements of cell dimensions and assuming spherical or ellipsoidal shape. Microplankton biovolumes were determined from measurements of their linear dimensions and using volume equations of appropriate geometric shapes. Biovolume estimates were converted to carbon biomass for each of the plankton categories using published conversion factors. Phototrophic and heterotrophic nanoplankton and diatom biovolumes were converted to carbon values using the modified Strathmann equation (Smayda, 1978). For other microplankton, conversion factors were $140\,\mathrm{fg\,C\,\mu m^{-3}}$ for dinoflagellates (Stoecker et al., 1994b), $190\,\mathrm{fg\,C\,\mu m^{-3}}$ for non-loricate ciliates (Putt and Stoecker, 1989), and $53\,\mathrm{fg\,C\,\mu m^{-3}}$ for tintinnid ciliates (Stoecker et al., 1994b). Conversion factors of 3.33 and $13.6\,\mathrm{pg\,C\,cell^{-1}}$ were used for flagellated, single cells and non-motile colonial cells of *P. antarctica*, respectively (Mathot et al., 2000). Estimates of *P. antarctica* colonies include only the carbon biomass associated with the colonial cells; mucus-associated carbon was not included in this analysis.

Depth-integrated values of abundance and biomass were calculated for the 0–60 m interval. Comparison of these values to 0–60 m depth-integrated particulate organic carbon (POC) were

