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The temporal dynamics of the flagellated and colonial stages of *Phaeocystis antarctica* in the Ross Sea

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Abstract

Phaeocystis antarctica in the Ross Sea forms colonies, and blooms of colonial *P. antarctica* often occur over large areas in the southern Ross Sea. Sites where colonies occur often have significant vertical fluxes of carbon in the form of aggregated and flocculent material. *P. antarctica* also is a key component of the sulfur cycle; therefore, the species is critically important in many of the biogeochemical cycles in the Ross Sea. Despite this fundamental role, the life history and temporal dynamics of this species are poorly known. This study investigated the contribution of solitary, flagellated forms and colonial cells of *P. antarctica* to phytoplankton abundance and autotrophic carbon, and the factors that might control the relative importance of these two morphological forms. Solitary *P. antarctica* cells numerically dominated the phytoplankton assemblage early in austral spring, although colony formation occurred almost immediately upon the onset of net population growth. The percentage of solitary cells relative to total cells (colonial + solitary) was high in early austral spring but decreased to a minimum during late spring; specifically, nearly 98% of the *P. antarctica* cells were in colonies in late spring, coinciding with the seasonal chlorophyll maximum. Significant phytoplankton mortality rates were positively correlated with high ratios of solitary: total *P. antarctica* cells. Highest mortality rates were observed during austral spring when solitary cells dominated the *P. antarctica* population. The abundance of solitary *P. antarctica* cells began to increase again during late summer, but colonial cell numbers were always greater than those of solitary cells during this period. This increase in the contribution of solitary forms during summer may have been a consequence of more severe micronutrient limitation for the colonies (relative to solitary cells), life history processes of *P. antarctica*, reduced microzooplankton grazing at that time, or a combination of these and other factors. We conclude that the relative abundance of solitary and colonial forms of this prymnesiophyte alga may be a consequence of seasonal changes in these factors. The outcome of these interactions affects the contribution of this alga to the vertical flux of carbon and the degree to which *P. antarctica* participates in the microbial food web of the Ross Sea.

1. Introduction

There has been the recognition during the past few decades that phytoplankton assemblage composition exerts a strong control over pelagic carbon transformations and biogeochemical cycles.

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For example, the dominance of primary production by small cyanobacteria in oligotrophic systems results in the utilization and remineralization of much of the production within the euphotic zone by the microbial food web. In contrast, diatoms are largely consumed by mesozooplankton, and thus contribute significantly to the vertical flux of organic carbon by virtue of their incorporation into sinking fecal material. Other forms, such as some prymnesiophytes, overwhelmingly contribute to sulfur cycling by releasing large amounts of dimethylsulfide (DMS) to the water, which then volatilizes and exchanges with the atmosphere. Coccolithophorids, another type of prymnesiophyte, form calcium carbonate tests, and hence exert control over the alkalinity and carbon cycles when present. Thus, not all phytoplankton affect elemental and energy flow equally, and present models are beginning to incorporate the critical roles of individual taxa in biogeochemical cycles (Armstrong, 1999).

The Southern Ocean has long been considered to be a diatom-dominated system, and indeed many locations have substantial numbers of these forms (e.g., Wilson et al., 1986; Brown and Landry, 2001). More recently it has been recognized that *Phaeocystis antarctica*, a prymnesiophyte with a relatively complex life cycle, is extremely important in some regions. *P. antarctica* forms large blooms in areas of the Southern Ocean such as Prydz Bay (e.g., Davidson and Marchant, 1992) and the southern Ross Sea (El-Sayed et al., 1983). Indeed, it is often the dominant species in the latter region (DiTullio and Smith, 1996; Arrigo et al., 1999; Mathot et al., 2000; Dennett et al., 2001).

P. antarctica is one of the four species of *Phaeocystis* that can occur either as solitary, flagellated unicells or as colonies of hundreds of non-flagellated cells (Rousseau et al., 1994; Lancelot et al., 1998; Zingone et al., 1999). The colonies are spherical to cylindrical in shape and hollow, and the algal cells are embedded in an organic matrix that is the basis of the colony like those of *P. globosa* (Hamm et al., 1999). It has been reported that *P. pouchetii* cells are liberated from the colonial matrix as the colonies sink in the water column, resulting in the generation of large numbers of solitary cells (Wassmann et al., 1990).

Little is known concerning the environmental factors that regulate the dominance of solitary and colonial forms of the alga, although it has been suggested that inorganic nutrients and grazing may influence the ratio of these forms. In the North Sea when phosphate is reduced to limiting concentrations, flagellated cells of *P. pouchetii* appeared to be favored (Riegman et al., 1992). Similarly, solitary cells of the same species tend to be favored when ammonium is the dominant form of nitrogen available to the alga (Lancelot et al., 1998). Riegman and van Boekel (1996) concluded that colonial cells of *P. globosa* are more effective competitors for nitrate and are favored at irradiances above 50 μmol photons $m^{-2} s^{-1}$. A recent laboratory study of *P. globosa* found that colony formation and survival were enhanced under conditions of enhanced microzooplankton grazing (Jakobsen and Tang, 2002), confirming the role of grazing. However, no clear relationship between environmental conditions and life cycle stage for *P. antarctica* can, at present, be determined.

