where maximum tintinnid abundances were recorded in ice-covered areas (Weddell Sea, Bransfield Strait, Bellingshausen Sea), or at approximately 60 meters below the surface (Weddell-Scotia confluence: Alder unpublished data).

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Studies on the nutrient status in sea ice and underlying platelet layer of McMurdo Sound

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Past studies of the sea-ice microbial communities (SIMCO) in the land-fast ice of McMurdo Sound, Antarctica, have concentrated on the role of light in microalgal growth in the congelation and underlying platelet ice (Bunt and Lee 1970; Palmisano et al. 1987; SooHoo et al. 1987). Due to sampling difficulties, comparatively little attention has been paid to the nutrient regime in this habitat.

In antarctic waters, concentrations of major nutrients are high compared to other oceanic regions and are, thus, generally considered to be nonlimiting for algal growth. Recent studies on sea ice, however, have indicated that the nutrient concentrations in sea ice can differ considerably from the underlying water column. One reason for this may be restricted exchange between sea ice and seawater, concomitant with enhanced biological activity.

The bottom 20 centimeters of congelation ice and the platelet layer which underlies a large portion of the fast ice of McMurdo Sound in spring and summer has been observed to harbor a SIMCO of exceptionally high biomass (Palmisano and Sullivan 1983). To improve our understanding of the development and growth of this unique microbial community, we studied the nutrient environment of the platelet ice and the upper water column.

Our main sampling site (ice falls) was located in McMurdo Sound approximately 3 kilometers north of McMurdo Station (77°49.48′S 166°41.45′E). The ice cover consisted of 2-year-old congelation ice approximately 2.5 meters thick underlaid by roughly 65 centimeters of platelet ice. Snow cover in the region ranged from 0 to 10 centimeters, although we concentrated our sampling efforts in clear ice areas. Sampling took place at 1- to 5-day intervals starting 26 September 1989 and ending 3 December 1989. All sampling holes were located within our 200-square-meter study site. We had a second sampling site approximately 5 kilometers west of ice falls located near the ice runway and a third 10 kilometers north of ice falls located west of the cinder cones between McMurdo Station and Turtle Rock. The ice runway site was characterized by 3.5 to 4 meters of multiyear congelation ice over 70 centimeters of platelet ice all covered by 40 centimeters of snow. This site was used to determine nutrient concentrations in areas of low biological activity. The cinder cones site contained 1.9 to 2.0 meters of first-year ice overlying 50 to 65 centimeters of platelet ice and covered by 0 to 50 centimeters of snow. The latter two sites will not be discussed here.

Nutrients in congelation ice were studied in melted core sections obtained by standard ice coring procedures; however, these results will not be discussed here. A new sampling device, ADONIS (Arrigo/Dieckmann Nutrient Ice Sampler, figure 1), was developed to profile at high resolution the entire platelet layer and underlying water column down to a depth of approximately 1 meter. ADONIS consists of a 4-meter length of 5.7-centimeter diameter PVC pipe through which six lengths of 0.6-centimeter diameter polyethylene tubing are fed. The tubing remain inside the pipe until the unit is inserted into a 7.5-centimeter diameter hole drilled into the ice with an ice auger. At this time, the tubing is forced out from the pipe to a distance of 25 centimeters through a series of guide holes placed at 12-centimeter intervals at the base of the pipe. The tubing is guided by additional small PVC inserts with a 90° bend glued into the interior of the pipe so that the tubing exits

