

A high-resolution sampler for nutrient and chlorophyll *a* profiles of the sea ice platelet layer and underlying water column below fast ice in polar oceans: preliminary results

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ABSTRACT: A device (ADONIS) for collecting interstitial water samples, at closely spaced intervals, from the platelet ice layer and upper water column beneath congelation ice in McMurdo Sound, Antarctica, was designed, developed, and tested. Fourteen profiles of inorganic nutrients and chlorophyll *a* (chl *a*) were obtained using ADONIS under fast ice near McMurdo Station. All profiles revealed highest chl *a* concentrations at the congelation/platelet ice interface. Maximum chl *a* concentration, under 2.5 m congelation ice, ranged between 5.20 and 853 $\mu\text{g l}^{-1}$ from 26 October to 3 December 1989, but was only 0.35 $\mu\text{g l}^{-1}$ under 4 m thick ice with a 0.4 m snow cover. Ammonium concentrations in the interstitial water of the platelet ice layer always exceeded those in the underlying water column by at least an order of magnitude, with maximum values per profile ranging from 3.20 to 178 $\mu\text{mol NH}_4 \text{l}^{-1}$. Concentrations of phosphate, nitrate, and silicic acid in the platelet ice layer differed only slightly from those in the water column, except in the presence of high algal biomass, where they were somewhat depleted but never exhausted. By the end of November, ammonium and phosphate at the interface of the congelation/platelet ice layer had increased slightly relative to water column concentrations, indicating that regeneration exceeded uptake. Growth of the sea ice microbial community in the platelet layer does not appear to be nutrient-limited, as nutrients are apparently replenished by an adequate and efficient water exchange mechanism between platelet layer and underlying water column. ADONIS proved to be an effective tool with which to obtain high-resolution profiles of nutrients and chl *a* in interstitial waters of the platelet ice layer and upper water column under congelation ice up to 4 m thickness.

INTRODUCTION

The platelet ice layer is a feature usually observed under fast ice surrounding Antarctica (e.g. Moretskiy 1965, Bunt 1968, Dayton, Robilliard & DeVries. 1969, Sullivan & Palmisano 1984, Dieckmann et al. 1986, Garrison et al. 1986, Smetacek et al. 1992). Ice platelets, ranging in diameter from a few millimeters to 15 cm and in thickness from 1 to 3 mm, are produced in super-cooled water advected from under-

neath ice shelves, both at depth (Foldvik & Kvinge 1974, Dieckmann et al. 1986) and under sea ice (Dayton, et al. 1969, Barry 1988). The basal plane of these platelet ice crystals has a characteristic roughness which may facilitate the attachment of microorganisms. Under ice shelves or sea ice, ice platelets aggregate into relatively loose layers up to several meters in thickness (Moretskiy 1965, Dayton et al. 1969, Engelhardt & Determann 1987, Kipfstuhl 1991), constituting stable habitats which, provided sufficient light is available, are colonized by microalgae and other microorganisms (Bunt 1968, Palmisano & Sullivan 1985a, Garrison et al. 1986, Grossi et al. 1987, Cota & Sullivan 1990, Smetacek et al. 1992). Such

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microbial communities may attain extraordinarily high biomasses of up to 13 mg chlorophyll *a* ($\text{chl } a$) l^{-1} (Arrigo, Robinson and Sullivan unpubl.). In addition, Smetacek et al. (1992) have described another type of platelet layer associated with fast ice in the same region, and noted that in contrast to the platelet layers under pack ice, where algae were only found in the interstitial water, algae here also grew attached to ice platelets. Furthermore, they concluded that the accumulation of $\text{chl } a$ up to concentrations of $65 \mu\text{g l}^{-1}$ in the interstitial water of the fast ice platelet layer, in the presence of nitrate, indicated that the water between these platelets was not stagnant.

Most studies of sea ice microbial communities (SIMCO) in McMurdo Sound, Antarctica, have focused on the role of light in controlling microbial growth in the congelation ice and underlying platelet layer (Bunt & Lee 1970, Palmisano et al. 1987a, SooHoo et al. 1987, Arrigo et al. 1991). However, indirect evidence, such as microalgal biochemical composition, patterns of carbon allocation (Palmisano & Sullivan 1985b), and calculations of nutrient demand (Cota & Sullivan 1990), suggests that the availability of inorganic macronutrients may limit microalgal growth in McMurdo Sound. Furthermore, Smetacek et al. (1992) observed nutrient exhaustion concurrently with $\text{chl } a$ concentrations of $34 \mu\text{g l}^{-1}$ in stabilized interstitial waters of platelet layers up to 100 cm deep under drifting pack ice near the Filchner Ice Shelf in the southern Weddell Sea.