P. antarctica is critical to primary production, elemental transformations and vertical flux in the Ross Sea. For example, massive blooms of this species occur in the southern Ross Sea, and they have been reported to produce some of the highest concentrations of DMS observed in the ocean (DiTullio and Smith, 1995; Kettle et al., 1999). Furthermore, *P. antarctica* colonies appear to be relatively ungrazed by microzooplankton in this region (Caron et al., 2000), and thus its role in carbon export and flux is substantial. Dunbar et al. (1998) compared the vertical fluxes of two sites (one dominated by diatoms and the other dominated by *P. antarctica)* in the southern Ross Sea and found that carbon flux rates were approximately equal (although silica flux rates were an order of magnitude greater at the site dominated by diatoms). The material collected in the traps at the *P. antarctica*-dominated site was largely aggregates and amorphous organic material, implying that the material was exported without transformation by the food web. It has also been suggested that *P. antarctica* contributes to substantial fluxes during periods of rapid growth during austral spring (DiTullio et al., 2000), but these flux events have not yet been confirmed by

sediment trap collections in the Ross Sea. Collectively, this information indicates that detailed knowledge of this species is essential for understanding ecosystem function in this and other Antarctic coastal waters.

This study investigated the contribution of solitary and colonial *P. antarctica* cells to the overall temporal dynamics of the phytoplankton assemblages of the southern Ross Sea. We hypothesized that the morphological form of the species was important in determining its fate in the planktonic food web, given that we know that solitary cells were actively grazed by microzooplankton during spring, while rates of phytoplankton mortality were low (mostly undetectable) when *P. antarctica* colonies dominated the phytoplankton. Because a variety of factors (nutrients, irradiance and grazing pressure) may influence the proportion of total cells in colonies, we sought to understand these dynamics within the seasonal phytoplankton bloom in the southern Ross Sea.

2. Materials and methods

This study was part of AESOPS, the US Southern Ocean Joint Global Ocean Flux Study (Smith et al., 2000a). All samples were collected in the southern Ross Sea from the R.V.I.B. *Nathaniel B. Palmer*. Cruises were completed in early spring (October–November 1996), in late spring (November–December 1997), in summer (January–February 1997) and autumn (March–April 1997). Data from all of the cruises were merged to produce a temporal composite (Smith et al., 2000a, b). Much of the sampling occurred along 76°30′S at a series of eight stations, each separated by ca. 60 km (Fig. 1). Ice concentrations were variable during the study with 100% ice cover being observed in early spring and in autumn and ice-free conditions occurring during summer (Smith et al., 2000a).

Water samples were collected from the upper 100 m using a trace-metal clean rosette or standard Niskin bottles (with Teflon-coated internal springs) mounted on a rosette. Chlorophyll *a* concentrations were determined fluorometrically after filtration and extraction for 24 h in 90% acetone (Smith et al., 2000b). Depths sampled for enumeration of nano- (2–20 μm) and microplankton (20–200 μm) varied depending upon water-column characteristics (e.g., depth of the chlorophyll maximum or euphotic zone). Up to five depths were routinely sampled from each vertical profile. Samples for the enumeration of phototrophic (i.e. chloroplast-bearing) nanoplankton were preserved with 1% formalin or 0.5% glutaraldehyde (from 10% stock solutions prepared with filtered seawater) and refrigerated until

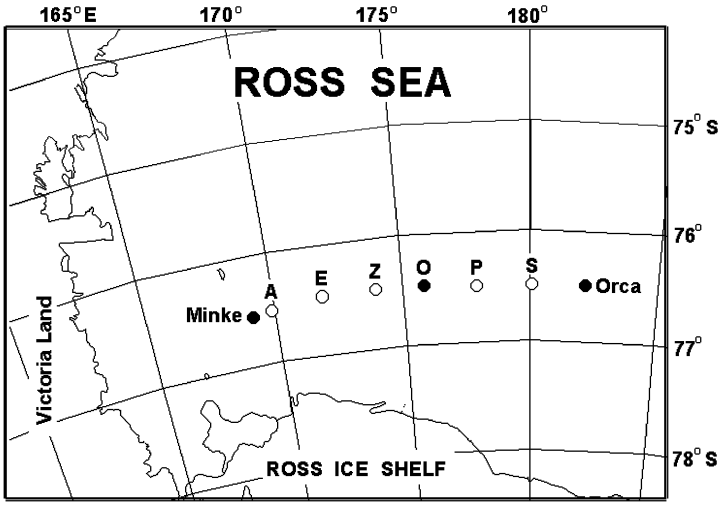

Fig. 1. Map showing the location of samples collected during the four cruises. Exact station locations are provided in Dennett et al. (2001).

processed for epifluorescence microscopy (within 24 h of collection). Aliquots were stained with DAPI (50 μg ml^{-1} final stain concentration), filtered onto black 0.8 μm polycarbonate filters, sealed with paraffin onto microscope slides, and 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 phototrophic nanoflagellates were identified by the autofluorescence of chlorophyll *a* using blue light excitation. Presumptive solitary *P. antarctica* cells were distinguished from other phototrophic protists based on cell size and shape, chloroplast arrangement, and the presence of flagella. *P. antarctica* colonies generally fall in the range of microplankton or larger. Numbers of flagellated, solitary and colonial (within an organic matrix) *P. antarctica* were counted on all samples.