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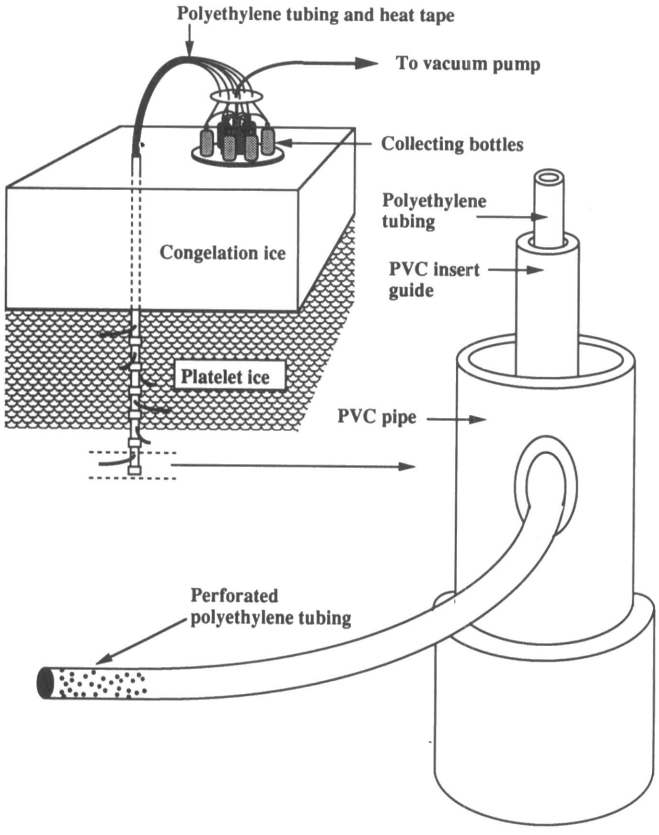

Figure 1. Schematic representation of ADONIS illustrating its method of deployment, and an expanded view of a sampling tube.

at an angle perpendicular to the pipe and well into the unconsolidated platelet ice matrix. The submerged end of the tubing is capped to prevent clogging and a series of holes 1 millimeter in diameter are drilled extending to 5 centimeters from the cap. The opposite ends of the six tubes are connected to an apparatus consisting of six collecting bottles with in line shut-off valves connected to a single vacuum flask so that all six samples can be drawn simultaneously. To keep the lines from freezing, heat tape is run parallel to the tubing from the base of ADONIS to where the tubes attach to the collection bottles. After the first set of samples are collected, ADONIS is lowered further into the ice to sample greater depths including the upper boundary of the water column.

Samples were transported within 1 hour of sampling to a shore laboratory in McMurdo where they were filtered on Whatman GF/F for flourometric determination of chlorophyll *a* and pheopigment (Parsons, Miata, and Lalli 1984). The filtrate was used for analyzing inorganic nutrients. The concentration of ammonia was immediately determined using the alternative method of Parsons et al. (1984). The remainder of the filtrate was frozen for later determination of phosphate, nitrate, nitrite, and silicic acid using an Alpkem Rapid Flow Analyzer RFA-300 at the University of Southern California.

Although ADONIS was effective in obtaining accurate profiles of dissolved organic material, inorganic nutrients, salinity, alkalinity, and pH in the platelet layer, chlorophyll concentrations obtained by this method are underestimates of levels contained within the platelet ice layer since only interstitial water was sampled and a substantial fraction of sea ice microalgae were observed to adhere to ice crystals. This method, however, does provide valuable qualitative information on microalgal distributions within the platelet layer.

Chlorophyll profiles at each of our sampling sites indicate that when present, microalgal biomass was concentrated in the upper 20 centimeters of the platelet ice layer throughout the spring bloom, with the highest concentration (70 percent of total biomass) found immediately beneath the congelation ice (figures 2 and 3). Chlorophyll concentrations in the upper 2 meters of the water column were less than 1 milligram per cubic meter throughout the sampling period.

Ammonium concentrations in the platelet ice at the ice fall site were always at least an order of magnitude higher than that found in the water column. Furthermore, maximum ammonium concentrations in the platelet ice changed dramatically throughout the early part of the season, with a peak concentration on 26 September of approximately 3.4 micromole which increased dramatically to a maximum of 177 micromole on 8 October. By 12 October, however, peak ammonium concentrations had dropped to 6 micromole and varied only from 5.5 to 11 for the remainder of the season.

From the early (26 October) to the middle (19 November) part of our sampling season, profiles of ammonium, nitrate, phosphate, and silicic acid showed significant nutrient depletion (but not limitation) coinciding with maximum chlorophyll concentrations in the upper platelet ice (figure 2). After 19 November, however, while profiles of silicate and nitrate continued to follow this pattern, ammonium and phosphate concentrations increased in the upper platelet ice (figure 3).

