Physical control of chlorophyll \( a \), POC, and TPN distributions in the pack ice of the Ross Sea, Antarctica

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[1] The pack ice ecosystem of the Ross Sea was investigated along a 1470-km north-south transect during the spring 1998 oceanographic program Research on Ocean-Atmosphere Variability and Ecosystem Response in the Ross Sea (ROAVERRS). Snow and sea ice thickness along the transect varied latitudinally, with thinner snow and ice at the northern ice edge and thin new ice in the vicinity of the Ross Sea polynya. Relative to springtime observations in other sea ice regions, algal chlorophyll \( a \) (Chl \( a \)) concentrations were low. In contrast, particulate organic carbon (POC), total particulate nitrogen (TPN), and POC:Chl \( a \) were all high, indicating either that the ice contained substantial amounts of detritus or nonphotosynthetic organisms, or that the algae had a high POC:Chl \( a \) ratio. The abundance of Chl \( a \), POC, and TPN in the sea ice was related to ice age and thickness, as well as to snow depth: older ice had thinner snow cover and contained higher algal biomass while new ice in the polynya had lower biomass. Older pack ice was dominated by diatoms (particularly \textit{Fragilariopsis cylindrus}) and had vertical distributions of Chl \( a \), POC, and TPN that were related to salinity, with higher biomass at the ice-water interface. Fluorescence-based measurements of photosynthetic competence (Fv/Fm) were higher at ice-water interfaces, and photosynthesis-irradiance characteristics measured for bottom ice algae were comparable to those measured in pack ice communities of other regions. Nutrient concentrations in extracted sea ice brines showed depletion of silicate and nitrate, depletion or regeneration of phosphate and nitrite, and production of ammonium when normalized to seawater salinity; however, concentrations of dissolved inorganic nitrogen, phosphorous, and silica were typically above levels likely to limit algal growth. In areas where pack ice and snow cover were thickest, light levels could be limiting to algal photosynthesis. Enrichment of \( \delta^{13}C \)-POC in the sea ice was correlated with the accumulation of POC, suggesting that carbon sources for photosynthesis might shift in response to decreasing CO\(_2\) supply. Comparisons between new ice and underlying waters showed similar algal species dominance (\textit{Phaeocystis antarctica}) implying incorporation of phytoplankton, with substantially higher POC and TPN concentrations in the ice.

INDEX TERMS: 4207 Oceanography: General: Arctic and Antarctic oceanography; 4540 Oceanography: Physical: Ice mechanics and air/sea/ice exchange processes; 4805 Oceanography: Biological and Chemical: Biogeochemical cycles (1615); 4815 Oceanography: Biological and Chemical: Ecosystems, structure and dynamics; KEYWORDS: sea ice, algae, Antarctic, nutrients, ecosystem


1. Introduction

[2] During each austral autumn, the surface of the ocean surrounding the Antarctic continent begins to freeze, eventually forming a layer of sea ice up to a meter or more thick. This ice cover generally extends over an area ranging from \( 4 \times 10^6 \) km\(^2\) in the summer to approximately \( 19 \times 10^6 \) km\(^2\) in late winter, most of which consists of annual pack ice [Cavalieri et al., 1999]. The presence of sea ice increases surface albedo, restricts air-sea gas exchange, and provides a stable habitat for diverse microbial assemblages.

[3] Most of what is currently known about Antarctic pack ice is based on investigations in the Weddell Sea sector of...
the Southern Ocean. These studies have documented the
dynamic nature of the Antarctic ice pack, which is con-
stantly moving and shifting in response to local near-surface
ocean currents and winds [Kottmeier and Sellmann, 1996;
Fisher and Lytle, 1998]. In areas where the snow cover is
sufficiently thin to allow adequate light transmission, dia-
tom-based microbial communities often form within the ice
pack in spring and early summer [Legendre et al., 1992;
Lizotte and Sullivan, 1992; Gleitz et al., 1996b]. Microbial
communities in the pack ice of the Weddell Sea can be quite
productive, with maximum photosynthetic rates comparable
to those of pelagic phytoplankton sampled in the same
region [Lizotte and Sullivan, 1992].

[4] Pack ice within the Ross Sea sector of the Southern
Ocean is less well studied than in the Weddell Sea, but has
received an increasing amount of scientific interest of late.
The first large-scale study of the Ross Sea ice pack was a
géophysic survey conducted during the austral autumn of
1995. Based on observations made during that study,
Jeffries and Adolphs [1997] proposed that the pack ice in
the Ross Sea sector of the Southern Ocean consists of three
distinct zones (Figure 1). The outer pack, extending from
600 km north of the Ross Ice Shelf to the northern ice edge,
was composed of relatively young sea ice with a mean
thickness of 0.36–0.48 m. Snow cover was relatively thin
(mean = ca. 0.1 m) in this zone during the short time
available for accumulation. The central pack (200–600 km
north of the Ross Ice Shelf) comprised older and thicker
(mean = 0.6–0.7 m) sea ice with a heavier and more
variable accumulation of snow (mean = ca. 0.15 m). The
inner pack (0–200 km north of the Ross Ice Shelf) was
influenced strongly by the Ross Sea polynya located at the
northern edge of the Ross Ice Shelf. During winter and early
spring, sea ice continually forms in this polynya but is
adveected northward by strong katabatic winds blowing off
of the Ross Ice shelf [Bromwich et al., 1992]. Consequently,
sea ice in this zone decreases in age, thickness (0.22–
0.47 m), and snow depth (0.03–0.08 m) with increasing
proximity to the Ross Ice shelf.

[5] We know of no published studies focused on the
microbial communities of Ross Sea pack ice, although
extensive work has been done on the nearshore fast ice of
this region, particularly in McMurdo Sound. Fast ice of the
Ross Sea differs significantly from the pack ice of the
region in thickness and structure [Gow et al., 1998], which
imposes differences in light and nutrient availability that
impacts algal growth. Reviews of Antarctic sea ice biology
show that pack ice is usually dominated by species different
from those dominating nearshore ice communities [Horner,
1985]. Antarctic pack ice communities have been shown to
be more similar to nearby phytoplankton with respect to
species composition [Garrison et al., 1987] and algal
physiology [Lizotte and Sullivan, 1992] leading Priddle et
al. [1996] to hypothesize that pack ice and the upper water
column comprise a “two-phase” ecosystem. Thus we
anticipated that the biology of Ross Sea pack ice would
differ considerably from fast ice in the region. Furthermore,
structural differences between pack ice of the Ross Sea and
the pack ice of other Antarctic regions [Jeffries and Adolphs,
1997] and oceanographic differences such as larger, more persistent polynyas open the possibility that
pack ice microbial communities of the Ross Sea might
differ from counterparts studied previously in other regions
of the Southern Ocean.

[6] During the spring of 1998, the Research on Ocean-
Atmosphere Variability and Ecosystem Response in the
Ross Sea (ROAVERRS) program sampled the pack ice
along a complete north-south transect in the Ross Sea in a
location near that sampled earlier by Jeffries and Adolphs
[1997]. This has allowed us to (1) determine how the
springtime snow and pack ice thickness distributions in
the Ross Sea differ from the autumn values reported by
Jeffries and Adolphs, and (2) investigate the relationship
between the physical characteristics of the pack ice habitat
and the resident microbial communities. In particular, we
studied how physical and chemical conditions in pack ice
are related to the abundance, physiology, and elemental
composition of sea ice microalgae in the Ross Sea.

2. Materials and Methods

[7] The R.V. B. Nathaniel B. Palmer was the sampling
platform for the ROAVERRS program. En route to the Ross

Figure 1. Sea ice station locations for the 1470 km long
north-south transect sampled between 6 November and
14 November 1998 as part of the Research on Ocean-
Atmosphere Variability and Ecosystem Response in the
Ross Sea (ROAVERRS) program. Stations denoted by black
symbols correspond approximately to the inner pack zone of
Jeffries and Adolphs [1997]; gray symbols denote stations in
the central pack, and white symbols, in the outer pack.
Sea polynya, a 1470-km long north-south transect through the pack ice (centered approximately on 176°E) was sampled between 6 November and 14 November 1998. A total of 27 stations were sampled along this transect providing a spatial resolution of approximately 0.5° in latitude (Figure 1). Cores were typically collected along a 4-core transect at 1 m intervals after measurements were made of snow thickness and ice surface temperature. We did not sample the ridged or rafted ice that comprised relatively small area on some floes. Stations 1–6 and 21–23 had discernible floes 10–100 m across, from which we sampled in transects starting at the edge of the floe. Stations 7–20 were located in consolidated pack ice with no discernible edges. Stations 24–29 were sampled in new pancake ice.

2.1. Satellite Measurements of Sea Ice Distribution and Circulation

Sea ice concentrations were measured remotely using the Special Sensor Microwave Imager (SSM/I). Seasonal and interannual changes in sea ice area were calculated for the region bounded by 60°S–79°S and 162°E–155°W which contained both our transect and the transect sampled by Jeffries and Adolphs [1997]. Total sea ice area was calculated every other day (2 January 1979 to 9 July 1987) or daily (10 July 1987 to 31 December 1998) by summing the product of the size and the fractional sea ice concentration of all pixels.

Maps of sea ice motion (velocity and direction) for the Ross Sea, Antarctica, were produced as described by Meier et al. [2000] by C.W. Fowler at the University of Colorado, Boulder.

2.2. Surface Water Column Sampling

A rosette of 10-l Bullister Bottles was used to collect water samples from surface waters (3 m). Suspended particles were collected by filtration of water samples through Whatman GF/F glass-fiber filters for analysis of chlorophyll a (Chl a), particulate organic carbon (POC), and total particulate nitrogen (TPN).