Samples for the enumeration of phototrophic microplankton (20–200 μm algae, including colonies of *P. antarctica*) were preserved in amber glass bottles with acid Lugol's and/or glutaraldehyde-Lugol's solution (35%, v/v) at a final concentration of 1% or 10% (Rousseau et al., 1990). All samples were stored in the dark (Stoecker et al., 1994). Settled volumes varied between 50 and 400 ml depending upon microplankton abundance. Samples with low abundance of microplankton (primarily from the early spring and autumn) were allowed to settle in the sample bottle, and then a known volume of supernatant was removed before transfer of the sample and settling into counting chambers for enumeration using an inverted microscope (Utermöhl, 1958). A minimum of 50–100 microplankton were counted within 10–20 fields of view (160 × magnification); all cells were grouped by major taxa. Formalin-preserved samples of microplankton were filtered onto 0.8-μm black, polycarbonate filters, and phototrophic and heterotrophic forms were distinguished using epifluorescence microscopy (Booth, 1993). The coefficient of variation is generally <10% using this procedure (Venrick, 1981).

Biovolume estimates were determined for nanoplankton from microscopic measurements of cell dimensions and assuming spherical or ellipsoidal shape. Microplankton biovolume was determined from measurements of the linear dimensions and using volume equations of appropriate geometric shapes. Volume estimates were converted to carbon biomass using published conversion factors (Eppley et al., 1970; Garrison et al., 1998; Mathot et al., 2000). Conversion factors of 3.33 and 13.6 pg C cell^{-1} were used for flagellated, solitary cells and non-motile colonial cells of *P. antarctica*, respectively (Mathot et al., 2000). Carbon estimates of *P. antarctica* colonies include only the carbon associated with the colonial cells. Depth-integrated abundance and biomass values were calculated for the upper 60 m. All data are available via the internet (http://usjgofs.whoi.edu/).

3. Results

3.1. Temporal variations in solitary and colonial cell abundance

During early austral spring (i.e., "pre-bloom" conditions) phytoplankton biomass was extremely low with surface chlorophyll levels less than 0.1 μg l^{-1} (Smith et al., 2000b) and integrated (0–100 m) chlorophyll concentrations less than 10 mg m^{-2} (Fig. 2a). Numbers of *P. antarctica* cells were also low. The mean abundance of solitary cells during the first portion (prior to October 26) of the early spring cruise was 0.22×10^6 cells l^{-1} (Fig. 2b), whereas the average number of colonial cells for the same period was 0.027×10^6 cells l^{-1} (Fig. 2c). Hence, most *P. antarctica* cells present in the water column prior to significant biomass increase in spring were solitary forms (Fig. 2d). As phytoplankton biomass increased during the spring, the numbers of flagellated cells relative to the total *P. antarctica* abundance decreased, although there was considerable scatter in this ratio as a function of spatial heterogeneity along the transect line (Fig. 2d). The lowest ratios (i.e. the highest dominance of colonial cells) were observed near the time of maximal phytoplankton biomass in late spring (ca. December 16). The percentages of solitary cells in several of these samples were less than 5%. In addition, the numbers of diatoms (both smaller