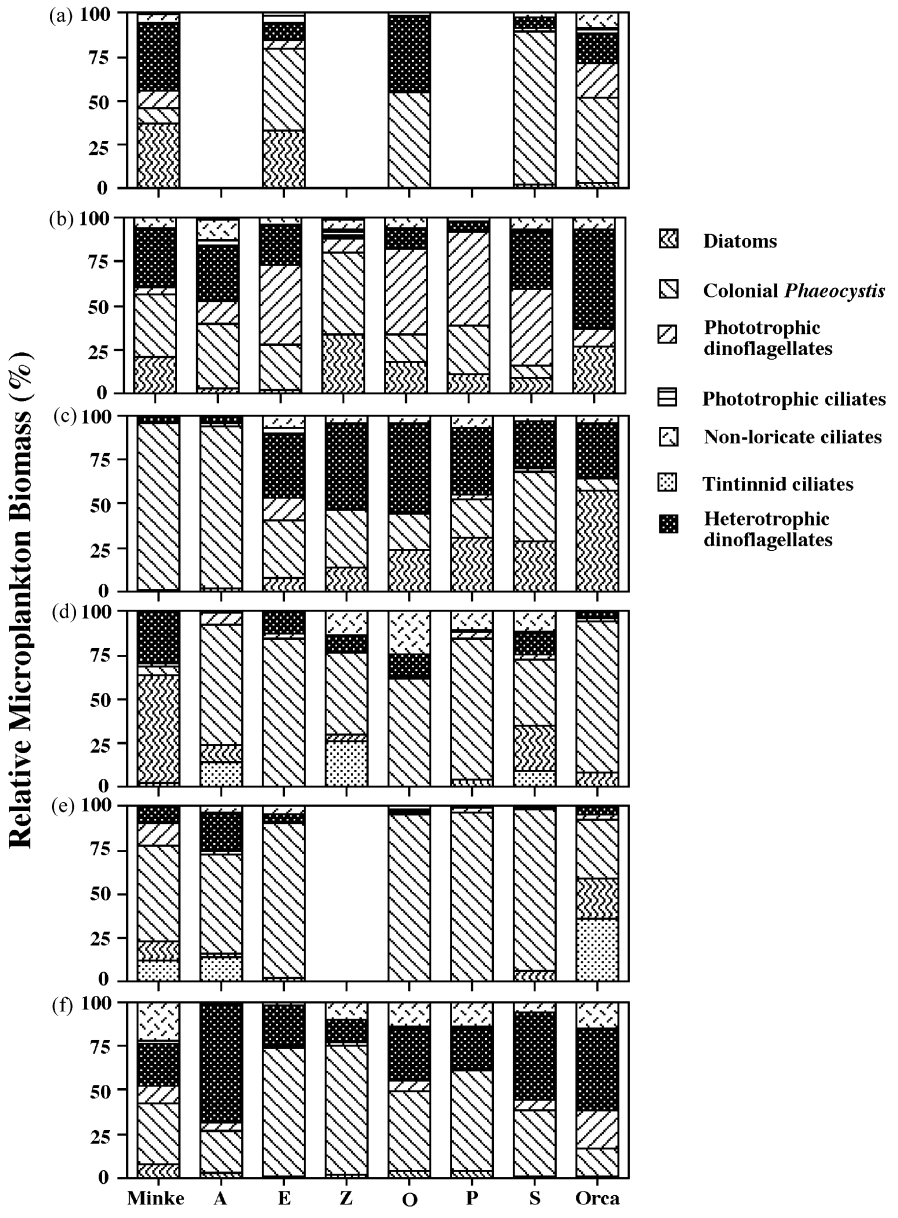


Fig. 5. Relative microplankton biomass of major taxonomic groups as a percent of total microplankton at stations along 76°30′S. See Fig. 2 for description of sample dates for panels a–f.

performed using POC values from equal or similar depths which were derived from the filtration (precombusted 25 mm Whatman GF/F filters) of 0.5–21 of whole water samples and high temperature pyrolysis (Smith et al., 2000b). All data are available via the internet (http://usjgofs.whoi.edu/jgofs. html).

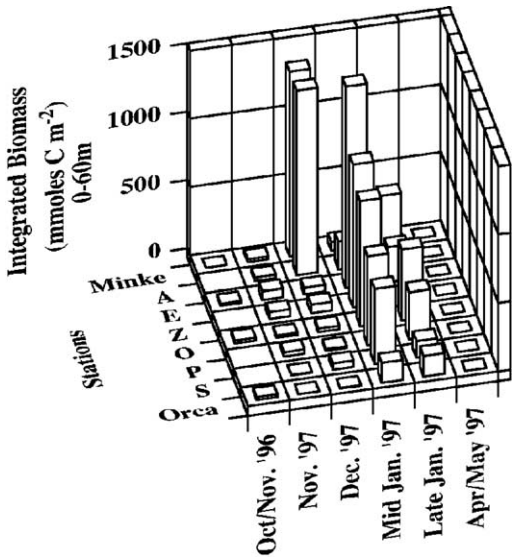


Fig. 6. Integrated carbon biomass (0–60 m) of colonial *P. antarctica* cells at stations along 76°30′S from early spring (October/November) to late autumn (April/May).

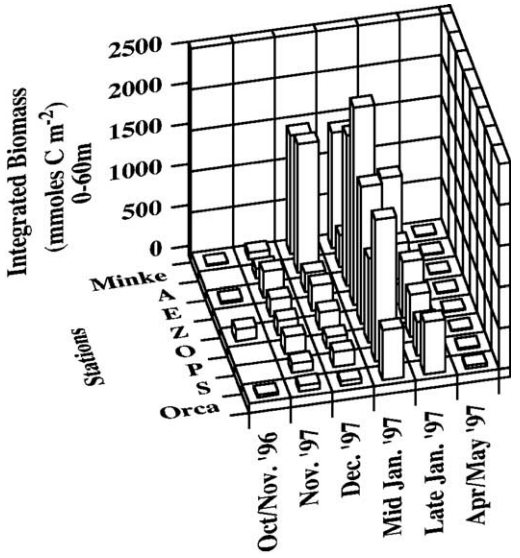


Fig. 7. Integrated carbon biomass (0–60 m) of total nano- and microplankton at stations along 76°30′S from early spring (October/November) to late autumn (April/May).