2.3. Sea Ice Sampling

Sea ice was sampled by deployment of personnel either directly onto the ice pack, or, in the case of thin ice (<0.2 m), from a basket hung over the side of the ship and positioned just above the ice surface. On thick ice, sea ice samples were obtained using a SIPRE corer (0.076 m interior diameter); an ice saw was used to obtain sea ice samples from thin ice. Ice cores longer than 0.2 m were sectioned at 0.1–0.2 m intervals and each segment was placed in individual labeled polyethylene bags. All sea ice samples were stored in the dark in a thermally insulated cooler until they could be processed on board ship (within 0.5 hours). In the cold room of the ship, one set of ice samples was measured for length (0.05–0.27 m), placed in 2 or 4 l polyethylene bottles, a sufficient quantity of 0.2-μm-filtered seawater added to maintain salinity ≥28 psu (to minimize osmotic shock to the microbial community), and the sample allowed to melt in the dark. Brine samples were collected from replicate, sectioned (ca. 0.1 m length) cores that were centrifuged in the cold room within 10 min of collection. Brine was decanted, its volume measured, and the brine analyzed for salinity, nutrient concentration, and variable fluorescence; the remaining ice was melted for volume and salinity determination.

Brine samples were collected from duplicate core sections for analysis of salinity and nutrients. Each 0.2 m ice core section was spun rapidly in a large (1 l volume) centrifuge to accelerate the discharge of brine from the ice matrix. Work was done in a −2°C freezer to prevent melting of sea ice.

2.4. Snow and Ice Thickness

At least four holes (usually spaced 1 m apart) were drilled at each sea ice station for determination of sea ice thickness. A tape measure attached to the center of a brass rod was inserted into each hole, and the tape was pulled tight until the brass rod held securely to the bottom sea ice surface. The thickness was then read off the tape measure at the snow/ice interface. Before drilling, snow thickness was measured by inserting a ruler through the snow to the snow/ice interface. The mean ice and snow thickness for each station was calculated by averaging the thickness at all core locations at that station.

2.5. Sea Ice Salinity and Temperature, Brine Salinity and Volume

Ice surface temperature at each core location was measured by inserting the tip of a digital temperature probe (Corning Science Products) approximately 0.01 m into the ice surface. The reading was taken after the temperature had stabilized (ca. 10 s). The mean surface temperature at a given station was calculated from the measurements made at each ice core location at that station.

Sea ice salinity was measured after bulk ice cores sections had melted. Brine volume was calculated from the salinity and density of sea ice and brine according to the equations of Cox and Weeks [1986].

2.6. Sea Ice Nutrients

Inorganic macronutrient concentrations in sea ice brines were determined on board ship within 1 hour of collection using a Technicon AutoAnalyzer II system according to the JGOFS protocols described by Knap et al. [1996]. Detection limits were 0.03 mmol m⁻³ for NO₃, 0.005 mmol m⁻³ for NO₂, 0.005 mmol m⁻³ for NH₄, 0.008 mmol m⁻³ for PO₄, and 0.1 mmol m⁻³ for Si(OH)₄. Nutrient-free artificial seawater water was used to dilute brine samples exhibiting very high salinity which were suspected of having nutrient concentrations above the analytical range.

2.7. Pigments POC, δ¹³C POC, and TPN Analyses

2.7.1. Pigments

Suspended particles were collected by filtration of melted sea ice samples through Whatman GF/F glass-fiber filters for analysis of algal pigments. Filters were immediately frozen in liquid N₂ and stored at −80°C until they could be processed. High performance liquid chromatography (HPLC) analysis of pigment composition, including chlorophylls and carotenoids, was performed using the method of Wright et al. [1991] as described by DiTullio and Smith [1996].

2.7.2. POC and TPN

POC and TPN (mostly organic N) samples also were measured following Knap et al. [1996] with the addition of
a rinse with 10 ml of 0.01 N HCl in filtered (0.2 μm) seawater immediately after filtration. Sea ice particulates were collected by filtration of 200–1000 ml of melted and diluted sea ice samples through precombusted 25 mm Whatman GF/F glass-fiber filters. Filters were rinsed with 0.1 N HCl to remove any carbonate phases and air-dried and analyzed for total organic C and TPN using a Carlo Erba NA1500 elemental analyzer/Conflo II device and Finnigan Delta Plus mass spectrometer at Stanford University. Filters were packed into tin envelopes, purged in ultrahigh purity He within a sealed sample carousel for >30 min, and flash combusted at ca. 1700°C. Elemental composition is determined by integrating mass 28 and 44 beam intensities (as voltage) on the Delta Plus, calibrated with at least five elemental standards analyzed during each run. Amount of total organic C and total N reproducibility, as determined by replicate analyses of acetanilide standard (n = 81) is 0.9 and 1.2%, respectively. The concentration of POC and TPN in the sea ice is then calculated from the known volumes of melted sea ice and particle-free diluent water added to keep salinities above 28 psu.

[19] δ13C-POC was also analyzed with the elemental analyzer and Finnigan mass spectrometer, simultaneous with the POC and TPN determinations. Isotopic compositions were calibrated against the NBS-21 and IAEA-N1 standards that were run before and after each set analyses. Isotopic reproducibility is on the order of 0.11‰.

2.8. Cell Counts

[20] Sea ice microalgae were fixed (2% gluteraldehyde final concentration) for several minutes and then concentrated by filtration of the melted sea ice sample under low pressure through a 0.2-μm Poretics filter. Filters were mounted on glass slides using Type FF nonfluorescing immersion oil and stored frozen. Cells were counted at both 400× and 1000× using epi-fluorescence microscopy.

2.9. Sea Ice Algal Photophysiology

2.9.1. Photosynthesis-Irradiance Incubations

[21] Photosynthesis versus irradiance (P-E) relationships for algae were determined using a modification of the 14C-bicarbonate technique of Lewis and Smith [1983] as described by Robinson et al. [1995] and Arrigo et al. [2000]. Melted sea ice samples (300 ml) were spiked with 14C-bicarbonate (NEN) solution to a final activity of 1 μCi ml−1. After thorough mixing, triplicate 100 μl subsamples were withdrawn and added to 7 ml scintillation vials containing 0.1 ml of phenethylamine and 5 ml of scintillation cocktail (Ecolume, ICN) to determine total activity of the spiked sample. The remaining spiked sample was distributed in 10 ml aliquots into 27 scintillation vials (20 ml). Three vials were immediately processed by vacuum filtration to obtain a time-zero value for radioactivity. The remaining 24 vials were placed in separate chambers within a temperature-regulated aluminum block (−1°C). Illumination was provided by a 500-W tungsten-halogen lamp (Sylvania). Light levels within each chamber were adjusted with neutral density filters to produce a complete P-E curve with illumination ranging from 0 to 350 μmol photons m−2 s−1. The incubations were initiated when the light source was turned on and terminated after 2 hours when illumination was discontinued. The contents of each vial were passed through Whatman GF/F glass-fiber filters under low vacuum pressure to collect algal cells. The filters were transferred to a scintillation vial containing a dilute acid solution to drive off inorganic radioisotope and then dried. Radioactivity associated with all filters was assayed using liquid scintillation (ICN Biomedicals Inc.) counting.

[22] The photosynthetic parameters Pm (maximum photosynthetic rate, mg C mg−1 Chl a h−1) and α (photosynthetic efficiency, mg C mg−1 Chl a h−1 (μmol photons m−2 s−1)−1) were estimated from a fit of P-E data to the equation of Platt et al. [1980] after spectrally correcting for the output of the tungsten-halogen lamp as described by Arrigo and Sullivan [1992]. Doubling times were calculated by log-transforming specific growth rates derived from Pm and the Chl a:C ratio. The photoadaptive index (Eh_chl μmol photons m−2 s−1) was calculated as Pm/α.

2.9.2. Quantum Yield of Photosynthesis

[23] The quantum yield of photosynthesis (φp) was calculated as

\[
\phi_p = \frac{\alpha}{43.2 \alpha \phi}.
\]

where \(\alpha\) is the mean pigment-specific absorption coefficient. Suspended particulates for \(\alpha\) determination were collected by filtration of water samples through Whatman GF/F glass-fiber filters for analysis of pigments and light absorption properties. Filters were immediately frozen in liquid nitrogen and stored at −80°C until they could be processed. Particulate absorption spectra, \(a_p(\lambda)\), were measured between 300 and 800 nm using a Perkin-Elmer Lambda 6 spectrophotometer. All spectra were corrected for optical path length amplification effects using the procedure of Mitchell and Kiefer [1988] and the coefficients of Bricaud and Stramski [1990]. Detrital absorption (actually absorption by nonmethanol extractable particles, including algal cell material, detritus, microbioplankton, bacteria, lithogenic material, etc.), \(a_{det}(\lambda)\), for each sample was determined using the methanol extraction technique of Kishino et al. [1985]. The Chl a-specific absorption coefficient \(a_{ph}^a\) was calculated by subtraction of \(a_{det}\) from \(a_p\) and normalization by Chl a.

2.9.3. Fluorescence Measurements

[24] Brine samples were stored in acid washed plastic bottles in the dark (dark adapted) for 30 min at 0°C prior to measuring fluorescence. The dark adapted samples were poured into 12 mm diameter glass cuvettes and fluorescence measurements (Fo) were made 30 s after insertion of a cuvette into the sample chamber of a Turner Designs Model 10 AU digital fluorometer. Addition of a neutral density filter reduced the excitation energy from the fluorometer, preventing overestimation of Fo for algae acclimated to low light [Parkhill et al., 2001]. The cuvettes were removed from the sample chamber, spiked with 10 mM DCMU (dissolved in 90% ethanol) to produce a final concentration of 10 μM, and returned to the sample chamber for measurement of DCMU-enhanced fluorescence (Fm).
[25] Measurements of Fo and Fm are related to the maximum quantum efficiency of photochemistry at photosystem II ($\phi_{PSII}$) by the relationship [Butler, 1978]

$$\phi_{PSII} = \frac{Fm - Fo}{Fm} = \frac{Fv}{Fm}. \quad (2)$$

where $Fv$ is variable fluorescence ($Fm - Fo$).