In order to study the nutrient regime in the platelet layer under fast ice in McMurdo Sound, we developed a device capable of relatively high-resolution sampling of interstitial waters. Here we provide a detailed description of this device, along with data on nutrient status and $\text{chl } a$ in the platelet ice layer and upper meter of the water column beneath the ice/water interface.

MATERIAL AND METHODS

Two sampling sites were located in McMurdo Sound, one about 3 km to the northwest and the other 2 km to the west of McMurdo Station (Fig. 1). At Stn 1 the fast ice cover consisted of 2 yr old congelation ice about 2.5 m thick with a 0.65 m loosely structured layer of platelet ice underneath. Snow cover in the region ranged from 0 to 0.1 m, but sampling was restricted to snow-free areas. Samples were collected at 1 to 5 d intervals from 26 October to 3 December 1989, in an area of 200 m^2 that was demarcated by flags on bamboo poles frozen into the ice.

Stn 2 was sampled once on 2 December. The congelation ice here was 3.8 m thick with a 0.4 m snow cover. The platelet layer underneath was ca 1 m deep.

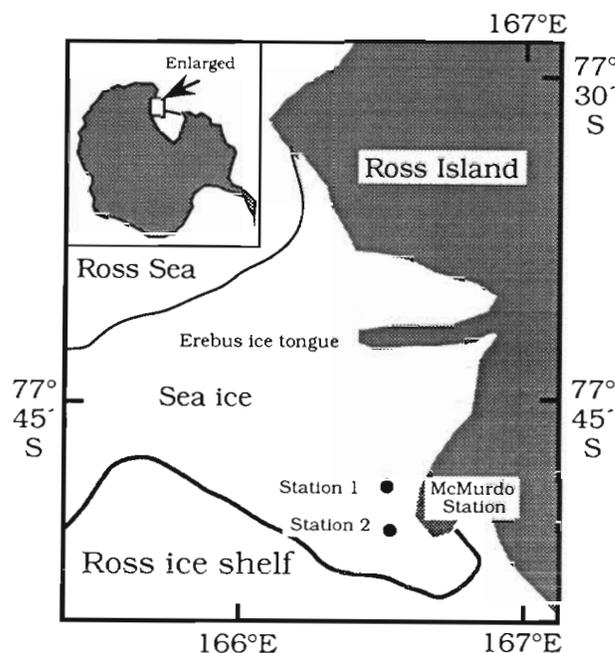


Fig. 1. Sampling stations in McMurdo Sound, Antarctica

During field studies in 1982 and 1984 SCUBA divers collected bulk samples of the platelet ice layer near Cape Armitage, as described in Grossi et al. (1987), in order to estimate the proportion of the algal community which was attached to ice crystal surfaces. The interstitial water was carefully decanted into a separate vessel and the platelet ice was retained. A known amount of filtered seawater was then added to the platelet ice and was allowed to melt at 0 to 5 °C. $\text{Chl } a$ concentration ($\mu\text{g l}^{-1}$) was estimated for each pair of samples by the fluorometric method (Parsons et al. 1984) and then converted to total $\text{chl } a$ (μg) by multiplying by the sample volume. The relative distribution of $\text{chl } a$ between interstitial water and platelet ice was estimated by assuming the ice comprised 20 % and the interstitial waters 80 % of the volume of the platelet ice layer (Bunt 1968).

The new sampling device, ADONIS (Arrigo Dieckmann Original Nutrient Ice Sampler) (Fig. 2), was designed to profile (at 12 cm intervals) the entire platelet ice layer as well as the underlying water column to a depth of ca 1 m, with as little disturbance of the structure of the platelet layer as possible. ADONIS is operationally divided into sampling and collecting units, which are described below and in Fig. 2. The sampling unit consists of a probe which is inserted in the platelet layer through a hole 5 cm in diameter, drilled only through the congelation ice with an ice auger. The last few centimeters of congelation ice are carefully drilled to prevent penetration and disruption of the platelet layer with the ice auger.