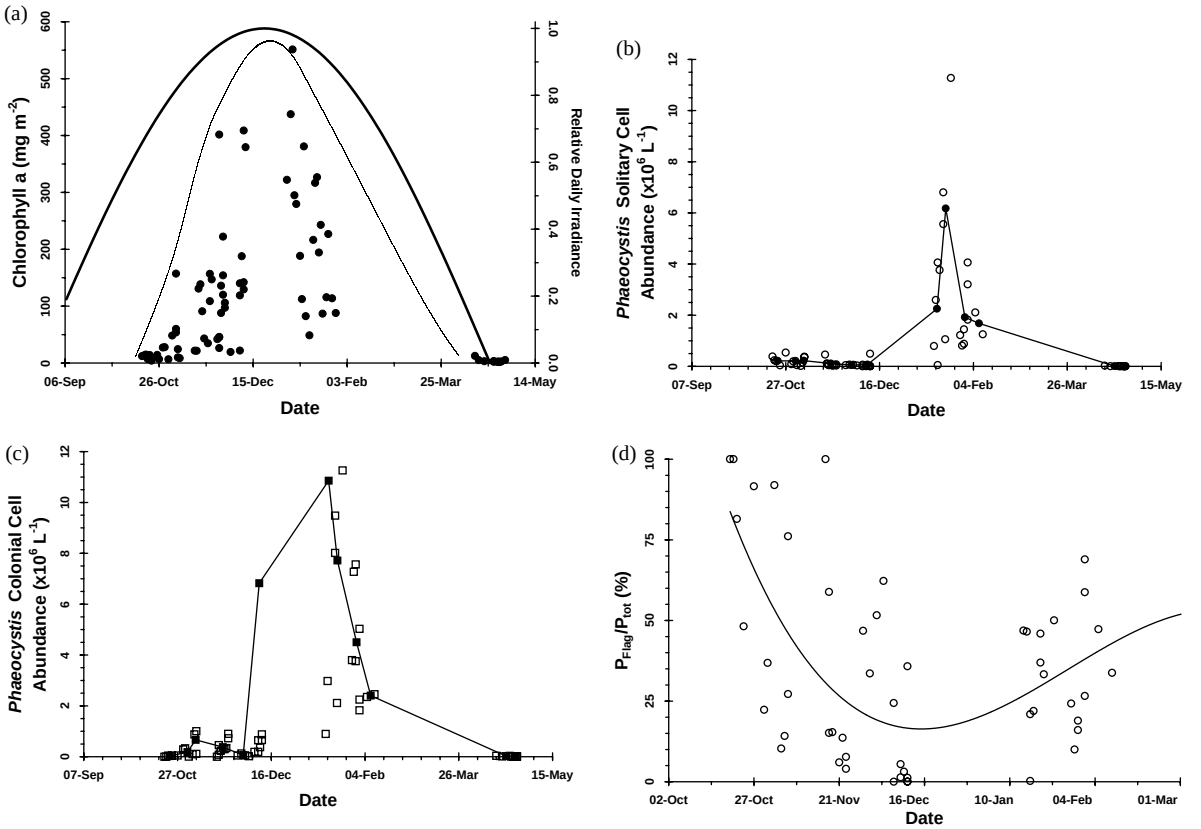

Fig. 2. (a) Integrated (0–100 m) chlorophyll *a* concentrations (solid circles) and clear-sky irradiance (heavy line) along 76°30′S as a function of time of sampling (from Smith et al., 2000b). The thin line represents a hand-drawn "envelope" of maximum concentrations; (b) abundance (average, depth-weighted from 0–60 m) of solitary, flagellated *Phaeocystis antarctica* cells in the southern Ross Sea as determined from microscopy. The filled circles and connecting line represent weekly averages; (c) abundance (average, depth-weighted from 0–60 m) of *Phaeocystis antarctica* colonial cells in the southern Ross Sea as determined from microscopy. The filled squares and connecting line represent weekly averages; (d) Percentage of solitary, flagellated cells (P_{flag}) relative to the total abundance of cells (P_{tot}; colonies + flagellates) of *P. antarctica*.

and larger than 20 μm), dinoflagellates, and other autotrophic flagellates also increased (Table 1). The appearance of colonial *P. antarctica* was not correlated with any other taxa (dinoflagellates, nano- or microplanktonic diatoms, or photosynthetic flagellates); however, the abundance of diatoms (both size classes) significantly correlated with that of flagellated forms of *P. antarctica* ($R^2 = 0.87$ and 0.86 for nano- and microplanktonic diatoms, corresponding to $p = 0.01$ and $p < 0.001$, respectively).

During the summer, the numbers of solitary cells increased to the maximum observed abundance of 11.3×10^6 cells l^{-1} on January 13, which represented 50% of the total *P. antarctica* cells on that date. The abundance of colonial cells also was maximal in summer (on January 10) and equaled 21.7×10^6 cells l^{-1}. Low abundance of solitary cells on that date resulted in colonial cells constituting 99.7% of the total number of *P. antarctica*.

3.2. Temporal variations in P. antarctica organic carbon biomass

The amount of organic carbon in each morphological form of *P. antarctica* followed similar trends to the abundance data with a few

Table 1
Mean abundance (cells l^{-1}) of cells for stations within a certain sampling period

Date	n	Microplanktonic dinoflagellates	Microplanktonic diatoms	Microplanktonic flagellates	*Phaeocystis antarctica* colonial cells	Nanoplanktonic diatoms	Nanoplanktonic flagellates	*Phaeocystis antarctica* flagellated cells
22 Oct	5	138	922	0	26,900	2860	8770	280,000
1 Nov	4	496	2150	1	181,000	2490	24,600	83,800
5 Nov	3	231	655	22	666,000	1300	19,300	293,000
20 Nov	8	9090	42,900	161	380,000	ND	ND	110,000
1 Dec	4	2920	63,100	114	63,400	ND	ND	50,304
9 Dec	9	2250	108,000	162	6,826,000	ND	ND	69,246
15 Jan	5	3240	153,000	0	10,860,000	138,000	68,000	2,251,000
20 Jan	4	6140	1,002,000	31	7,718,000	1,395,000	190,000	6,172,000
30 Jan	7	2150	128,000	26	4,501,000	130,000	84,300	1,918,000
7 Feb	2	2400	17,300	0	2,404,000	2430	132,000	1,679,000
20 Apr	5	205	162	6	24,800	ND	ND	8590
25 Apr	6	71	333	0	16,400	ND	ND	2120