2.10. Sea Ice Irradiance

[26] Although subice irradiance was not measured directly during this study, the downwelling spectral irradiance at the depth of maximum algal biomass was approximated using the sea ice radiative transfer model of Arrigo et al. [1991]. Model forcing data included air temperature (used to determine snow wetness and sea ice brine volume), snow and sea ice thickness, and Chl $a$ concentration. Downwelling photosynthetically active radiation (PAR) was calculated by integrating spectrally from 400 to 700 nm. Percent transmission of PAR was calculated from PAR at the snow surface and at the depth of the maximum algal biomass; this was done both with and without Chl $a$ to determine the effects of the algal biomass on light transmission.

3. Results

3.1. Sea Ice and Snow

3.1.1. Sea Ice Dynamics

[27] Both 1995 (the year of the Jeffries and Adolphs [1997] study) and 1998 (the year of our study) had particularly extensive sea ice cover, ranking among the highest years in terms of sea ice extent for the 20-year period between 1979 and 1998 (Figure 2), a trend that continued throughout most of both years. The decline in sea ice extent in both years was delayed, resulting in particularly high spring and summer ice cover. Because of the similarity in the dynamics of sea ice concentration and extent between the 2 years, we feel confident that it is appropriate to interpret differences in sea ice and snow thickness between the autumn 1995 study and the spring 1998 study as being indicative of seasonal changes rather than reflecting interannual variability, which would confound a seasonal comparison.

[28] Like sea ice extent, sea ice circulation patterns in 1998 also were similar to those of 1995. Maps of sea ice motion in both years show a general cyclonic pattern, with sea ice ultimately moving northward and then eastward out of the southwestern Ross Sea (Figures 3 and 4). Early in the growth season (February), ice velocities were very low, generally 2 cm s$^{-1}$ or less. By March, ice velocities in both years had increased to a maximum of 6–8 cm s$^{-1}$ (Figures 3b and 4b), with the general direction of flow aligned parallel to the Ross Ice Shelf in the southeast and then shifting northward in the southwest (Figures 3f and 4e). As sea ice extent increased throughout autumn, mean sea ice velocities reached their maximum value, coinciding with the annual maximum in daily average wind speed [Arrigo et al., 1998a]. Peak sea ice velocity during the year averaged approximately 10–12 cm s$^{-1}$, although occasionally speeds increased to as high as >18 cm s$^{-1}$ in response to a strong storm event (e.g., Figure 3d). Although sea ice circulation was generally cyclonic (Figures 3h, 4f, and 4k), there were some days when sea ice moved in a predominantly northward direction (e.g., Figures 3g and 4l).

[29] Sea ice velocity in the vicinity of our study averaged approximately 6 cm s$^{-1}$ between the time of initial ice pack formation and our study in November. At this rate of speed, sea ice that had formed in the Ross Sea polynya immediately north of the Ross Ice Shelf would take approximately 340 days to travel the 1800 km distance to the furthest northern boundary of the pack ice. Even at near-maximum speeds of 10 cm s$^{-1}$, the distance could not be covered in less than 200 days. Given that pack ice in the Ross Sea does not begin to form until sometime in March, moving at a speed of 6 cm s$^{-1}$, pack ice formed north of the Ross Ice Shelf would have traveled, at most, 1250 km by the time of our study in November. Sea ice velocities suggest that despite the generally northward flow of sea ice in the southwestern Ross Sea, the oldest sea ice would never reach the northern ice edge, and thus would be concentrated in the interior of the pack, in agreement with observations of Jeffries and Adolphs [1997].

3.1.2. Sea Ice Concentration

[30] Sea ice concentration determined by SSM/I (Figures 1 and 5a) varied markedly along the sea ice transect. At the northern boundary of the ice pack, sea ice concentrations formed a sharp delineation between partially ice covered waters to the south and ice-free waters to the north (Figure 5a). Sea ice concentrations remained between 80 and 96% as far south as 75°S. South of 75°S, there was substantial northward advection of ice associated with the Ross Sea polynya, and as a result, sea ice concentrations declined rapidly in this region. At the southernmost sea ice station near the Ross Ice Shelf, ice concentrations were only approximately 32%.

Figure 2. Temporal changes in area coverage by sea ice for the years 1995 and 1998 in the Ross Sea. Thin gray lines denote annual sea ice cycle for all other years between 1978 and 1998. For this analysis, the boundaries of the Ross Sea were defined as: north-160°S, south-Antarctic continent, east-155°W, and west-162°E. Note that both 1995 (the year of the Jeffries and Adolphs [1997] study) and 1998 (the year of our study) were relatively high sea ice years.
Figure 3. Seasonal changes in (a–d) sea ice velocity (cm s$^{-1}$) and (e–h) sea ice trajectory between the onset of ice freeze-up in February and the study of Jeffries and Adolphs [1997] in May 1995.
3.1.3. Sea Ice and Snow Thickness

[31] The mean sea ice thickness (Figure 5b) along our November transect through the Ross Sea ice pack was 0.54 ± 0.25 m, with the frequency distribution being skewed toward the thinner ice thickness classes (Figure 6). This is similar to the mean autumn ice thickness reported by Jeffries and Adolphs [1997] which ranged from 0.51 ± 0.27 to 0.65 ± 0.33 m, depending upon sampling method employed (direct measurements versus ship-board observation of overturned floes). Seventy percent of the ice cores sampled during our study were between 0.25 and 0.75 m in length and less than 2% of the ice cores were greater than 1.0 m thick. Ridging was far less prevalent in the pack ice along our transect than was the case for other regions of the Ross Sea, such as nearby Terra Nova Bay where ridged ice accounted for 44–66% of total ice mass [Jeffries et al., 2001].

[32] Our ice thickness data suggest that the three distinct zones proposed by Jeffries and Adolphs [1997] for autumn were also present in the Ross Sea during the austral spring, although the characteristics of these zones differed markedly between seasons. Springtime ice thickness was greatest in the broad, outer pack between the northern margin of the ice pack and 72°S (equivalent to the 600–1200 km outer pack of Jeffries and Adolphs), averaging 0.65 ± 0.20 m, with a high degree of latitudinal variability (Figure 5b). In the

Figure 4. Seasonal changes in (a–c, g–i) sea ice velocity and (d–f, j–l) sea ice trajectory between the onset of ice freeze-up in February and our study in November, 1998.
central pack between 72°S and 75°S (equivalent to the 200–600 km central pack of Jeffries and Adolphs), sea ice thickness decreased to an average of 0.41 ± 0.05 m (Figure 5b). In contrast to the outer pack, the thickness of sea ice in the central pack was substantially lower than values measured by Jeffries and Adolphs during the autumn. Within the inner pack between 75°S and the Ross Ice Shelf (equivalent to the 0–200 km inner pack of Jeffries and Adolphs), springtime sea ice thickness diminished rapidly from 0.41 ± 0.05 m at the boundary between the inner and central pack to <0.05 m in the extreme south, which was dominated by dark nilas (Figure 5b).

Springtime snow thickness did not exhibit a meridional pattern proportional to sea ice thickness, as was observed in autumn (Figures 5b and 5c). Snow depth was greatest and most variable (0.18 ± 0.17 m) in the central pack near 68°S (Figure 5c) and declined both northward toward the sea ice margin (0.03 ± 0.02 m) and southward toward the Ross Ice Shelf (<0.01 m). Between 72°S and 78°S, snow thickness averaged <0.02 m. Spring and autumn snow thickness distributions were only similar in the northern reaches of the ice pack. Autumn snow accumulation in the southern two thirds of the ice pack was 2- to >10-fold greater than springtime values, with the peak thickness in autumn (ca. 0.15 m) located much further south, between 75°S and 76°S. If the spring and autumn snow distributions shown in Figure 5c are representative of their respective seasons, then approximately 90% of the autumn snow cover
south of 69°S disappears or is transformed into snow ice by spring.

3.1.4. Sea Ice Temperature, Salinity, and Brine Volume

The temperature measured at the snow/ice interface (or the pack ice surface when snow was absent) varied along our transect from −9.0°C to −2.7°C (Figure 5d). There was no obvious latitudinal trend in surface temperature, with most of the variation being a function of smaller-scale weather events that varied both spatially and temporally during the 8-day study. Temperatures at the sea ice interior (in the vertical center of the ice slab), assuming a linear temperature gradient from the pack ice surface to the bottom, were less variable, ranging from −5.4°C to −2.3°C.

In contrast to temperature, bulk sea ice salinity (the mean salinity of the entire pack ice slab) exhibited a significant ($p < 0.01$) latitudinal trend (Figure 5e), increasing with proximity to the Ross Ice Shelf where the pack ice was relatively thin. The mean pack ice salinity along the transect was 5.6 psu, with values being lowest north of 68°S (mean = 4.1 psu) and highest south of 75°S (mean = 9.4 psu). Brine salinity, the salinity of the liquid fraction of the sea ice, is controlled by temperature due to the

Figure 5. Latitudinal variability in (a) sea ice concentration, (b) sea ice thickness, (c) snow thickness, (d) sea ice temperature (both at the surface and at the midpoint of the ice slab), (e) sea ice salinity, (f) brine salinity (both at the surface and at the midpoint of the ice slab), (g) brine volume (both at the surface and at the midpoint of the ice slab), and (h) percent light transmission along the north-south sea ice transect. In Figures 5b and 5c, data were binned so as to conform to autumn data from Jeffries and Adolphs [1997], which is also shown.