## 3. Results

The water characteristics of the Ross Sea conducive to increases in phytoplankton biomass were bracketed by the four cruises conducted as part of this study (Fig. 2). Density of the upper water column was relatively uniform during cruises conducted in early spring (October–November,

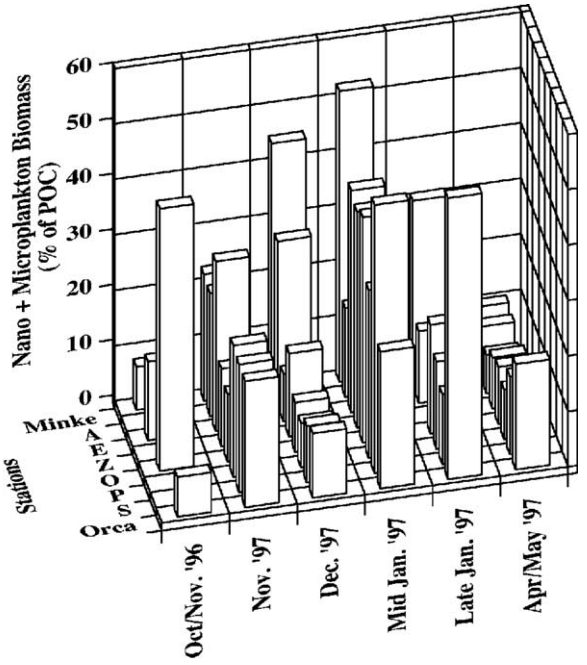


Fig. 8. Nano- and microplankton biomass as a percent of particulate organic carbon (POC) at stations along 76°30′S from early spring (October/November) to late autumn (April/May).

1996) and late autumn (April–May, 1997). Mixed layer depths (0.02 change in $\sigma_T$ from the surface) ranged from 26 to $>500$ m (with a mean of 165 m) for the early spring cruise, while mixed-layer depths during the autumn cruise ranged from 59 to 285 m. The depths of the 1% isolumes for stations during early spring averaged 74 m and ranged 53–122 m. During the late autumn cruise these depths were all $\geqslant 100$ m. These physical features were paralleled by low standing stocks of phytoplankton. Chlorophyll concentrations along 76°30′S during these periods were consistently low, with values $<1$ μg chl $a$ $l^{-1}$ during the early spring cruise and $<0.05$ μg chl $a$ $l^{-1}$ during late autumn (Figs. 2a and f).

Mixed-layer depths and 1% light depths were considerably shallower at the times of the mid- and late-spring transects (November–December, 1997, Fig. 2b and c). Chlorophyll concentrations during spring (late November, 1997) more than doubled across the transect ($\sim$1–2 μg chl $a$ $l^{-1}$ within the mixed layer; Fig. 2b) relative to values observed during early spring the previous year. A minor sub-surface chlorophyll maximum was present at 30 m during the late spring transect at one station (Station S; 2.4 μg chl $a$ $l^{-1}$). By late spring both mixed-layer depths and 1% light depths were generally less than 30 m and within a few meters of each other, particularly in the western portion of the transect (Fig. 2c). Chlorophyll concentrations were dramatically greater at these latter stations. At station Minke, chlorophyll increased to approximately 15 μg chl $a$ $l^{-1}$ over a period of 21 days (Fig. 2c).

Mixed-layer depths and 1% light depths remained shallow during the first transit of 76°30′S during austral mid-summer (January, 1997; Fig. 2d). Chlorophyll concentrations increased generally from east to west, with maximal surface values $>6$ μg chl $a$ $l^{-1}$. Deep chlorophyll

maxima of approximately 8 μg chl $a\,l^{-1}$ were clearly present at 60 and 70 m for most stations in the central and western portions of the transect during this period. On the eastern end of the line, chlorophyll profiles remained fairly uniform with depth.

Overall, chlorophyll concentrations indicated declining phytoplankton biomass during late-summer (February, 1997; Fig. 2e). A slight deepening of the mixed layer occurred on the eastern portion of the line during late summer. The magnitudes of the chlorophyll maxima also decreased on the central and western end of the transect to approximately 4.5 μg chl $a\,l^{-1}$.