The date represents the median date of sampling, and n =number of stations within that sampling period. Microplankton are cells > 20 μm, and nanoplankton are cells < 20 μm. ND=not detected.

exceptions. Integrated carbon in solitary cells and colonies was maximal in summer (Fig. 3a and b), with the greatest values being 2.25 and 17.7 g C m^{-2}, respectively. The contribution of solitary cells to total *P. antarctica* biomass carbon biomass was greatest early in spring, while the smallest contributions were observed during the time of the maximal chlorophyll concentration in late spring (Fig. 3c). The flagellate-associated carbon increased during summer and decreased in autumn, similar to the trend seen in abundance (Figs. 2b and 3a). The ratios of the average abundance of solitary cells relative to colonial cells in early spring, late spring and summer were 58.3%, 23.2% and 33.7%, respectively, whereas these ratios based on carbon during each period were 41.2%, 11.6% and 12.6%.

3.3. Spatial patterns of *P. antarctica* and diatoms

Spatial variations in the contribution of flagellated and colonial cells to total *P. antarctica* biomass were examined by pooling data from each station regardless of the time of sampling. Solitary cells were most abundant in the eastern portion of the transect, where solitary cells formed an average of nearly 53% of *P. antarctica* abundance at Station Orca (Fig. 4a). In contrast, in the western portion of the transect only ca. 20% of the total number of *P. antarctica* cells were solitary cells. Organic carbon associated with the cells showed a similar pattern. Thirty-five percent of the *P. antarctica* carbon was contributed by solitary cells at Orca, but less than 10% of *P. antarctica* carbon was derived from flagellates in the western region. Diatom abundance was greatest at the ends of the transect and did not show a clear relationship to the ratio of solitary and colonial forms of *P. antarctica* (Fig. 4b).

4. Discussion

Members of the genus *Phaeocystis* occur throughout the world's oceans, often forming large blooms in a variety of diverse locations, such as the Ross Sea, North Sea, Greenland Sea, Bering Sea shelf break, the Arabian Sea, and the