Figure 6. Frequency distribution for sea ice core length along the north-south sea ice transect.
increased temperature (Figure 5d) and higher sea ice salinity, respectively. This increase in brine volume in the interior layers of the sea ice pack (Figure 5f) along the length of our transect. Within the interior layers of the sea ice, where temperatures were somewhat higher, salinities would have ranged from about 43 to 93 psu. South of 75°S where the depth of maximum Chl \(a\) varied widely along the length of our transect (Figure 5g). South of 75°S, however, brine volume increased dramatically, to an average of 14 and 18% at the pack ice surface and the sea ice surface (Figure 5d) during our study would have resulted in near-surface brines having salinities ranging from 50 to 134 psu (Figure 5f) along the length of the north-south transect. Within the interior layers of the sea ice, where temperatures were somewhat higher, salinities would have ranged from about 43 to 93 psu. 

Brine volume, the fractional volume of an ice slab taken up by liquid brine, was relatively uniform between 64°S and 75°S, averaging about 4% in the interior layers of the ice pack and about 6% at the surface (Figure 5g). South of 75°S, however, brine volume increased dramatically, to an average of 14 and 18% at the pack ice surface and interior, respectively. This increase in brine volume in the southern part of our transect was due to a combination of increased temperature (Figure 5d) and higher sea ice salinity (Figure 5e) in this region.

### 3.1.5. Light Transmission

The percent transmission of total surface downwelling PAR to the depth of the sea ice microalgal community (i.e., the depth of maximum Chl \(a\)) varied widely along the length of our transect (Figure 5h). Irradiance transmission was lowest (almost zero) at the stations near 68°S where both the ice pack (Figure 5b) and the surface snow cover (Figure 5c) were thickest. The percent transmission at these stations responded much more strongly to changes in snow thickness than to changes in pack ice thickness (Figure 7). In the absence of snow, a 0.2-m increase in pack ice thickness resulted in a 20% reduction of the transmitted irradiance. In contrast, when sea ice was thin, a similar 0.2 m increase in snow thickness yielded an 80% reduction of the transmitted irradiance. Of course, these effects are diminished as both sea ice and snow thickness increase. At snow depths >0.2 m, an increase in ice thickness has little effect on the percent irradiance transmission. Similarly, as pack ice thickness increases beyond approximately 1.2 m, changes in snow depth have only a minor impact on irradiance transmission. Irradiance was much higher in sea ice at the southern portion of the transect where thin, snow-free, dark nilas transmitted >80% of the incident radiation.

### 3.1.6. Sea Ice Nutrients

Concentrations of PO\(_4\)_3 were highly variable within the sea ice, ranging from 0.20 to 68.5 \(\text{µM}\) (Figure 8a). Because nutrients were measured in the liquid portion of the sea ice (e.g., the brine), some of this variation is due to changes in PO\(_4\)_3 concentration related to changes in temperature. At reduced temperatures, brine salinity will increase to maintain phase equilibrium, and nutrient concentrations will change in proportion to salinity (the solid line in Figure 8a), assuming that no other processes are influencing nutrient abundance. However, concentrations of PO\(_4\)_3 were often much higher than would have been expected from thermodynamic equilibrium. The cause for this is likely to be degradation of biological material in older sea ice and the resulting regeneration of PO\(_4\)_3 \cite{Arrigo et al., 1995}. This is supported by the fact that elevated PO\(_4\)_3 was only observed in the older sea ice found in the central and outer pack ice regions (Figure 8a). PO\(_4\)_3 concentrations in more recently formed ice within the inner pack were in the same proportion to salinity as the water column prior to significant biological activity in the spring, suggesting that there had been little biological remineralization or removal of PO\(_4\)_3 in young ice prior to our study \cite{Sweeney et al., 2000}. In the lower layers of the sea ice within the central and outer pack, PO\(_4\)_3 concentrations were often well below the levels expected when PO\(_4\)_3 is conservative with salinity, indicating that substantial drawdown of PO\(_4\)_3 by sea ice algae had taken place prior to our study. Nevertheless, PO\(_4\)_3 remained consistently above 0.5 \(\text{µM}\) throughout the pack ice, suggesting that PO\(_4\)_3 availability was not limiting the rate of microalgal growth during the early spring.

Silicic acid (Si(OH)\(_4\)_3), an element required by the diatoms that dominate sea ice microbial communities, exhibited much less variation with salinity than did PO\(_4\)_3, with concentrations consistently at or below levels expected from the salinity of the brines from which they were measured (Figure 8b). Unlike PO\(_4\)_3, there was no indication of Si(OH)\(_4\)_3 enhancement in the pack ice, indicating that even in older sea ice, there was little dissolution of empty diatom frustules. Like PO\(_4\)_3, Si(OH)\(_4\)_3 in the inner pack showed no sign of depletion at the time of our study, whereas Si(OH)\(_4\)_3 in the central and outer pack was substantially reduced. Still, Si(OH)\(_4\)_3 remained above 20 \(\text{µM}\) throughout our study region and was not likely to be limiting rates of algal growth.

The pattern of nitrate (NO\(_3\)) abundance was very similar to that of Si(OH)\(_4\)_3, with ice brines collected from the inner pack exhibiting little, if any, depletion, and those from the central and outer pack showing evidence of substantial NO\(_3\)_3 removal (Figure 8c). One major difference, however, is that unlike Si(OH)\(_4\)_3, NO\(_3\)_3 occasionally was completely exhausted within the lower layers of the
It is unlikely, however, that nitrogen supplies were limiting algal growth in the sea ice because concentrations of ammonium (NH$_4$) were extremely high (Figure 8e), probably due to remineralization of TPN (similar to that observed for PO$_4$). As a result, concentrations of total inorganic nitrogen (TIN) were nearly always above 10 $\mu$M.

Interestingly, the N:P ratio implied by these data is low (8–10), but similar to values measured in pelagic diatom blooms in the Ross Sea [Arrigo et al., 1999, 2000, 2002; Sweeney et al., 2000]. Overall, the patterns of nutrient drawdown and accumulation in Ross Sea pack ice are similar to observations in pack ice of the Weddell and Amundsen Seas [e.g., Thomas et al., 1998].

### 3.2. Horizontal Variability of Ice Microalgal Biomass

#### 3.2.1. Chlorophyll $a$

The mean concentration of Chl $a$ in the Ross Sea ice pack was 4.62 ± 5.71 mg m$^{-2}$ and depth-integrated Chl $a$ abundance averaged 2.53 mg m$^{-2}$ over the entire transect. Chl $a$ was highest at Station 001 along the northern margin of the ice pack (64°S), with concentrations averaging 16.0 mg Chl $a$ m$^{-2}$ and depth-integrated biomass of 11.2 mg Chl $a$ m$^{-2}$ (Figure 9a). Between 64.5°S (Station 002) and 70.5°S (Station 014), Chl $a$ concentration was relatively uniform, averaging 3.68 ± 2.56 mg m$^{-2}$. Further south, Chl $a$ increased with latitude, peaking at 8.41 mg m$^{-2}$ and 5.10 mg Chl $a$ m$^{-2}$ at 72°S (Station 017). South of 74°S, concentrations of Chl $a$ were the lowest observed during our study, averaging 0.89 ± 0.41 mg m$^{-2}$ with Chl $a$ accumulations of only 0.24 ± 0.15 mg m$^{-2}$. Over the entire transect, depth-integrated Chl $a$ exhibited a distinctly bimodal distribution in its frequency distribution (Figure 10a), with most of the ice cores containing either 2 – 3 mg Chl $a$ m$^{-2}$ or ≤0.5 mg Chl $a$ m$^{-2}$. Algal biomass accumulation consistently was greatest in the pack ice with snow cover of <0.05 m thick and never exceeded 4 mg Chl $a$ m$^{-2}$ when snow cover was greater than this thickness (Figure 11).

#### 3.2.2. POC, TPN, and $\delta^{13}$C-POC

On average, Ross Sea pack ice contained 634 mg POC m$^{-2}$ and 83 mg TPN m$^{-2}$ (Figures 10b and 10c) and...
exhibited depth-integrated latitudinal patterns similar to that of Chl $\text{a}$ (Figures 9a–9c). Unlike Chl $\text{a}$, which was low compared to other pack ice habitats, the average POC abundance in the Ross Sea pack ice was quite high, comparable to values reported for the highly productive land-fast ice of McMurdo Sound [Grossi et al., 1987; Dunbar and Leventer, 1992]. Furthermore, POC concentrations were >10-fold greater than the highest accumulation of ice algae measured in the Baltic Sea (49.2 mg C m$^{-2}$) during the winter and spring of 1994 [Haecky et al., 1998] and >2-fold higher than in the fast ice algal community in Ellis Fjord, eastern Antarctica, which attained standing crops ranging from 22 to 231 mg C m$^{-2}$ [McMinn, 1996].

Like Chl $\text{a}$, POC and TPN were greatest at the northern boundary of the ice pack, averaging 2000 mg m$^{-2}$ and 250 mg m$^{-2}$, respectively (Figures 9b and 9c). Although depth-integrated POC and TPN were much lower to the south (minimum of 300 mg POC m$^{-2}$ and 40 mg TPN m$^{-2}$ between 64°S and 72°S), each attained a clear local maximum at 72°S (1000 mg POC m$^{-2}$ and 150 mg TPN m$^{-2}$), similar to that exhibited by Chl $\text{a}$. The abundance of POC and TPN was lowest between 76°S and 78°S in the newly formed sea ice associated with the Ross Sea polynya. Although peak POC abundance was 3659 mg m$^{-2}$, >90% of the ice cores contained POC below 1100 mg m$^{-2}$ (Figure 9b).