Judging from spectral irradiance and from chlorophyll and inorganic nutrient profiles, we determined that distributions of algae in the platelet ice appear to be controlled by light, not by nutrient availability, since at no time during the course of the spring algal bloom did the concentration of any measured major nutrient fall to levels that might be expected to be limiting. Conversely, because surface irradiance potentially available to the platelet ice community is rapidly attenuated by snow, sea ice, and particulates present in the congelation ice (including microalgae), irradiance it the top of the platelet layer is usually quite low (0 to 50 microeinsteins per square meter per second depending upon congelation ice thickness, snow cover and particle concentration). Also, a steep light gradient exists in the platelet ice due to the high concentrations of algae (2-5 grams of chlorophyll per cubic meter) present there (Arrigo et al. unpublished data). The result is that light available to microalgae growing in the lower platelet ice is of relatively poor spectral quality due to the absorption of the optimum wavelengths by the community above. Thus, the highest biomass is located in the upper platelet ice where the majority of the high-quality light is available and growth is optimized.

Although nutrients do not appear to limit algal growth in the platelet ice, the nutrient dynamics do indicate that a rich and highly regenerative community develops there. Ammonium is regenerated throughout the season, although depletion, presumably due to algal uptake at the top of the platelet layer, is evident early in the season. In the latter half of the season, however, regenerative ammonium production exceeds ammonium uptake as concentrations in the upper platelet ice begin to increase relative to the layers below. In addition, a parallel regeneration of phosphate in excess of uptake by microalgae is apparent later in the season in the upper platelet ice.

It is interesting to note that in the upper platelet ice, nitrate is depleted in the presence of high ammonium concentrations. This is contrary to evidence indicating that nitrate uptake by phytoplankton ceases when ambient ammonium concentrations exceed a threshold level of 0.5 to 1.0 milligrams of nitrogen per cubic meter (Eppley, Coatsworth, and Solarzano 1969;