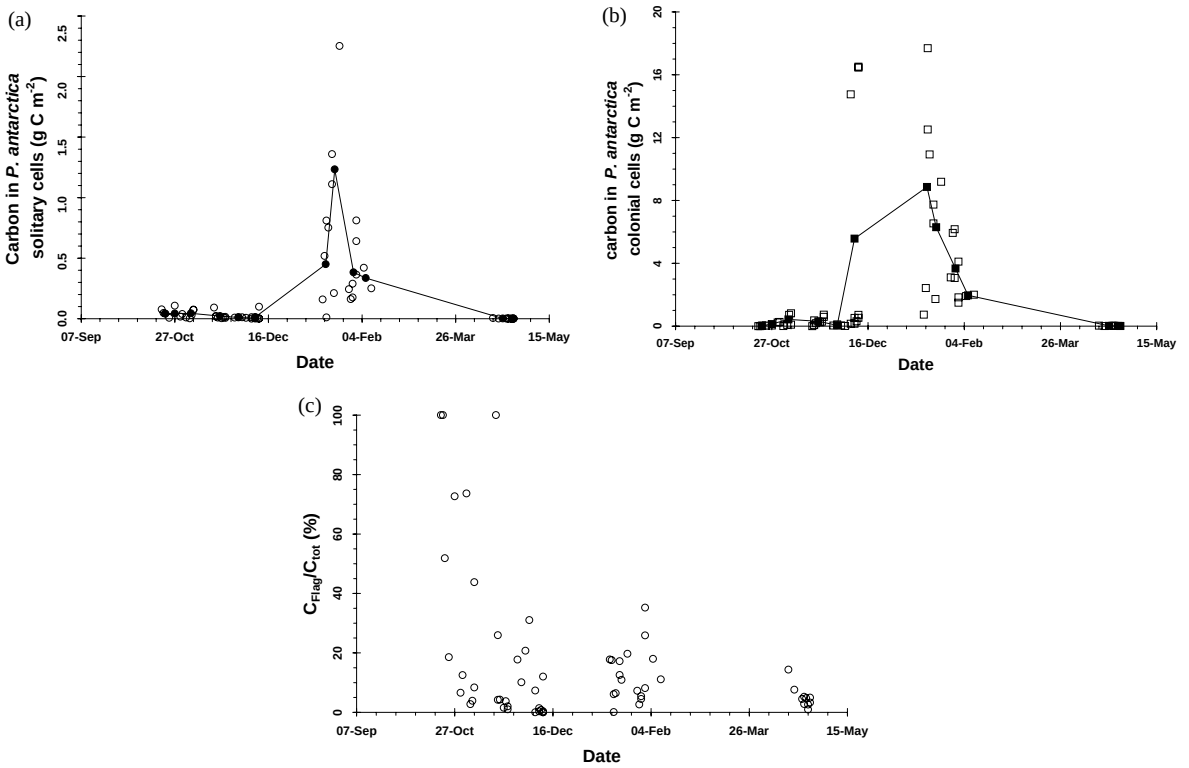

Fig. 3. Microscopically-derived carbon abundance of (a) solitary, flagellated cells and (b) colonial cells. (c) Percentage of carbon contributed by flagellated cells relative to the total *P. antarctica* cells present. The solid symbols and lines in (a) and (b) represent weekly averages. Note the different axes in (a) and (b).

Barents Sea (see Lancelot et al., 1998). In some locations (e.g., North Sea) it is believed that *Phaeocystis* growth occurs after diatoms have depleted silicic acid, but in other locations the environmental stimulus for its growth is poorly known. In the Arabian Sea a *Phaeocystis* bloom occurred in a water column with a relatively deep mixed layer (Garrison et al., 2000). Arrigo et al. (1999) also suggested that deep mixed layers in some portions of the Ross Sea favor the growth of *P. antarctica* relative to diatoms, as a result of the potentially greater photosynthetic rates of *P. antarctica* at lower irradiances (Moisan and Mitchell, 1999). However, mixed layers in the Ross Sea were not statistically different between stations dominated by diatoms or *Phaeocystis* (Smith and Asper, 2001). Furthermore, the photosynthetic responses (van Hilst and Smith, 2002) and growth rates (determined from silicon and carbon tracers; Smith et al., 1999) of diatoms and *Phaeocystis* were not significantly different in this environment. Therefore, the causes for the establishment of *P. antarctica* blooms in the Ross Sea do not appear to be related to mixed-layer depth or photophysiology.

The contribution of solitary, flagellated forms of *P. antarctica* to the total bloom biomass and carbon fixation in the Ross Sea is even more poorly understood. Arrigo et al. (1999) mapped the distribution of *P. antarctica* in the southern Ross Sea and found that diatoms were more commonly encountered in the west and in the east (near the melting ice edge). Smith and Asper (2001) also found a similar result in a different year. Our results suggest that the spatial variations in the contribution of flagellated or colonial forms to the total *P. antarctica* abundance or carbon (Fig. 4) also vary spatially, with greater

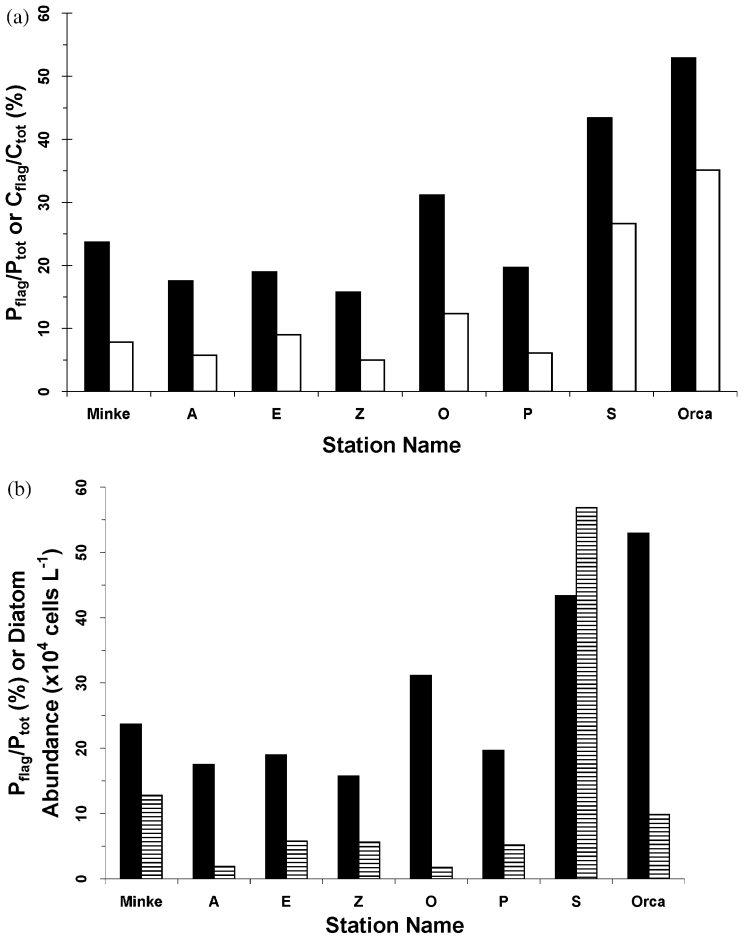

Fig. 4. The spatial variations of (a) abundance of flagellated *P. antarctica* cells to total (solitary + colonial) *P. antarctica* (solid bar) and of organic carbon of flagellated *P. antarctica* relative to that of all *P. antarctica* cells (open bar), and (b) the relative abundance of flagellated *P. antarctica* cells (solid bar) and absolute diatom abundance (gray bar). Abundances determined microscopically and organic carbon estimated from abundance data and appropriate equations (see text for details).