[45] The ratio of POC:TPN exhibited a highly significant ($p < 0.001$) correlation with latitude, decreasing with proximity to the Ross Ice Shelf (Figure 9d). In contrast, the POC:Chl $\text{a}$ ratio in sea ice increased with proximity to the Ross Ice Shelf, being on average twofold greater in the inner and central pack (486 ± 488) than in the outer pack (249 ± 110). The sea ice at the two southermost stations (Stations 027 and 029) had by far the highest POC:Chl $\text{a}$ ratios (1834 and 1973) measured anywhere along the transect. Gleitz and Thomas [1993] reported a similar range of POC:TPN and POC:Chl $\text{a}$ ratios in the Weddell Sea, with POC:Chl $\text{a}$ much higher in new ice than in older ice.

[46] The $\delta^{13}$C of the POC ($\delta^{13}$C-POC) collected from the bottom of the ice pack, where algal biomass was generally greatest, varied with latitude from −27.3 to −17.2 (Figure 12) in a manner similar to that of Chl $\text{a}$, TPN, and POC. There was a highly significant correlation ($R^2 = 0.80, p < 0.001$) between the $\delta^{13}$C-POC of the material associated with the highest algal population density at each station and the depth-integrated POC.

3.3. Vertical Variability of Ice Microalgal Biomass

Within individual ice floes of a thickness sufficient to obtain vertical profiles, vertical distributions of microbial...
biomass varied markedly between the ice floe edge and its center. For example, at Station 001, an approximately oval ice floe 7 m wide and 10 m long (Figure 13a) with \(0.04 \text{ m}\) of snow cover, sea ice gradually increased in thickness from 0.35 m at the edge of the floe to 0.83 m near its center. Concentrations of Chl \(a\) (Figure 13b), POC (Figure 13c), and TPN (Figure 13d) increased with depth within this floe, peaking at the bottom (0–0.1 m) near the center of the floe where the sea ice was thickest. Generally, vertical gradients of particulate organic matter (POM) were sharpest at the interior of the floes and weaker near the edges. In addition, biomass near the sea ice surface was higher at the edges of the floe than at its center.

At Station 001, the POC:Chl \(a\) ratios were very high (Figure 13e) and POC:TPN ratios (Figure 13f) were elevated (>10), well above the Redfield value of 5.7 (g:g), near the surface of the thickest portion of the ice floe (Cores 1 and 2). The POC:Chl \(a\) ratio averaged 242 for the entire transect but ranged from 57 to >4000, with the highest values found near the surface of the ice floes (mean surface POC:Chl \(a = 1147\)) and the lowest being associated with layers where algal biomass was maximal. Approximately 95% of the stations showed a strong decrease in POC:Chl \(a\) with depth. This pattern was not as pronounced for POC:TPN, which decreased with depth at 27% of the stations (there was no depth dependence at 64% of the stations; POC:TPN increased with depth at only 9% of the stations).

Algal Chl \(a\) peaked most often (77% of cores) in the lower layers of the sea ice cores (e.g., Station 001, Figure 13), suggesting that bottom ice microalgal communities dominated the Ross Sea pack ice. This is supported by profiles of POC and TPN which also exhibited enhanced concentrations at the bottom of the sea ice. Surface communities and interior ice microalgal communities dominated only 16 and 7% of the ice cores, respectively.

### 3.4. Ice Microalgal Species Composition

The diatom *Fragilariopsis cylindrus* was by far the most numerically abundant algal species in the pack ice, particularly north of 74.5°S where, on average, it made up more than 56% of the microalgal assemblage, by cell number (Figures 14a and 15). South of 74.5°S, the pack ice was dominated by the prymnesiophyte *Phaeocystis antarctica*, where it accounted for 72% of algal numbers in predominantly young ice (Figures 14b and 15). It was far less abundant in the thicker sea ice north of 74.5°S, making up slightly more than 10% of the microalgal community. *Corethron criophilum*, another diatom, was also found only in young ice near the Ross Ice Shelf, accounting for 10 and 24% of the algal population at Stations 24 and 27, respectively (Figure 15).

Distribution patterns of other diatom species were much less regular. On average, *Fragilariopsis curta* and two *Nitzschia* species (*Nitzschia prolongatoides* and *Nitzschia turgidiloides*) comprised 8.8 and 7.8% of the algal assemblage.
Nitzschia stellata, commonly found in the fast ice near McMurdo Sound [Palmisano et al., 1987a; Arrigo et al., 1993, 1995], and Nitzschia subcurvata were both present in small numbers, each averaging just over 2% of the algal population. Both species were more common in the thicker sea ice north of 72°S than in the sea ice associated with the Ross Sea polynya. Other microalgae, including Navicula glacei, Amphiprora sp., Tropidoneis sp., and various cryptomonad species, were present in numbers averaging less than 1% of total algal abundance, although at a few stations some of these algae accounted for an appreciable (5–10%) component of the population (Figure 15).

3.5. Ice Microalgal Photophysiology

3.5.1. Photosynthesis Versus Irradiance (P-E) Parameters

The maximum Chl a normalized photosynthetic rate ($P_{max}$) for microalgae located in peak biomass layers of the ice pack ranged from 0.4 to 0.8 mg C mg$^{-1}$ Chl a h$^{-1}$ (Table 1). The lowest rates were observed at those stations with the thickest cover of snow (Station 009, 0.07 m) and sea ice (Station 013, 0.93 m). The values for $P_{max}$ observed during our study are intermediate between the higher rates typically reported for phytoplankton in the water column of the Ross Sea [Palmisano et al., 1986; Smith et al., 1996; Lazzara et al., 2000] and the lower rates for microalgae growing in land-fast sea ice of McMurdo Sound [Palmisano et al., 1987b; Arrigo et al., 1993; Robinson et al., 1995] and in the Terra Nova Bay sector of the Ross Sea [Guglielmo et al., 2000]. They are within the range of values (0.09–1.20, mean 0.56) measured for annual ice floes in the Weddell Sea [Lizotte and Sullivan, 1991], which are significantly higher than measured in Ross Sea fast ice communities (see review by Lizotte and Sullivan [1992]). The lower values for $P_{max}$ in Ross Sea pack ice are probably due to strong shade acclimation of the algal assemblages, which were located at the bottom of the ice pack where light levels are lowest.

Photosynthetic efficiencies normalized to Chl a ($a^{*}$) were equally variable, ranging from 0.008 to 0.016 mg C mmol photons m$^{-2}$ s$^{-1}$ Chl a h$^{-1}$ (Table 1), similar to the range of values (0.004–0.030, mean 0.011) measured for annual ice floes in the Weddell Sea [Lizotte and Sullivan, 1991]. These are much lower than the reported mean $a^{*}$ of 0.26 mg C mmol photons m$^{-2}$ s$^{-1}$ Chl a$^{-1}$ for sea ice algae in Resolute Passage [Suzuki et al., 1993].

Figure 13. (a) Physical dimensions of the ice floe and locations of ice cores at Station 001 (Figure 1). Vertical profiles of (b) Chl a, (c) POC, (d) TPN, (e) POC:Chl a, and (f) POC:TPN for the four ice cores collected at Station 001. Ice thickness was greatest near the center of the floe (0.83 m) and decreased with proximity to the edge (0.35 m).

Figure 14. Latitudinal variability in the abundance of (a) F. cylindrus and (b) P. antarctica as a percent of total algal cell number for sea ice stations sampled along the north-south sea ice transect. F. cylindrus dominated the sea ice community in the high biomass regions north of 74°S while P. antarctica dominated in the low biomass regions south of 74°S.
al., 1997], but slightly higher than values obtained from nearby Terra Nova Bay [Guglielmo et al., 2000]. Unlike $P_m, a^*$ did not exhibit any obvious trends with either snow depth, sea ice thickness, or percent light transmission.

The photoadaptation parameter, $E_k$, for microalgae growing in the Ross Sea ice pack reflects the dependence of photosynthetic rate on ambient light levels. Values for $E_k$ ranged from 33 to 88 $\mu$mol photons m$^{-2}$ s$^{-1}$, indicating that the sea ice microalgae were shade adapted (Table 1). These $E_k$ values are within the range of values (14–126, mean 61) measured for annual ice floes in the Weddell Sea, where this parameter decreased with depth in the ice column [Lizotte and Sullivan, 1991]. In the fast ice of McMurdo Sound, $E_k$ was 37–45 $\mu$mol photons m$^{-2}$ s$^{-1}$, well above the daily average irradiance, indicating that the algae were not completely acclimated to their relatively low-light environment [Robinson et al., 1998]. The lowest values of $E_k$ for our study were measured in areas where light levels should be minimal, i.e., where the sea ice cover was thick (Station 013) or where snow was abundant (Station 009). Regressing the measured $E_k$ for a particular station against its calculated percent light transmission values yielded an extremely high $R^2$ value of 0.98, illustrating the strong relationship that exists between ice microalgal $E_k$ and light availability.

The absorption characteristics of sea ice microalgae were also consistent with a shade acclimated population, with mean Chl a-specific absorption coefficients ($a^*$) ranging from 0.006 m$^2$ mg$^{-1}$ Chl a at Station 020 to 0.011 m$^2$ mg$^{-1}$ Chl a at Station 009. This relatively low $a^*$ coupled with moderate $a^*$ resulted in calculated values for the quantum yield of photosynthesis ($\phi_p$) that also were low (0.018–0.053 mol C [mol photons]$^{-1}$), but typical of values measured previously for sea ice microalgae from the Ross Sea [SooHoo et al., 1987; Arrigo and Sullivan, 1992].