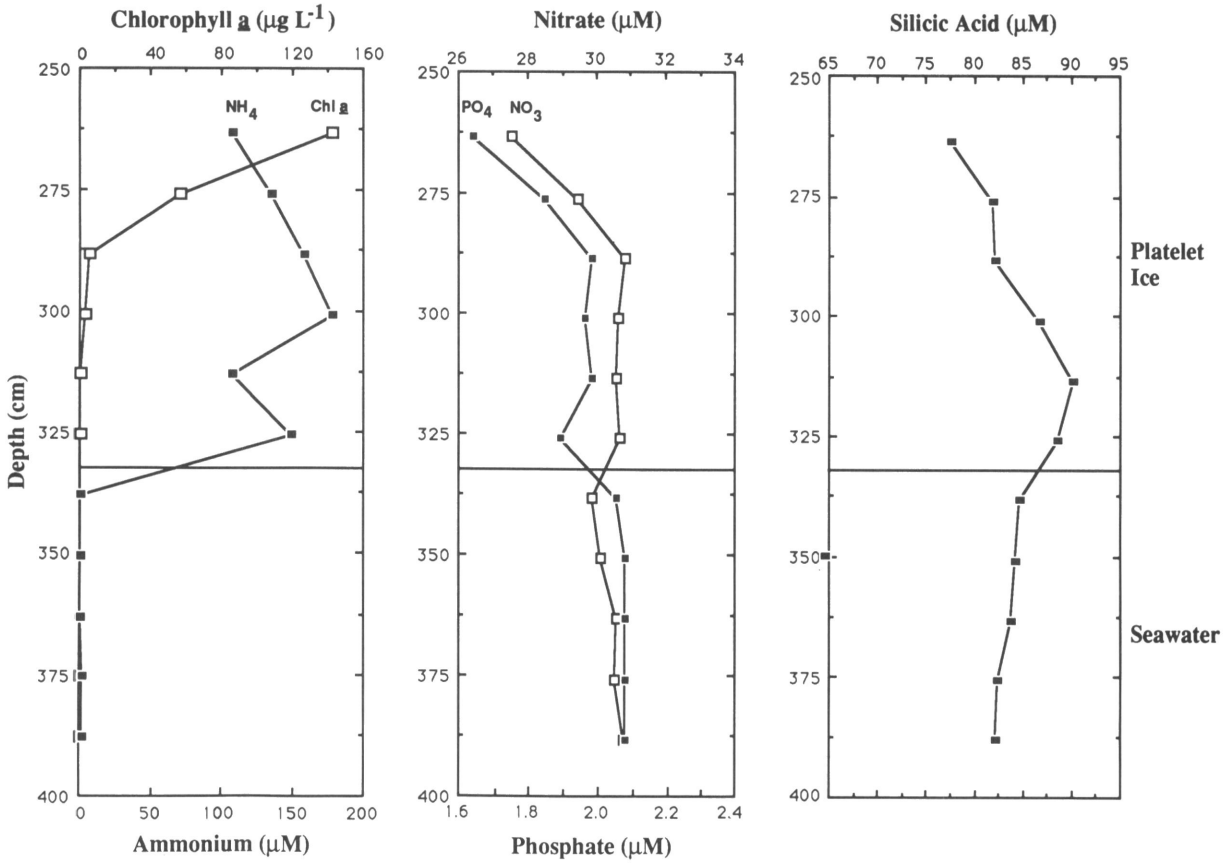

Figure 2. Profiles of chlorophyll *a* and inorganic nutrients at Ice Falls Station, McMurdo Sound, Antarctica, 8 November 1989. (cm denotes centimeter. μM denotes micromole. μg L^{-1} denotes micrograms per liter.)