The abundances and biomasses of PNAN and HNAN varied by orders of magnitude between the four cruises. Overall, depth-integrated (0–60 m) abundances at the principal sampling stations ranged from $0.20 \times 10^4$ to $7.07 \times 10^6\,l^{-1}$ for PNAN and $2.48 \times 10^4$ to $4.97 \times 10^6\,l^{-1}$ for HNAN (Fig. 3a and b). Average abundances of nanoplankton for each of the four cruises ranged from $1.24 \times 10^4$ to $3.26 \times 10^6$ PNAN $l^{-1}$ and $2.66 \times 10^4$ to $1.90 \times 10^6$ HNAN $l^{-1}$ (Table 1). In contrast, depth-integrated PNAN and HNAN abundances along 76°30′S for any one transect typically varied by less than an order of magnitude. An exception to this generality was one of the transects during austral summer when depth-integrated PNAN abundances ranged from $0.13 \times 10^6$ to $7 \times 10^6\,l^{-1}$ (Fig. 3a).

Similarly, nanoplankton biomass over all stations and sampling dates varied more than three orders of magnitude between the four cruises (ranges of 0.1–359 mmol C $m^{-2}$ and 1.5–268 mmol C $m^{-2}$ for PNAN and HNAN, respectively). Also analogous to abundances, nanoplankton biomass at stations within any particular transect varied by less than an order of magnitude (Fig. 3c and d). Overall, PNAN and HNAN biomasses were fairly similar. Cruise averages of PNAN and HNAN biomass differed by less than 50% except in autumn when HNAN accounted for 97% of the total nanoplankton biomass (Table 1).

Mean cruise abundance (0–60 m) of PMIC (including colonial cells of *P. antarctica*) varied by more than two orders of magnitude between the four cruises ($2.41 \times 10^4$–$6.57 \times 10^6\,l^{-1}$). However, depth-integrated PMIC abundance for individual stations on the four cruises covered a range of five orders of magnitude ($0.02 \times 10^4\,l^{-1}$ in early spring to $2.17 \times 10^7\,l^{-1}$ in mid-summer; Table 1). Orders of magnitude changes were also seen in PMIC biomass with an overall range of 0.1–1530 mmol C $m^{-2}$ (early spring to mid summer), and means for each cruise ranging from 2.5 to 530 mmol C $m^{-2}$ (Table 1, Fig. 4a). The average depth-integrated abundance of HMIC for each of the four cruises varied by less than a factor of 10 ($0.13$–$0.89 \times 10^4\,l^{-1}$; Table 1) whereas average HMIC biomass for each cruise varied by nearly two orders of magnitude (3.8–193 mmol C $m^{-2}$). Individual stations had values as high as 1090 mmol C $m^{-2}$ at Station Z during mid-summer, 1997 (Fig. 4b).

Taxonomic composition of the microplankton assemblages varied both seasonally and spatially along 76°30′S between 1996 and 1997. Colonial *P. antarctica* dominated the low biomass of the eastern portion of the transect in the early spring, while diatoms and dinoflagellates (primarily heterotrophic dinoflagellates) dominated on the western end. During November/December 1997, colonial *P. antarctica* had not yet established a dominance at any station along the transect (Fig. 5b), but a diverse mixed assemblage of both PMIC and HMIC existed. By early December 1997, however, more than 90% of the microplankton biomass on the western portion of the transect line was colonial *P. antarctica* (Fig. 5c). This dominance greatly diminished within a distance of 2° to the east, and diatoms and dinoflagellates became prevalent eastward to Station Orca.

Colonial *P. antarctica* dominated the microplankton biomass during mid-austral summer at most stations during January/February, 1997 (Fig. 5d and e). The western end of the transect line in mid-January had significant contributions of diatoms and heterotrophic dinoflagellates (Fig. 5d), but more than 90% of the microplankton biomass at four stations in late January 1997 was attributable to *P. antarctica* (Fig. 5e). The eastern end at the beginning of February was dominated by diatoms and tintinnid ciliates. By autumn 1997, absolute abundance and dominance of colonial *P. antarctica* in the central stations had diminished, and HMIC constituted nearly 50% of the microplankton biomass at 6 of the 8 stations along the transect (Fig. 5f).