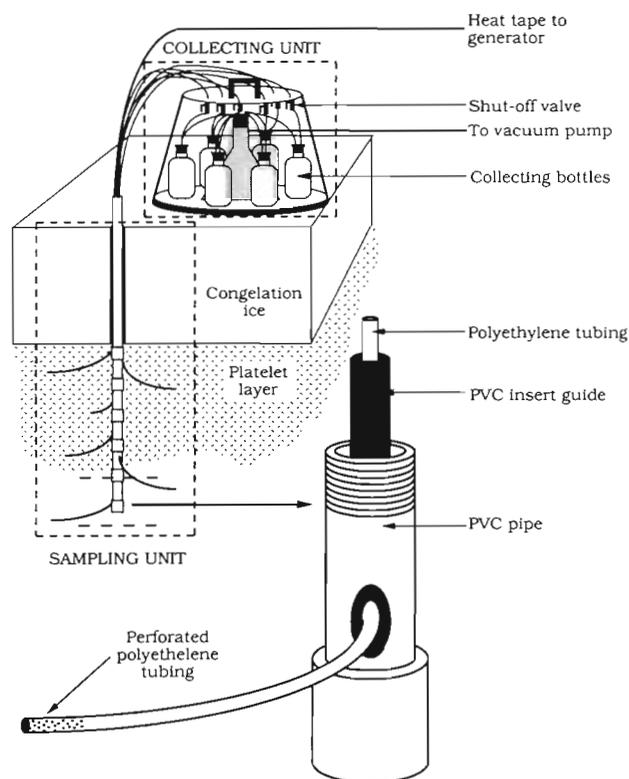


Fig. 2. Schematic diagram of ADONIS, illustrating method of deployment and expanded view of a portion of the sampling probe (not drawn to scale)

The probe is constructed of 2 or 3 (depending on congelation ice thickness) PVC pipes, each 2 m long and 3.4 cm in o.d. (outside diameter), joined together with sleeves (4.4 cm o.d.). Six lengths (each ± 6 m long) of 0.6 cm (o.d.) polyethylene tubing are fed through the pipes. During sampling these tubes draw water simultaneously from 6 discrete depths within the platelet layer and/or the underlying water column. However, during insertion into the congelation ice the sampling tubes remain retracted inside the probe until it is in position. The tubes then are forced out from the probe to a distance of 25 cm through a series of holes placed at 12 cm intervals along the lower 60 cm of the probe. Each sampling tube is offset about 30° from the tube above so as to maximize the distance between the tube intakes. To ensure that the sampling tubes exit at an angle perpendicular to the probe and well into the unconsolidated platelet ice matrix, they are guided by small PVC inserts [1.5 cm o.d. and 0.7 cm inner diameter (i.d.)], bent at a 90° angle and glued to the interior of the probe. The tubes themselves are perforated with 1 mm holes extending inwards over the distal 5 cm and the ends are capped to prevent clogging. To prevent freezing of the tubes during sampling, heat tape, which is connected to a portable

generator, is run along the full length of the sampling unit inside the probe.

The free ends of the 6 sampling tubes are attached to the collecting unit, which draws each sample into an individual bottle marked with an appropriate sample number. The collecting unit consists of 6 acid-washed 1 l glass bottles with single-hole stoppers through which glass tubes are inserted. The glass tubes are attached to 6 in-line shut-off valves with rubber tubing. The opposite ends are attached to the sampling tubes so that the flow of water to any bottle can be stopped when necessary using the shut-off valves. To allow vacuum pressure to be simultaneously applied to all sample bottles, a vacuum flask, attached to a vacuum pump, is connected to each of the 6 sample bottles by vacuum tubing and large-bore hypodermic needles which penetrate the rubber stoppers.

Once ADONIS is in place, ca 30 ml of water are drawn into each bottle to rinse them and to ensure that water which has entered the sampling tubes during deployment (30 ml void volume) is displaced by water from the area to be sampled. After the first set of samples are collected, the sampling tubes can be retracted and ADONIS removed or lowered further into or through the platelet layer to sample greater depths.

Water samples collected using ADONIS were stored on ice in the dark and transported within 1 h of sampling to the laboratory at McMurdo Station. Samples were immediately filtered (< 5 mm Hg) on Whatmann GF/F Filters which were used for fluorometric (Turner 111 fluorometer) determination of chl *a* (Parsons et al. 1984). The filtrate was subsequently used for analysis of inorganic macronutrients.

Ammonium concentrations were determined immediately using the 'Alternative method' by Parsons et al. (1984). Initially we also analyzed nitrate, phosphate and silicate samples immediately using methods by Parsons et al. (1984). After the first 2 profiles, nutrients were frozen in polypropylene bottles for later analysis using an Alpkem Rapid Flow Analyzer RFA-300 at the University of Southern California. Replicates of nutrient samples which had been analyzed immediately were reanalyzed and showed little or no detectable change in the concentration of any nutrient.