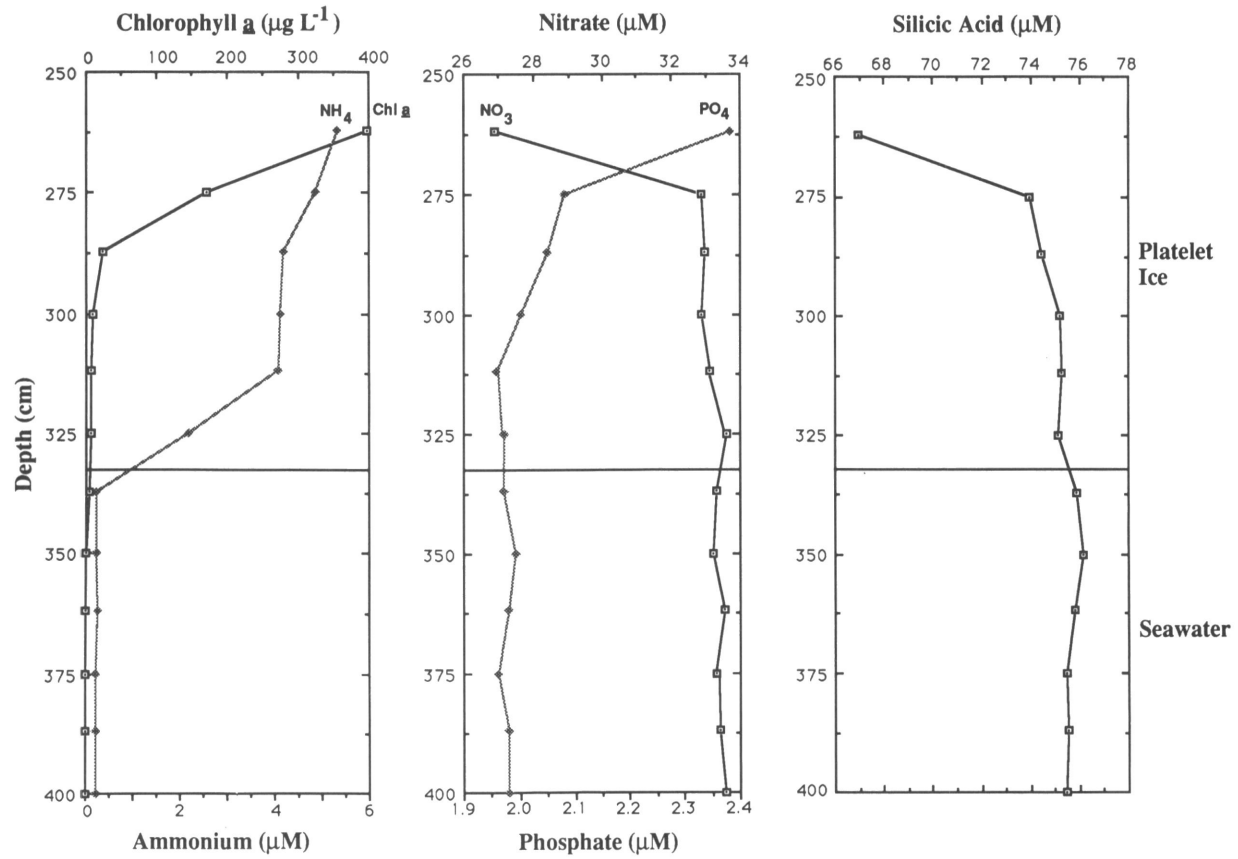

Figure 3. Profiles of chlorophyll a and inorganic nutrients at Ice Falls Station, McMurdo Sound, Antarctica, 3 December 1989. (cm denotes centimeter. μM denotes micromole. μg L^{-1} denotes micrograms per liter.)

MacIsaac and Dugdale 1969; Olson 1980). It agrees very well, however, with suggestions that oyster pond algae, a group of diatom species which inhabit an environment similarly high in ammonium, nitrate, and organic nitrogen sources (concentrations of dissolved amino acids were also high in the upper platelet ice, Welborn personal communication), have higher ammonium threshold levels than similar pelagic species so that alternative nitrogen sources may be assimilated when ammonium is high (Collos, Maestrini, and Robert 1989).

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Temperature dependence of the photosynthetic parameter alpha in antarctic sea-ice microalgae

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The environments inhabited by antarctic sea-ice microalgae are characterized by low ambient temperatures near −2.0 °C. Numerous studies have been undertaken to determine which adaptive strategies are employed by antarctic microalgae to cope with such low temperatures and to evaluate to what extent temperature may limit algal growth. In general, these algae are psychrophiles, having optimal growth temperatures below 15 °C, and maximum and minimum temperatures for growth at or below 20 °C and 0 °C, respectively, suggesting that they are adapted to low-temperature environments. Field observations of low photosynthetic rates may indicate, however, that polar microalgae have not overcome limitations imposed by low temperature (Tilzer et al. 1986).

Several studies have reported that both maximal photosynthetic rate (P^bmax) and photosynthetic efficiency (alpha) are temperature dependent (Palmisano, SooHoo, and Sullivan 1987; Tilzer et al. 1986). The temperature dependence of P^bmax (maximum photosynthetic rate obtained at saturating irradiances) is well documented and thought to result from temperature sensitivity of the diffusional or enzymatic processes regulating Pmax. The temperature dependence of alpha (linear portion of the photosynthesis-irradiance curve) is surprising, since it is thought to be regulated by temperature independent photochemical reactions. Consequently, Tilzer et al. (1986) has proposed that at very low temperatures photochemical reactions are replaced by other temperature dependent reactions as rate limiting steps in "light limited" photosynthesis. Alternately, there are other factors that can bring about an apparent change in alpha in response to temperature without proposing a special interpretation of light-limited photosynthesis at low temperature. These factors including light harvest, energy transfer to the reaction center of photosystem II, and carbon fixation pathways.

The aim of our study was to characterize the temperature dependence of alpha and, through a systematic approach, to identify the temperature sensitive steps responsible for the observed effect. Fresh samples of sea-ice microalgae were collected from beneath approximately 2 meters of congelation ice at McMurdo Sound during the 1988–1989 and 1989–1990 field seasons. P^bmax and alpha were determined from isotopic sodium bicarbonate ($NaH^{14}CO_2$) incorporation at 6.0, −2.0, and −6.0 °C. Similarly, assimilation of carbon into proteins, polysaccharides, lipids, and low-molecular-weight compounds was determined by incorporation of $NaH^{14}CO_2$ followed by biochemical fractionation of photosynthetic products. In parallel, measurements of algal absorption, fluorescence, and pigment concentration were taken to calculate mean specific absorption (light harvest), relative energy transfer efficiency from pigments to the reaction center, pigment ratios, and quantum yield. Enzymatic activities were determined for ribulose disphosphate carboxylase (RUBPC) and phosphoenolpyruvate carboxykinase (PEPCK) from −6.0 to 25 °C.

Our data demonstrate that temperature can effect alpha, confirming the observations of other workers (Tilzer et al. 1986; Palmisano et al. 1987). Using the values at 6.0 °C for comparison (0.014 milligrams of carbon per milligram of chlorophyll