### 3.5.2. Fluorescence Characteristics

The photosynthetic capacity of sea ice microalgae also was measured in terms of the efficiency of energy conversion at photosystem II (Fv/Fm). In contrast to the more laborious $P$-$E$ parameter determination, Fv/Fm is a rapid measurement and was performed at all stations for which adequate algal biomass was available (algal biomass was too low to measure Fv/Fm at stations 22 and 24–29). Values for Fv/Fm from field-collected samples generally do not exceed 0.65, which is the maximum value typically observed for healthy phytoplankton [Robinson et al., 1998]. Fv/Fm for the bottom ice communities during our study ranged from 0.20 to 0.42 (Figure 16a), with no obvious latitudinal pattern, although there was a significant

### Table 1. Photosynthetic Parameters in the Bottom of Pack Ice Cores From the Ross Sea

<table>
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<tr>
<th>Station</th>
<th>Ice Depth</th>
<th>Snow Depth</th>
<th>$P_m$</th>
<th>$a^*$</th>
<th>$a^*_m$</th>
<th>$\phi_p$</th>
<th>$E_k$</th>
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</table>

*Ice and snow depth units are in meters; $P_m$ units are in mg C mg$^{-1}$ Chl a h$^{-1}$; $a^*$ units are in mg C mg$^{-1}$ Chl a; $a^*_m$ units are in m$^2$ mg$^{-1}$ Chl a; $\phi_p$ units are in mol C Ein$^{-1}$ absorbed; and $E_k$ units are in $\mu$mol photons m$^{-2}$ s$^{-1}$.\n
![Figure 15. Stacked column plot showing abundance of various algal types as a percent of total algal cell number for sea ice stations sampled along the north-south sea ice transect. Cell counts were made on core sections that contained the highest biomass, usually the bottom section. Nitzschia spp. is a combination of N. prolactatoideas and N. turgidiloides.](image-url)
inverse correlation ($R^2 = 0.56, p < 0.001$) between Fv/Fm and sea ice thickness (Figure 16b). Similarly, Fv/Fm for fast-ice algae in McMurdo Sound ranged from 0.24 to 0.43 [Robinson et al., 1998]. Vertical profiles of Fv/Fm (Figure 16c) collected during our study illustrate that values were typically highest in the bottom layer of the ice where biomass was maximal, salinity was lowest, and access to nutrients would be expected to be greatest.

4. Discussion

4.1. Sea Ice and Snow

The north-south variation in sea ice thickness from the northern margin of the Ross Sea polynya to the Ross Ice Shelf is controlled by the balance between rates of sea ice advection and new ice production, both of which vary spatially and seasonally. In the absence of coastal polynyas, sea ice begins to form first near the continental margins, increasing in thickness and expanding northward over time. Consequently, sea ice age and thickness usually decrease with distance from the Antarctic coast. Within the outer pack (72°S–64°S), this increased sea ice age is reflected by the increase in ice thickness between autumn and spring (Figure 5b). However, because new ice in the Ross Sea is continually being formed in the vicinity of the Ross Sea polynya and advected northward by strong katabatic winds (Figures 3 and 4), the oldest and thickest sea ice in the Ross Sea sector of the Southern Ocean is located in the interior of the pack, with younger, thinner ice both to the north and to the south. A comparison of our ice thickness data with that of Jeffries and Adolphs [1997] suggests that the region of maximum age and thickness is located further north in the spring (between 68°S and 72°S) than it is in the previous autumn (75°S–76°S), likely reflecting both wintertime advection of the ice and the springtime enlargement of the Ross Sea polynya associated with increased atmospheric temperatures. This 6° northward shift between autumn and spring of the region of maximum ice thickness implies an ice advection rate of 4.3 cm d$^{-1}$, consistent with rates of sea ice motion inferred from satellite data in the vicinity of our study (Figures 3 and 4).

The loss of snow cover during winter (between the autumn and spring studies) may be due to a number of factors. Of course, interannual variability may play a role. However, in the vicinity of the Ross Sea polynya (south of 72°S), sea ice is continually being advected northward (Figures 3 and 4) and replaced by newly formed ice near the Ross Ice Shelf. Because of lower temperatures and higher sea ice concentrations in the autumn, advection is slower at that time (Figure 4c) than in the spring (Figure 4i), and restricted to a zone nearer the Ross Ice Shelf where the winds are particularly strong [Bromwich et al., 1992]. The greater thickness of snow in the south in autumn (relative to spring) probably reflects the lower rate of sea ice advection and increased time for snow accumulation during that season.

However, this process is not likely to be responsible for the autumn-spring differences in snow thickness observed between 69°S and 72°S, which is too far north to be impacted by processes associated with the Ross Sea polynya. Metamorphosis of accumulated snow into snow ice [Jeffries and Adolphs, 1997] may have been responsible for some of the apparent decrease in snow cover between winter and spring in this region. Indeed, ice cores collected during the spring of 1998 occasionally contained surface layers that appeared to be snow ice (though $^{18}$O measurements were not made to confirm this observation). Additionally, ablation of the snow surface by the strong winds that characterize the Ross Sea region can scour large areas of pack ice free of snow cover. Much of this snow is redistributed into drifts that form at the edges of rafting and cracked ice floes. Some snow also may be lost as the snow blows into cracks, leads, and other areas of open water within the sea ice interior. Finally, melting can result in a loss of snow cover, although this was probably not the case prior to our study. The sea ice temperature at the snow/ice interface varied from −2.7°C to −9.0°C along the north-south transect (Figure 5d) and was highly correlated with surface air temperature ($R = 0.95$). These low temperatures indicate that the ice pack had not yet warmed to the point of becoming isothermal and that little melting of either sea ice or snow had probably taken place.

4.2. Controls on Sea Ice Microalgal Distributions

4.2.1. Temporal Considerations

Mean Chl $a$ abundance in the pack ice of the Ross Sea (2.53 mg Chl $a$ m$^{-2}$) was lower than Chl $a$ standing crops measured in other polar sea ice habitats, including Weddell Sea pack ice where mean spring-summer values are about twice this level [Dieckmann et al., 1998], first year
Sea ice in Saroma-ko Lagoon, Japan (2–119 mg Chl $a$ m$^{-2}$) [Kudoh et al., 1997; Robineau et al., 1997] and Resolute Passage, Canadian Arctic (3.7–160 mg Chl $a$ m$^{-2}$) [Suzuki et al., 1997; Michel et al., 1996], and even some winter values reported for the Weddell and Scotia Seas (<0.01 to >29 mg Chl $a$ m$^{-2}$) [Garrison and Close, 1993]. Chl $a$ abundance in the Ross Sea pack ice was more than two orders of magnitude below the peak measured in the Ross Sea land-fast ice [$Palmsano and Sullivan, 1983$; Arrigo et al., 1995]. However, based on photosynthetic rates measured during our study (Table 1), doubling times for pack ice algae in the Ross Sea averaged <5 days, similar to values reported for other sea ice habitats [$Grossi et al., 1987$], suggesting that low algal growth rates were not responsible for their low biomass. In large part, the low Chl $a$ concentrations throughout our study region likely can be attributed to the early timing of our sampling program. In many sea ice habitats, microalgae continue to increase in abundance until early December, when elevated temperatures cause the sea ice habitat to degrade to the point where it can no longer sustain a viable microbial community [$Grossi et al., 1987$; Arrigo et al., 1995; Gleitz et al., 1996a, 1996b]. Our program ended almost a full month before sea ice microbial communities in the fast ice of McMurdo Sound have been reported to reach their peak biomass levels [$Grossi et al., 1987$; $Palmsano et al., 1987a, 1987b$; Arrigo et al., 1993, 1995]. It is reasonable, therefore, to assume that had our sampling program been conducted a few weeks later in the season, microalgal biomass would have attained much higher levels than we measured. In some cases, the low biomass we observed was simply a reflection of the recent formation of the sea ice and the lack of time for the algae to grow and accumulate, such as in the vicinity of the Ross Sea polynya.

### 4.2.2. Physical Entrainment of Organic Material

Although Chl $a$ concentrations in newly formed sea ice have been reported to be enriched relative to concentrations in surface waters due to particle scavenging mechanisms [$Garrison et al., 1989$], during our study, Chl $a$ concentrations in young sea ice were similar to those in the underlying water column, averaging 0.75 mg Chl $a$ m$^{-3}$ and 0.98 mg Chl $a$ m$^{-2}$, respectively (Table 2). This suggests that while algal cells were likely being physically incorporated into newly formed pack ice, they either were not being concentrated to the degree reported for other pack ice systems [$Garrison et al., 1989$] or their Chl $a$ was being rapidly degraded prior to our sampling (see below). Substantial physical concentration of algal material within sea ice appears to require periodic wave-induced expansion and compression of the newly formed frazil ice layer. Under these conditions, enrichment factors for Chl $a$ calculated from the ratio between the concentrations in ice and underlying water have been reported to be as high as 53 [$Weissenberger and Grossmann, 1998$]. This suggests that the sea ice sampled during our study formed under conditions that were relatively quiescent when compared to other sea ice habitats. In addition, Melnikov [1998] reported that in the Weddell Sea in 1992, the biomass of ice algae was 10–20 times lower, in terms of Chl $a$, than that of the underlying phytoplankton, indicating that the lack of Chl $a$ enrichment observed in the Ross Sea during the spring of 1998 is not unique.

Interestingly, unlike Chl $a$, POC and TPN concentrations measured in newly formed sea ice (i.e., Stations 024–029) were considerably enriched relative to concentrations in surface waters. A similar pattern was observed during ice formation in the Weddell Sea [Gleitz and Thomas, 1993]. POC and TPN were an average of 6.8- and 4.1-fold higher, respectively, in the newly formed sea ice than in the underlying water column (Table 2). There are three possible explanations for the disparity between the level of enrichment of Chl $a$ and of POC and TPN in newly formed sea ice. First, non-Chl $a$ containing POC and TPN (e.g., bacteria, protists) may have been preferentially entrained into the sea ice during the initial stages of its formation. This scenario is unlikely, however, given the low abundance of both bacteria [$Ducklow et al., 2000$] and protists [$Caron et al., 2000$] measured in surface waters of the Ross Sea. Second, the young sea ice we sampled was being formed in waters where blooms of *P. antarctica* begin as early as October [$Smith et al., 2000$]. Cells within *P. antarctica* colonies are embedded within a carbon-rich, polysaccharide matrix surrounded by a proteinaceous skin [$van Rijssel et al., 1997$; Hamm et al., 1999]. This colonial matrix, with its high carbohydrate and protein content, endows the colony with a high TPN:Chl $a$ ratio [$Palmsano et al., 1986$]. However, the TPN:Chl $a$ and POC:Chl $a$ ratios of *P. antarctica* colonies are not high enough to explain the excess POC and TPN concentrations measured in newly formed sea ice, unless a disproportional amount of colonial matrix material was being incorporated into the ice without the associated algal cells (where the Chl $a$ is located), possibly due to *P. antarctica* cells abandoning their colonies upon incorporation into the ice (little evidence for this).