To obtain estimates of total algal standing stock in the platelet layer and the congelation ice, we also drilled larger holes adjacent to ADONIS holes using a SIPRE ice corer (7.6 cm i.d.) powered by a Jiffy motor. As the core is removed, ice platelets with attached organisms rise up in the hole and displace the extracted core. All the platelets and associated community were carefully scooped out of the hole using a Nalgene beaker fitted with a handle. They were collected in darkened 2 l Nalgene bottles, capped and

stored on ice during transport to McMurdo Station. The core was placed on a sheet of black plastic and cut into 20 cm sections. Each section was placed in a dark, 1 l Nalgene bottle and handled as the platelet ice samples above.

The platelet ice samples and core sections were allowed to melt at -1°C for a period of 12 h. The salinity of the platelet ice meltwater was monitored periodically and adjusted by adding measured quantities of $0.2\ \mu\text{m}$ filtered seawater to maintain salinities > 30 ppt. The melted core samples were analyzed in the same manner as the ADONIS water samples, and platelet ice samples were used for chl *a* determinations as well as other experiments not discussed here.

RESULTS

Congelation ice and skeletal layer

In the lower 20 cm of congelation ice, which included the densely populated skeletal layer, chl *a* concentrations in the core meltwater ranged from $0.35\ \mu\text{g l}^{-1}$ in the sample from Stn 2 to between 1145 and $3005\ \mu\text{g l}^{-1}$ in the cores collected at Stn 1.

Platelet ice layer

Bulk characteristics

Chl *a* was estimated for pairs of samples of the interstitial waters and platelet ice collected by SCUBA divers (Table 1). Approximately half of the chl *a* was associated with platelet ice, confirming visual inspection of the sample. However, this appears to be an underestimate of the amount of biomass actually associated with the ice platelet surfaces; although the cells were observed to adhere tightly to crystal surfaces, long strands comprising the diatom colonies were easily disrupted, even during the careful decanting procedure used to separate platelets from interstitial water. As a result they appeared in the interstitial water sample.

ADONIS profiles

A time series of 14 profiles was carried out at the 2 stations, only 3 of which are presented here in detail. Vertical profiles of the platelet layer at Stn 1 reveal that the distribution of microalgal biomass was highly stratified throughout the sampling season, with 39 to 91 % of the observed chl *a* concentrated in the top 12 cm of the platelet layer at the congelation ice/platelet layer interface (Figs. 3 & 4). Concentrations obtained from ADONIS in this upper layer ranged

from 5.20 to $853\ \mu\text{g chl a l}^{-1}$ of interstitial platelet ice water. In contrast, the maximum chl *a* concentration measured in the interstitial water of the platelet layer at Stn 2 was only $0.4\ \mu\text{g l}^{-1}$ (Fig. 5). Concentrations in the upper meter of the water column at Stns 1 and 2 were relatively low and never exceeded $1\ \mu\text{g chl a l}^{-1}$.

Like the distribution of algal biomass, ammonium concentrations often exhibited marked vertical stratification within the platelet layer, although the pattern differed substantially from that observed for chl *a*. Prior to 19 November, minimum ammonium concentration coincided with the depth of the chl *a* maxima, while the peak concentration occurred somewhat deeper (Fig. 3). Later, however, the pattern was reversed and peak ammonium concentration occurred in conjunction with maximum chl *a* concentration (Fig. 4). This was observed also at Stn 2, where relatively high ammonium concentrations were found despite very low chl *a* concentrations. Vertical ammonium gradients associated with the platelet layer often were extreme, the maximum occurring on 8 November. Between the sampling depths of 0 and 36 cm, ammonium concentrations varied from 107 to $178\ \mu\text{mol l}^{-1}$, representing a vertical gradient of $2.0\ \mu\text{mol l}^{-1}\ \text{cm}^{-1}$ over this interval. The concentration gradient was even more pronounced across the platelet layer/seawater interface, where ammonium concentration decreased from $149.4\ \mu\text{mol l}^{-1}$ in the lower platelet layer to $0.5\ \mu\text{mol l}^{-1}$ in the water column 12 cm below, representing a gradient of $12.5\ \mu\text{mol l}^{-1}\ \text{cm}^{-1}$.

Peak ammonium concentrations in the platelet layer changed dramatically throughout the early part of the season, yet were always at least an order of magnitude higher than those observed in the upper water column.