During early austral spring and autumn, colonial *P. antarctica* depth-integrated biomass was consistently $<83\,\mathrm{mmol\,C\,m^{-2}}$ (Fig. 6). At the easternmost station, the biomass of this species never exceeded $150\,\mathrm{mmol\,C\,m^{-2}}$ at any time. In contrast, a bloom of colonial *P. antarctica* was fully developed throughout the central region during summer. Transects in the following spring indicated that the *P. antarctica* bloom was not present along the transect line in late November, but was clearly apparent at the western portion of the transect line the following month (Fig. 6). A three dimensional plot of these data indicated a rapid development of the *P. antarctica* bloom starting at the western end of the transect and progressing east (Fig. 6). However, the data are taken from two successive seasons, and the extent of interannual variability in bloom assemblage composition and development is not known.

Colonial *P. antarctica* contributed significantly to total nano- and microplankton biomass at many stations even when this prymnesiophyte was not at high abundance (compare Figs. 6 and 7). For example, during the first occupation of stations Minke and A in November, 1997, colonial *P. antarctica* biomass was low (20 and $23\,\mathrm{mmol\,C\,m^{-2}}$, respectively), but these values still represented $\sim$25% of the total nano- and microplankton biomass (Fig. 7). Many of the late-spring to late-summer samples were strongly dominated by this species. Within 20 days colonial *P. antarctica* biomass had increased to $1350\,\mathrm{mmol\,C\,m^{-2}}$ (89% of the total nano- and

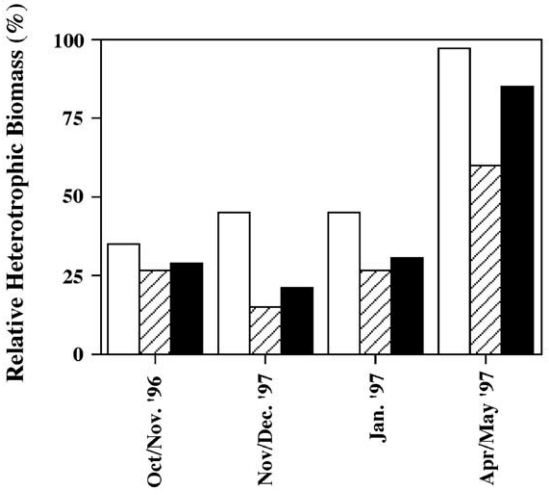


Fig. 9. Cruise average relative biomass of nano- and microplankton heterotrophs along 76°30′S from early spring (October/November) to late autumn (April/May). Open bars = percentage of HNAN to total nanoplankton (TNAN), diagonal patterned bars = percentage of HMIC to total microplankton, solid bars = percentage of heterotrophic nano- and microplankton to total plankton biomass (2–200 μm).

microplankton biomass) at this end of the transect. Mid-austral summer sampling at stations Minke and A showed low levels of colonial *P. antarctica* biomass (61 and 200 mmol C $m^{-2}$) at these two stations, while stations Orca-E increased from 144 to 1480 mmol C $m^{-2}$ along the length of the transect. By late January, colonial *P. antarctica* biomass was declining at most stations, with a range of 150–517 mmol C $m^{-2}$ for the 8 stations. Nevertheless, these values still accounted for more than 50% of the the total nano- and microplankton biomass at stations A, E, and O at the western portion of the line (compare Figs. 6 and 7).

Depth-integrated (0–60 m) biomass of total nano- and microplankton constituted a significant but variable proportion of the depth-integrated particulate organic carbon (POC). The overall average for all cruises was 21.8% of POC, with a range of 7.2–52.4% (Fig. 8). Colonial *P. antarctica* was an important component of this contribution. During transects when colonial *P. antarctica* was low ($<167$ mmol C $m^{-2}$), the percentage of total nano- and microplankton to POC varied by a factor of 2.7 with an average of 15.1%, with the exception of station O during October/November, 1996. When average colonial *P. antarctica* biomass exceeded 167 mmol C $m^{-2}$ (the period from late spring to late austral summer), total nano- and microplankton to POC averaged 26.1%.