contributions of flagellated *P. antarctica* cells in the east. The carbon contribution is less, largely because of the differences noted in the sizes of the cells of each form. Also, significant temporal variations in the ratio of solitary to colonial cells of the alga were apparent in our seasonal study (Fig. 2d). In addition to the variations in cells of *P. antarctica*, diatoms also varied spatially, and their abundance was positively correlated with that of flagellated *P. antarctica* (Table 1). The specific causes of these variations may be numerous, but our data indicate that at least two features of the ecology of *Phaeocystis* play important roles.

Microzooplankton grazing rates were extremely low in the Ross Sea during this study. Indeed, grazing rates as determined by the dilution technique revealed significant phytoplankton mortality rates at only 13 of 51 experiments (Caron et al., 2000). However, for those stations where significant phytoplankton mortality rates were measured, a positive relationship was observed between mortality rate and the percentage of solitary cells relative to the total number of *P. antarctica* cells (Fig. 5). This result appears to indicate that microzooplankton were capable of grazing solitary cells of *P. antarctica* but relatively

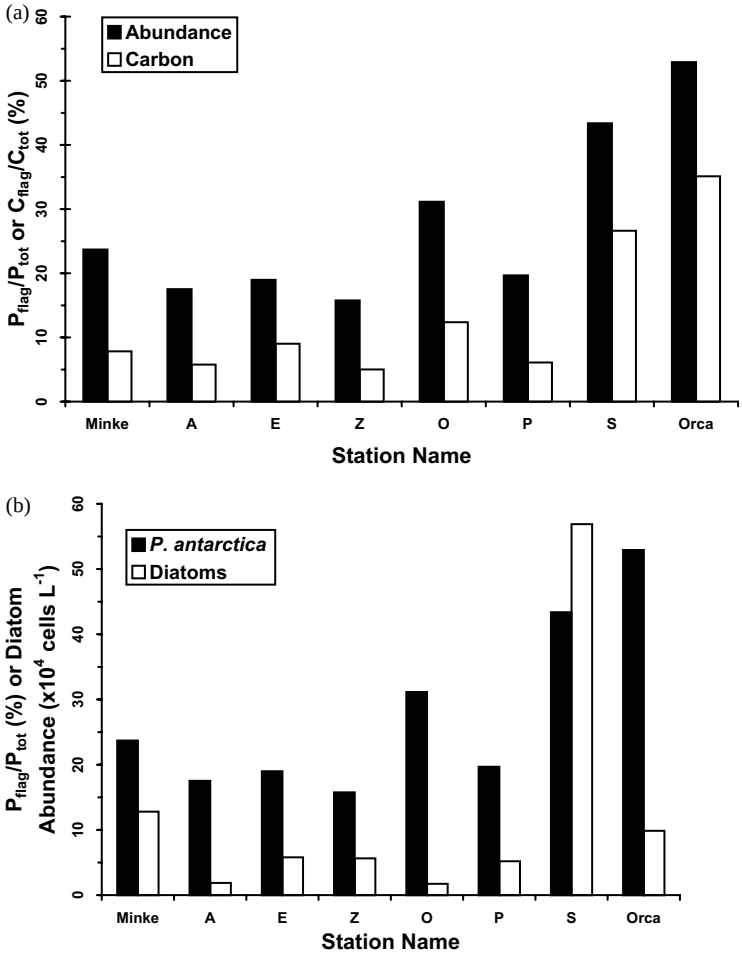

Fig. 5. Relationship between phytoplankton mortality rate, as determined from dilution experiments (Caron et al., 2000), and the percentage of flagellated cells relative to the total abundance of *P. antarctica*.

incapable of ingesting cells in colonies. The results of previous studies support the finding that solitary, flagellated cells of *Phaeocystis* spp. are readily ingested by microzooplankton (e.g., Verity et al., 1988; Weisse and Scheffel-Möser, 1990; Weisse et al., 1994; Tang et al., 2001).

It has been hypothesized that colony formation is a strategy of *Phaeocystis* species for avoiding grazing pressure (Lancelot et al., 1998; Jakobsen and Tang, 2002). Grazing on colonies may take place at some low level (indeed, this process has been noted in some systems; e.g., Weisse et al., 1994), but this rate appears to be insignificant relative to algal growth during much of the late spring and summer in the Ross Sea. Reduced grazing on the colonial form of *P. antarctica* combined with rapid grazing on solitary cells could result in a competitive advantage for colonial cells even if the solitary and colonial cells had similar gross growth rates. Of course, it is also possible that the life history of *P. antarctica* in the Ross Sea has intrinsic controls that favor colony formation during periods of growth initiation and rapid growth. This latter behavior would intensify any selective advantage that colonial cells might have due to release from grazing pressure.