### Table 2. Chl $a$, POC, and TPN in Newly Formed Sea Ice and Underlying Surface Waters

<table>
<thead>
<tr>
<th>Station</th>
<th>Sea Ice</th>
<th>POC</th>
<th>TPN</th>
<th>POCA:Chl $a$</th>
<th>POC:TPN</th>
</tr>
</thead>
<tbody>
<tr>
<td>024</td>
<td>1.06</td>
<td>0.82</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>025</td>
<td>1.07</td>
<td>2.04</td>
<td>339.0</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>027</td>
<td>1.13</td>
<td>1.07</td>
<td>660.3</td>
<td>195.9</td>
<td>16.5</td>
</tr>
<tr>
<td>029</td>
<td>0.21</td>
<td>0.28</td>
<td>378.3</td>
<td>31.3</td>
<td>6.5</td>
</tr>
<tr>
<td>Mean</td>
<td>0.78</td>
<td>1.05</td>
<td>134.3</td>
<td>108.0</td>
<td>14.0</td>
</tr>
</tbody>
</table>

*All units are in mg m$^{-3}$. Surface water values for Chl $a$, POC, and TPN are means for the upper 3 m; sea ice values are means from replicate cores at each station. POC:TPN ratios are presented as weight:weight. ND means no data are available.*
Finally, it is possible that Chl $a$, POC, and TPN were all initially concentrated to similar degrees within the newly formed pack ice, which at the time of our sampling was probably already a few days to weeks old. Therefore between the time of initial formation of this young sea ice and our sampling program, heterotrophic activity may have resulted in a transfer of POC and TPN to the heterotrophic community and a dramatic reduction in Chl $a$. This latter scenario is supported by phaseopigment (Chl $a$ degradation products generally thought to result from zooplankton grazing) concentrations, which are highest (relative to Chl $a$) in newly formed sea ice. It is also consistent with our NH$_4$ data, which suggest that a substantial amount of remineralization had taken place prior to our arrival, indicating a high degree of heterotrophic activity. Unfortunately, because grazing and other heterotrophic processes were not explicitly measured during our study, the exact cause of the high level of POC and TPN enrichment relative to Chl $a$ in young ice remains a topic for future research.

The high abundance of *P. antarctica* in newly formed sea ice is probably responsible for the shape of the frequency distributions for POC (Figure 10b) and TPN (Figure 10c), which did not exhibit the distinct bimodal distribution displayed by Chl $a$. The bimodality of the Chl $a$ frequency distribution is due to the abundance of samples collected from newly formed sea ice which contained a large proportion of *P. antarctica* but only a small amount of Chl $a$. However, because samples dominated by *P. antarctica* also had relatively high POC:Chl $a$ ratios, the POC frequency distribution does not contain a large number of low POC samples and is much less bimodal. The TPN frequency distribution does show an elevated number of low TPN samples (although not so extreme as for Chl $a$) which is probably a consequence of the fact that the POC:TPN ratio is somewhat reduced in the higher latitude samples that were dominated by *P. antarctica*.

### 4.2.3. Latitudinal Biomass Variability

Considering all of the processes that can influence microalgal biomass in sea ice, latitudinal variability in the abundance of Chl $a$, POC, and TPN must reflect a dynamic balance between rates of (1) sea ice formation, accretion, and degradation, (2) snow accumulation, (3) algal growth, and (4) heterotrophic activity. By the time of our study in November, satellite data show that the Antarctic ice pack had ceased its northward expansion (Figure 4I). Sea ice at the northernmost stations was 0.6 m thick (Figure 5b) and, based on measured sea ice velocities, at least 3–4 months old. The combined effect of low latitude and thin snow cover (Figure 5c) at these northern stations resulted in a relatively abundant flux of solar insolation to the pack ice algal community (Figure 5h). Consequently, these stations contained the highest algal Chl $a$ biomass of the entire ice pack (Figure 9a), and the highest photosynthetic rates (Table 1). Further south, snow thickness increased dramatically (sea ice thickness also increased, but only slightly), and the latitude of maximum snow thickness (Figure 5c) coincided with the local minimum in the depth-integrated Chl $a$ (Figure 9a), POC (Figure 9b), TPN (Figure 9c), light transmission (Figure 5h), and photosynthetic rate (Table 1). Decreasing snow thickness (Figure 5c) and increasing light transmission south of 68$^\circ$S was likely responsible for the increase in accumulated Chl $a$, POC, and TPN between 68$^\circ$S and 72$^\circ$S. The relationship between Chl $a$ and snow thickness observed during this study (Figure 11) was similar to trends observed previously under more extreme conditions in the thick fast ice in McMurdo Sound [e.g., *Sullivan et al., 1985*]. However, with the exception of the region between 66$^\circ$S and 68$^\circ$S, snow cover was generally thin, and despite the fact that the presence of snow has such a strong influence on light transmission through sea ice [SooHoo et al., 1987; *Arrigo et al., 1991*; this study], snow thickness was probably not a particularly important factor in controlling algal biomass accumulation over much of the Ross Sea pack ice.

Although snow thickness continued to decline and light availability continued to increase south of 72$^\circ$S, algal abundance did not increase steadily, resulting in the local biomass maximum observed at 72$^\circ$S (Figures 9a–9c). The latitudinal decline in algal biomass south of 72$^\circ$S was the result of dynamical processes associated with sea ice formation in the Ross Sea polynya. As was noted earlier, the sea ice nearest the Ross Ice Shelf was relatively young and thin and increased in both age and thickness to the north. During our study, the thin (~0.1 m) sea ice sampled near the Ross Ice Shelf was probably only a week old or less, and as a result, very little algal biomass had accumulated via algal growth (30–35 mg POC m$^{-2}$). Further to the north where the sea ice was older, the algae had more time to grow and biomass had attained higher levels. In the outer pack, the sea ice had most likely formed prior to the ice algal growth season and an increase in sea ice age would not be reflected by increased algal biomass. Therefore the local peak in algal biomass at 72$^\circ$S reflects a balance between processes to the south controlling the age of the sea ice (algal accumulation is limited by the amount of time available for ice algal growth) and processes to the north controlling ice thickness and the accumulation of snow (algal accumulation is limited by light-limited algal growth rates).

### 4.2.4. Dominance of Bottom Ice Communities

The predominance of bottom ice communities in the Ross Sea pack ice contrasts with similar pack ice habitats studied elsewhere in the Southern Ocean, studies which indicated that internal communities are as common as bottom-ice communities [Legendre et al., 1992; *Lizotte and Sullivan, 1992*; *Thomas et al., 1998*]. Internal communities generally dominate in sea ice that is composed of a sizable fraction of frazil ice. This is because frazil ice generally has a higher brine volume than congelation ice, facilitating increased nutrient exchange, and because as frazil ice is incorporated into the ice pack, it often entrains and concentrates pelagic diatom cells [Garrison et al., 1983, 1989] which may become the seed stock for the eventual ice algal bloom. Surface communities most often dominate in sea ice with a heavy snow cover or in rafted sea ice, conditions which force the ice surface below the freeboard level [Wadhams et al., 1987], facilitating the exchange of nutrients with the water column.

The scarcity of internal and surface ice communities in the Ross Sea pack was probably due to its relatively thin snow cover (Figure 5c) and to the fact that pack ice in the Ross Sea contains an unusually high proportion of congelation ice [Jeffries and Adolphs, 1997], giving it greater
similarity to land-fast ice than to the pack ice habitats of the Weddell Sea. Like the Ross Sea ice pack, congelation ice habitats in the Arctic [Smith et al., 1997; Michel et al., 1996], the Antarctic [Palmasano and Sullivan, 1983; Arrigo et al., 1993; Robinson et al., 1995; Archer et al., 1996; Stoecker et al., 1997, 1998], and in Saroma-ko Lagoon, Japan [Robineau et al., 1997; Kudoh et al., 1997; Suzuki et al., 1997] also are generally dominated by bottom ice communities.

4.2.5. Vertical Biomass Variability

Vertical distributions of ice algal biomass, whereby Chl a, POC, and TPN all increased with vertical and horizontal proximity to the ice/water interface, suggest that algal growth rates were highest in the bottom ice. One might assume from these distributions that algal growth rates were being controlled by the availability of nutrients which would be more readily available near the ice/water interface. This conclusion would be consistent with vertical patterns of Fv/Fm (Figure 16) which show increased photosynthetic capacity near the ice/water interface where nutrients should be most abundant. In addition, the high cellular POC:TPN (Figure 9) and POC:Chl a ratios measured in older sea ice are often indicative of nitrogen-limited algal growth.