Changes in heterotrophic biomass of both nano- and microplankton were compared to the total nano- and microplankton assemblage to examine the possibility of a seasonal shift in community structure in the Ross Sea (Fig. 9). HNAN biomass averaged 39% of the total nanoplankton (TNAN) biomass from early spring until the decline of the *P. antarctica* bloom in late summer when this value increased dramatically to 97% of TNAN biomass. Similarly, the contribution of HMIC to total microplankton (TMIC) biomass was minor (generally $<25\%$) during austral spring and summer. This percentage increased to 60% in autumn, but the absolute biomass constituted a minor percentage of the total heterotrophic biomass at that time (23%, Table 1). From early spring to the decline of *P. antarctica*, the relative percentage of total heterotrophic biomass (HNAN + HMIC ) to total nano- and microplankton biomass averaged $<30\%$, but this value rose to $\approx 87\%$ in autumn. At the end of the *P. antarctica* bloom, HNAN was a major component of the total nano- and microplankton biomass (66%).

## 4. Discussion

### 4.1. Phytoplankton biomass in the central Ross Sea

The colonial prymnesiophyte *P. antarctica* clearly plays a central role in the ecology of microbial populations within the Ross Sea. *P. antarctica* alone constituted a major fraction of the total nano- and microplankton biomass, and a significant fraction of the total POC concentration (Figs. 6 and 7). Moreover, the biomass of phototrophic microplankton varied by four orders of magnitude among seasons, largely due to dramatic seasonal changes in the abundance of this colonial prymnesiophyte. The strong dominance of *P. antarctica* in the Ross Sea in the present study is not a particularly surprising finding, having been demonstrated in previous studies of the region (DiTullio and Smith, 1996; Smith and Gordon, 1997; Smith and Dunbar, 1998).

It is important to note that our estimate of the contribution of *P. antarctica* does not include the contribution of particulate organic carbon contained in the colony matrix. A recent study

indicates that the latter material may constitute an additional 35% of the contribution of the algal cells during mid/late-summer (Mathot et al., 2000). This additional contribution would make *P. antarctica* biomass overwhelmingly dominant during bloom periods, and it would significantly increase our estimates of the contribution of this biomass to the concentration of total particulate organic carbon in the water at those times (Fig. 8).

It is difficult to accurately determine the contribution of flagellated, free-swimming cells of *P. antarctica* to PNAN biomass. It was not possible to categorically differentiate these cells from other phototrophic nanoplankton using our epifluorescence microscopy procedure, but cells resembling this species were common during the spring cruise. Inclusion of these cells as *P. antarctica* would further increase the importance of this alga to standing stocks of microbial biomass in the Ross Sea.

In contrast to our findings with *P. antarctica*, diatoms infrequently constituted a major fraction of the phytoplankton assemblage during our seasonal study (Fig. 5). These species were occasionally the dominant phytoplankton taxon at the eastern and western ends of the transect. In general, this pattern agrees with studies that have indicated largely non-overlapping (but not mutually exclusive) distributions of *P. antarctica* and diatoms in the Ross Sea (Arrigo et al., 1999; Smith and Asper, 2001).

### 4.2. Phototrophic vs. heterotrophic microbial biomass

We found that the phototrophic biomass exceeded heterotrophic biomass by a factor of 2-4X in all seasons except autumn. Both HNAN and HMIC biomass increased considerably during late austral summer (Table 1). However, the importance of heterotrophic biomass (relative to phototroph biomass) showed a dramatic increase only during austral autumn (April–May, 1997) compared to other seasons (Fig. 9). While this finding is not unexpected (one would anticipate an increase in heterotrophs at the end of a phytoplankton bloom and in the waning photoperiod), the composition of the heterotrophic biomass was somewhat unexpected.