In addition to differences in susceptibility to microbial grazing, there also may be physiological differences between solitary and colonial cells of *P. antarctica* that would result in different responses to changes in environmental conditions. Mathot et al. (2000) found that solitary cells were significantly smaller (mean spherical diameter=3.1 ± 0.60 μm) than those in colonies (mean spherical diameter=5.1 ± 1.1 μm). Furthermore, the calculated carbon content of solitary vs. colonial cells was 3.33 and 13.6 pg C cell^{-1}, a 4-fold difference (Mathot et al., 2000). It has been suggested that macronutrient limitation favors the smaller, flagellated forms relative to colonies of other species of *Phaeocystis* (Verity et al., 1988; Escaravage et al., 1995), and there is no reason to expect that micronutrient limitation would not favor solitary forms as well. Indeed, the diffusive flux of iron (calculated from Fick's Law) into a colony with a 4-mm diameter is ca. 10^6-fold lower than that into a 4-μm nanoflagellate at the same ambient iron concentration. Although colonial cells are on the exterior of the organic matrix, the size and nature of the colony may substantially reduce the iron (and other nutrient) availability to colonial *P. antarctica* cells.

However, it has recently been suggested that iron might complex with the colonial sheath of *Phaeocystis pouchetii*, thus making the absorbed iron more available to the colonial cells embedded in the mucilage (Schoemann et al., 2001). Lancelot and Mathot (1985) reported that *P. pouchetii* could utilize the carbon in the mucilage as an additional carbon source, and if this were true for *P. antarctica*, then it would provide a mechanism for enhanced iron uptake by colonial cells, providing them a competitive advantage over solitary cells. No data exist on the dependence of absorption of iron and its dependence on ambient dissolved concentrations, particularly in the Ross Sea, so the importance of this effect cannot be critically evaluated. However, such a mechanism might explain how colonial cells increase their relative contribution to biomass when iron is not limiting (e.g., during austral spring), particularly in concert with reduced losses due to grazing.

This effect presumably would be especially important during austral summer in the Ross Sea because iron is reduced to extremely low concentrations at that time (Sedwick et al., 2000; Fitzwater et al., 2000). Indeed, during our study iron concentrations during late summer at 20 m were (with only one exception) less than 0.04 nM (Coale et al., unpublished). Iron has been repeatedly shown to limit phytoplankton photosynthesis and growth in the region (Martin et al., 1990; Sedwick and DiTullio, 1997; Sedwick et al., 2000; Olson et al., 2000). Given that iron limitation in summer is a common occurrence in the Ross Sea, we suggest that the increase in flagellated, solitary cells in summer may represent a shift in the outcome involving the competition between solitary and colonial cells that arises from the conflicting impacts of grazing selectivity (which appears to favor colonies) and nutrient limitation (which appears to favor solitary cells).

The exact nature of that response, however, is unclear. It could simply be a reduced growth of colonial *P. antarctica* in concert with constant, unchanged losses resulting in a decrease in colonial cell abundance and a negative net growth rate for colonies. We also can speculate that if the colonial abundance decreased, the mean irradiance available to the remaining cells would increase, and the iron demand per cell would decrease due to the synergistic effect between irradiance and iron uptake (the Fe requirement is greater under low irradiance; Sunda and Huntsman, 1997). Alternatively, iron limitation could result in enhanced colony degradation and liberation of flagellated cells (Wassmann et al., 1990), thereby directly producing an increase in the net abundance of solitary cells. We cannot define the regulatory factor(s) at this time, and determination of the exact mechanism of the differential production of flagellated *P. antarctica* remains to be confirmed by further investigations.

The co-occurrence of flagellated *P. antarctica* cells with colonies of the same species is not unexpected, as the same situation has been reported in other systems (Lancelot et al., 1998) and of course colonial forms can give rise to flagellated forms of the species. However, based on the magnitude of the blooms attained by this species and the very different trophic pathways taken by solitary and colonial cells, the form of

P. antarctica in the Ross Sea has a disproportionately large and varied effect on carbon transformations and biogeochemical cycles. Flagellated cells seem to actively participate in the microbial food web, whereas colonial cells are less effectively controlled by microbial predators. Therefore, understanding the mechanisms by which the two morphological forms of this species are generated is critical to understanding the controls on the microbial food web in the Ross Sea. Similarly, an appreciation of the response of the forms of *P. antarctica* to varying environmental conditions (especially micronutrient concentrations and irradiance) should provide insights into the regulation of biogeochemical cycles of the area. While an understanding of the temporal and spatial dynamics of *Phaeocystis antarctica* is important, it is just as important to understand the controlling factors for the two phases of this species. Without such information our understanding of the role of this keystone species in present and past environments will remain incomplete.

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