Our nutrient data suggest, however, that nutrient concentrations in the sea ice never fell to growth-limiting levels (Figure 8), and therefore, could not have been limiting algal growth, even in the upper sea ice layers. With greater accumulation of algae, pack ice communities in other parts of the Southern Ocean have driven nutrient concentrations to much lower levels [Garrison and Buck, 1991; Gleitz and Thomas, 1993; Gleitz et al., 1996a; Thomas et al., 1998]. Except for those stations near 68°S where snow cover was thickest (Figure 5c), light availability (Figure 5h) would have been well above photosynthetic requirements as well [Palmasano et al., 1987b; Arrigo et al., 1991, 1993], even near the bottom of the ice floes. A more likely explanation for the observed vertical distributions of Chl a, POC, and TPN is that the autotroph community were being exposed to supraoptimal salinities near the sea ice surface (Figure 5f), and as a result, rates of algal growth and biomass accumulation in these levels were extremely low. Arrigo and Sullivan [1992] showed that algae in the fast ice of the Ross Sea exhibit greatly diminished photosynthetic rates at salinities above 50 psu and shut down photosynthesis altogether at 100 psu. Even in the interior layers of the ice floes, salinities were typically greater than 50 psu at the time of our study (Figure 5f). Considering that we sampled the algal assemblage during the spring, it is likely that temperatures prior to this time were even lower, and consequently, salinities would have been higher. Therefore algal populations in the upper layers of the ice would likely have become senescent by the time of our study, with increased rates of remineralization (evidenced by high PO4 and NH4), elevated detrital concentrations (clearly evident in particulate absorption spectra which show that detrital particles are the primary light absorbers in the upper sea ice [K. R. Arrigo et al., unpublished data, 1998]) and degraded Chl a, and hence, elevated POC:TPN and POC:Chl a ratios.

4.2.6. Exchange of Dissolved Material Between Ice and Ocean

Although nutrient concentrations suggest that algal populations were not nutrient stressed at the time of our study, and that light was generally at nonlimiting levels, there is some evidence that the availability of CO2 for photosynthesis may have been restricted (although it was not limiting). The strong relationship between δ13C-POC and POC (and Chl a) demonstrates that as algal biomass accumulation increased, the POC was becoming isotopically heavier. There are three reasons why this isotopic enrichment might be expected to occur. First, if exchange between the sea ice and the upper water column were restricted, uptake of light CO2 by ice algae could have resulted in brines that were enriched in 13C. Additional uptake of this enriched 13C pool by an increasing algal population would result in POC that was isotopically heavier than seawater (δ13C-POC = –25 to –28). Second, the depletion of ambient CO2 may have resulted in increased reliance by diatoms on the heavier bicarbonate ion as an inorganic C source during photosynthesis, a process observed previously [Gleitz et al., 1996b; Tortell et al., 1997; Laws et al., 1998; Matsuda et al., 2001]. Finally, the increased importance of the β-carboxylation pathway for C-fixation, an adaptation to reduced light availability [Robinson et al., 1995], would result in enhanced utilization of bicarbonate. This latter possibility is the least likely, however, because of the generally high light availability during our study, even in sea ice with the highest biomass levels (Figure 5b). It must be noted, however, that a higher proportion of heterotrophs and/or species-specific differences in isotopic fractionation may alter δ13C-POC values [Holm et al., 1997]. Unfortunately, neither of these factors was addressed during this study and their importance cannot be assessed.

If the cause for the high correlation between δ13C-POC and POC concentration was indeed reduced CO2 availability (i.e., Rayleigh fractionation), then this suggests that rates of exchange between the pack ice and the water column are relatively low, even in the bottom ice communities which are in close proximity to the ice/water interface and where the samples for analysis of δ13C-POC were collected. This conclusion is supported by the accumulation of high concentrations of NH4 and PO4 in the brines collected from all layers within the ice pack. If the sea ice were being rapidly flushed with seawater, PO4 and NH4 concentrations of the magnitude we measured would not have had sufficient time to build up. The sea ice is also clearly not a closed system with respect to exchange with the underlying ocean, as evidenced by the same elevated NH4, TIN, and PO4 concentrations. Were there no exchange between the sea ice and the water column, concentrations of PO4 and TIN could never exceed the nutrients: salinity dilution lines (Figure 8), which they clearly do in many cases.

These data provide indirect evidence that rates of exchange between the water column and the pack ice of the Ross Sea are probably low, even in the springtime when the porosity of the sea ice is increasing rapidly. Brine volume estimates at the time of our study suggest that the porosity of the ice over much of the transect was too low to provide for free seawater exchange, which requires brine volumes of approximately 5–7% [Cox and Weeks, 1986; Golden et al., 1998]. Although nutrients did not decrease to growth-limiting levels prior to our study, further growth by pack ice algae through the remainder of spring-summer could alter this
situation. On the other hand, the porosity of the sea ice will also increase as temperatures continue to rise, in which case the pack ice habitat may never become nutrient limited. Most likely, accumulation of microalgal biomass in the pack ice was being controlled by vertical gradients in salinity, with reduced algal photosynthetic rates in the upper layers of the ice where salinity was highest, and perhaps by zooplankton grazing, which was not measured during our study. Both high POC:Chl a ratios and elevated NH4 and PO4 concentrations suggest that heterotrophic processes may have been important in the early spring prior to our study.

4.3. A Coupled Ice-Ocean Ecosystem

[73] Our algal taxonomic data support the hypothesis that phytoplankton blooms in the Ross Sea are facilitated by the introduction of algal cells released from the degrading sea ice [Smith and Nelson, 1985]. Two of the most dominant algal species we found in the Ross Sea pack ice, F. cylindrus and P. antarctica, are known to be important components of pelagic phytoplankton blooms. The dominant diatom encountered in pack ice during our study, F. cylindrus, is commonly found in Antarctic pack ice [Leventer, 1998; Lizotte, 2001] and has been observed to dominate ice communities in areas such as Ellis Fjord in eastern Antarctica [McMinn, 1996]. Three of the diatom species (F. cylindrus, F. curta, and N. subcurvata) found in association with local pack ice (Figure 15) have all been reported to dominate diatom blooms in the marginal ice zone (MIZ) of the Ross Sea [Wilson et al., 1986; Cunningham and Leventer, 1998; Leventer, 1998; Arrigo et al., 1999].

[74] P. antarctica is also a dominant pelagic phytoplankton taxa in the Ross Sea, although blooms of this species are not generally associated with the MIZ. Instead, P. antarctica is most commonly associated with the Ross Sea polynya, where pelagic blooms of this species have been reported to attain Chl a concentrations of >10 mg m⁻³ over an area of tens of thousands of square kilometers [Arrigo and McClain, 1994; Arrigo et al., 1998a] and extending to depths >40 m [Smith and Gordon, 1997; Arrigo et al., 2000]. These blooms begin to form in early November, under conditions of minimal meltwater stratification [Arrigo et al., 1998a, 2000], while a considerable amount of sea ice is still being formed in the central Ross Sea. Although the dominance of P. antarctica in young ice south of 74°S during our study was probably more a reflection of its physical entrainment within the Ross Sea polynya than its competitive superiority in sea ice over other algal taxa, it was present in pack ice all along our transect, and possibly reduced in response to elevated snow thickness. North of this region (D), elevated algal standing crops were probably the result of less snow cover and the extended growing season that favors algal growth at lower latitudes.

[75] Diatoms were the most prevalent algal taxa in older ice where algal biomass was relatively high, while P. antarctica, which appeared to be preferentially incorporated into newly formed sea ice, dominated in younger, thin ice where algal biomass was always low. Because P. antarctica never dominated in areas of high algal biomass despite its high incorporation rate in new sea ice, it is likely that this species is not well adapted for growth within sea ice.

5. Conclusions

[76] Distributions of sea ice and snow thickness in the Ross Sea reflect latitudinal variability in sea ice age. The youngest and thinnest sea ice and the thinnest snow cover were located at the southern boundary of the pack, near the location of the Ross Sea polynya. Ice and snow thickness in springtime were greatest at the interior of the pack between 67°S and 69°S.

[77] Algal biomass was minimal in very young ice and in regions of unusually heavy snow cover. Except for areas of high snow cover where light likely controlled algal growth rates, algal growth over much of the ice pack was not yet resource limited. Low algal biomass accumulation prior to our study was largely a function of our early sampling period; older ice generally contained the highest biomass due to the increased length of time available for algal growth. Latitudinal trends in algal biomass observed during this study can therefore be explained in terms of sea ice thickness and age, and snow thickness as depicted in Figure 17. In the latitudinal segment labeled A in this figure, algal biomass increased with decreasing latitude and greater sea ice age, due to increasing time available for growth. At the latitude of peak algal biomass (A–B), the combination of older sea ice and low snow cover and ice thickness favored maximal algal growth rates. At B, algal biomass began to decline as sea ice thickened further, perhaps due to a combination of less light for bottom ice algal growth and increased heterotrophic activity (as implied by the high NH4 and PO4 concentrations observed there). The region of the pack ice denoted by C was under the control of light availability, and algal biomass was dramatically reduced in response to elevated snow thickness. North of this region (D), elevated algal standing crops were probably the result of less snow cover and the extended growing season that favors algal growth at lower latitudes.

[78] Ratios of POC:Chl a were high in the sea ice, particularly where P. antarctica was most abundant. This may reflect the high carbon content of the colonial matrix of this organism but it also may be due to a proliferation of microheterotrophs or rapid degradation of Chl a in the sea ice, neither of which were measured during this study. The
high correspondence between algal species composition in the sea ice of the Ross Sea and in the phytoplankton blooms which form there, both within the MIZ and in the Ross Sea polynya, suggests that the sea ice and oceanic regimes are tightly coupled systems that exchange a significant amount of particulate and dissolved material. The cycle of release from and incorporation into the annual ice pack by algae in the Ross Sea may represent an adaptive strategy to maximize growth rates in both habitats.

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References


Gleitz, M., S. Grossmann, R. Scharek, and V. Smetacek, Ecology of diatom and bacterial assemblages in water associated with melting summer sea ice in the Weddell Sea, Antarctica, Antarct. Sci., 8, 135–146, 1996a.


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