The relative absence of picophytoplankton and the predominance of colonial *P. antarctica* and diatoms might be expected to result in large increases in HMIC biomass in the autumn as the latter assemblage consumed PNAN and PMIC populations. While HMIC and PMIC biomass were similar in austral autumn, HMIC biomass as a percentage of total nano- and microplankton biomass was not dramatically higher (Table 1, Fig. 9). This result may simply have been a consequence of timing of the cruise. That is, a dominance of HMIC biomass may have occurred following the late-summer sampling period but before the autumn cruise. In a study conducted in McMurdo Sound, Stoecker et al. (1995) found HMIC biomass exceeding HNAN by a factor $>2$ during the decline of the colonial *P. antarctica* bloom. Alternatively, our findings may indicate that microzooplankton species were not consuming significant quantities of phytoplankton, or perhaps that HMIC biomass was being consumed rapidly (e.g., by mesozooplankton). The latter scenarios are consistent with observations of low rates of microbial herbivory by nano/microzooplankton in the Ross Sea (Caron et al., 2000), and with experimental studies demonstrating the consumption of microzooplankton by copepods during the summer (Lonsdale et al., 2000).

In contrast, HNAN occurred at high relative abundances during the autumn cruise compared to the biomasses of PNAN, PMIC and HMIC (Table 1, Fig. 9). The average biomass in autumn indicated that HNAN constituted approximately 65% of the total nano- and microplankton

biomass, and nearly all of the nanoplankton biomass along the transect line ($\approx 97\%$). The HNAN assemblage during late summer and autumn was dominated by small, bacterivorous flagellates, primarily choanoflagellates. These populations were actively consuming bacteria-sized particles in the water (Caron et al., 1999). The strong predominance of bacterivorous HNAN in the Ross Sea at the end of the seasonal phytoplankton bloom may indicate that much of the heterotrophic microbial biomass was supported by bacterial biomass rather than by the direct utilization of microalgal biomass.

### 4.3. Contribution of nanoplankton and microplankton to POC

As noted above, the contributions of PNAN, HNAN, PMIC and HMIC to total nanoplankton and microplankton biomass were rather unique, with a strong dominance of *P. antarctica* during much of the spring and summer, and the predominance of HNAN during the autumn. Nevertheless, the overall contribution of these assemblages to standing stocks of particulate organic carbon was remarkably similar to findings from other oceanic ecosystems. Averaged over all sampling dates, nano- and microplankton assemblages in this study constituted approximately 22% of the concentration of POC. This average is similar to values reported for such disparate locales as the North Atlantic (Caron et al., 1995; Buck et al., 1996) and the Arabian Sea (Garrison et al., 1998; Dennett et al., 1999). The highest values reported in the present study ($\approx 52\%$ of POC) are comparable to some of the highest percentages reported. Our estimates do not include the contribution of bacteria to total microbial biomass or that of mucus carbon within *P. antarctica* colonies.

It should be noted, however, that seasonal coverage of the Ross Sea, although bracketing the period of high biological activity in this ecosystem, was still limited to a 6–7 month period of the calendar year. The contribution of nano- and microplankton to total POC in the Ross Sea was lower during the early spring and autumn than during late spring and summer (Fig. 8). Thus, the inclusion of additional data for the late-autumn and winter periods might reduce the overall annual contribution of nano- and microplankton to the standing stock of POC.

### 4.4. Comparison to other Antarctic studies

There are few quantitative, seasonal studies of both phototrophic and heterotrophic microbial plankton in the Ross Sea with which to compare our data. In one of the few available data sets, Garrison et al. (1995) noted an increase in heterotrophic protists in diatom-dominated vs. *Phaeocystis*-dominated areas in November and December of 1994 at stations within the general vicinity of our study area.

These findings are consistent with findings in the present study. We observed that stations where diatoms were the dominant phytoplankton typically were associated with significant quantities of heterotrophic dinoflagellate biomass (Fig. 5). These situations occurred primarily at either end of the main transect. These two taxonomic groups (diatoms and heterotrophic dinoflagellates) accounted for up to 90% of the microplankton biomass at the eastern end of the line (Orca) during austral spring (Fig. 5c) and at the western end (Minke) during austral summer (Fig. 5d). In contrast, colonial *P. antarctica* comprised $>90\%$ of the total microbial (nano- and microplankton) biomass at several stations during austral spring and summer (Fig. 5c–e). This

difference in community structure presumably is a consequence of the ability of some heterotrophic dinoflagellates to prey on diatoms.

The results of studies in other coastal areas around Antarctica also agree with our results (Nöthig et al., 1991; Detmer and Bathmann, 1997; Klaas, 1997). As summarized by Garrison and Gowing (1993), microplankton biomass estimates in the upper 100 m of the Weddell/Scotia Sea ranged from 4.68 to 213 mmol C $m^{-2}$, which is within our range of averages for microplankton biomass exclusive of the austral summer peak of colonial *P. antarctica* (Table 1). Davidson and Marchant (1992) observed a maximum in the abundance of heterotrophic protists during and following a *Phaeocystis* bloom in waters offshore from the Australian Antarctic station (68°30′S, 77°50′E). Along 76°30′S in 1996–1997, average absolute HNAN biomass increased 25-fold while HMIC biomass increased 30-fold from early spring to late January (Table 1). Our study increases the resolution of the early observation by Davidson and Marchant, however, by quantifying the relative contribution of phototrophic and heterotrophic biomass among the nano- and microplankton. Our findings indicate that, despite substantial increases in the absolute biomass of HNAN and HMIC during the summer, the biomass of these assemblages did not dominate the phytoplankton biomass until well after the biomass of the bloom had decreased.

The seasonal shifts in phototroph:heterotroph biomass among the microbial plankton that we observed in the Ross Sea appear to be a pattern that is consistent with shifts observed in other Antarctic coastal waters. In the Weddell and Scotia Sea near the area of the Antarctic peninsula, Garrison et al. (1993) found similar biomass values for phototrophs and protozooplankton (50–300 μm protozoa) during austral winter, 1988 (range of 8.3–23 mmol C $m^{-2}$ for phototrophs and 15–34 mmol C $m^{-2}$ for heterotrophs). Phototroph biomass (predominantly diatoms) was substantually greater in this same area during austral spring 1983 (range for phytoplankton biomass at that time was 47.5–533 mmol C $m^{-2}$) while heterotrophs (protozooplankton) remained similar to the winter values. In autumn, 1986, the range of phototroph and protozooplankton biomass was comparable to biomass ranges recorded during austral spring, 1983. Similarly, Hewes et al. (1990) observed a roughly three-fold greater biomass of phototrophs relative to heterotrophs in surface waters of the continental shelf around Antarctica during austral summer (January–February, 1983).

In a general sense, shifts in the relative biomass of phototrophs and heterotrophs in the Ross Sea during early austral spring are in agreement with the findings of Garrison et al. (1993) and Hewes et al. (1990), but our values have slightly wider ranges. The ratio of phototroph:heterotroph biomass in austral spring during the development of a polyna in the Ross Sea gave rise to a bloom of the colonial *P. antarctica*, which dominated microbial biomass at a majority of stations along the transect through the summer (maximum of 1350 mmol C $m^{-2}$). Although heterotroph biomass increased during this period, phototroph biomass exceeded heterotroph biomass by a factor of $\approx 5$ (Table 1; Fig. 9). This dominance was reversed during austral autumn in the Ross Sea (heterotroph biomass exceeded phototroph biomass by a factor of $\approx 5$).

## 5. Conclusions

Phototrophic and heterotrophic nano- and microplanktonic assemblages in the southern Ross Sea, Antarctica, revealed some strikingly similar, and some uniquely different, aspects of these

assemblages relative to those found in other regions of the ocean. Averaged over all four cruises spanning three seasons, total nanoplankton and microplankton biomass constituted approximately 22% of the standing stock of particulate organic carbon in the top 60 m of the water column. This value is comparable to contributions of these assemblages in other oceanic ecosystems in which these assemblages have been quantified. The composition of these assemblages in the Ross Sea was unique, however, in that the colonial prymnesophyte *P. antarctica* strongly dominated the phytoplankton assemblage, as well as the biomass of the 2–200 μm plankton during much of the spring and summer. Heterotrophs (primarily choanoflagellates) were a dominant component of the nano- and microplanktonic size categories only during autumn, when *P. antarctica* declined and heterotrophic nanoplankton reached high relative abundance.

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