Table 1. Proportion of microalgal chlorophyll *a* (μg) associated with interstitial seawater and ice crystal surfaces within the platelet ice of McMurdo Sound, Antarctica

Date	Ice	Water	Total	% on ice	% in water
30 Oct 1982	7.81	7.55	15.37	50.85	49.15
12 Nov 1982	26.88	130.40	157.30	17.09	82.91
17 Nov 1982	1.16	0.77	1.93	60.25	39.75
27 Nov 1982	54.80	116.00	170.80	32.08	67.92
2 Dec 1982	1.96	5.13	7.09	27.67	72.33
19 Sep 1984	5.59	7.98	13.58	41.20	58.80
24 Sep 1984	0.08	0.10	0.18	46.07	53.93
5 Oct 1984	4.91	9.54	14.45	33.95	66.05
25 Oct 1984	4.35	0.99	5.34	81.44	18.56
31 Oct 1984	0.69	0.16	0.85	81.27	18.75
6 Dec 1984	1.70	1.86	3.57	47.73	52.27
Mean				47.24	52.27
SD				19.65	19.65

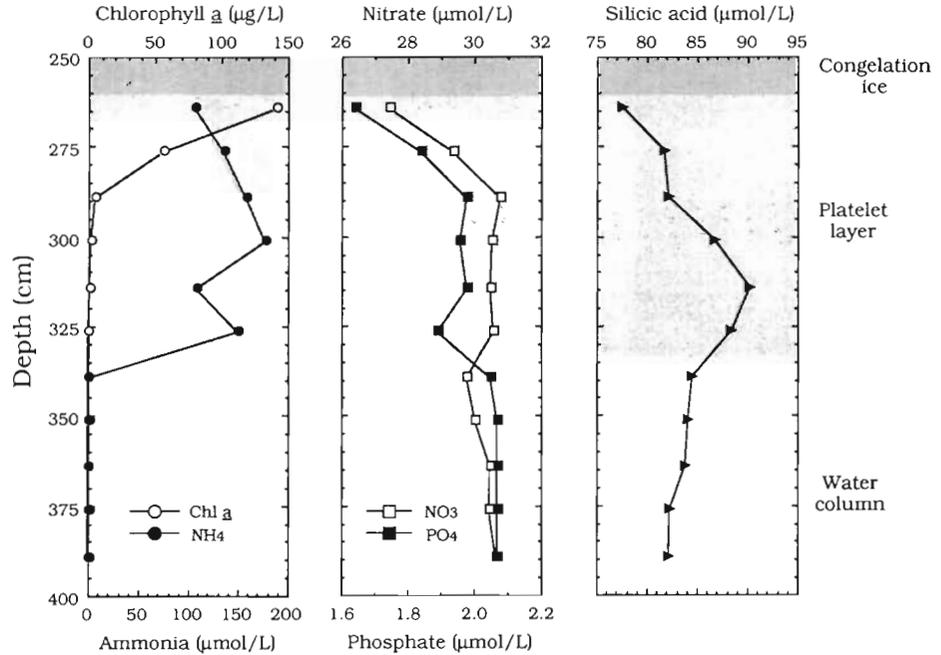


Fig. 3. Profiles of chlorophyll a and inorganic nutrients collected from the platelet layer and underlying water column at Stn 1 on 8 November 1989

On 26 October, the earliest sampling date, peak ammonium concentration within the platelet layer measured $3.40 \mu\text{mol l}^{-1}$ and increased dramatically by 8 November to the maximum observed value of $178 \mu\text{mol l}^{-1}$. By 12 November, however, peak ammonium concentrations had dropped to $5.80 \mu\text{mol l}^{-1}$ and varied between 5.30 and $10.8 \mu\text{mol l}^{-1}$ for the remainder of the season. Maximum ammonium concentration in the platelet layer at Stn 2 was $3.20 \mu\text{mol l}^{-1}$ (Fig. 5). Here too there was a steep gradient between the platelet layer and water column.

With the exception of the top of the platelet ice layer, concentrations of nitrate, phosphate, and silicic acid in the platelet layer generally were similar to those observed in the upper water column, averaging 32.1 , 72.3 and $2.00 \mu\text{mol l}^{-1}$, respectively, in the platelet layer, and 32.4 , 77.2 and $2.00 \mu\text{mol l}^{-1}$, respectively, in the water column. At the top of the platelet layer, corresponding to the depth of maximum chl a concentration, profiles of nitrate, phosphate, and silicic acid showed significant depletion (but not exhaustion) between 26 October and 19 November, similar to that observed for

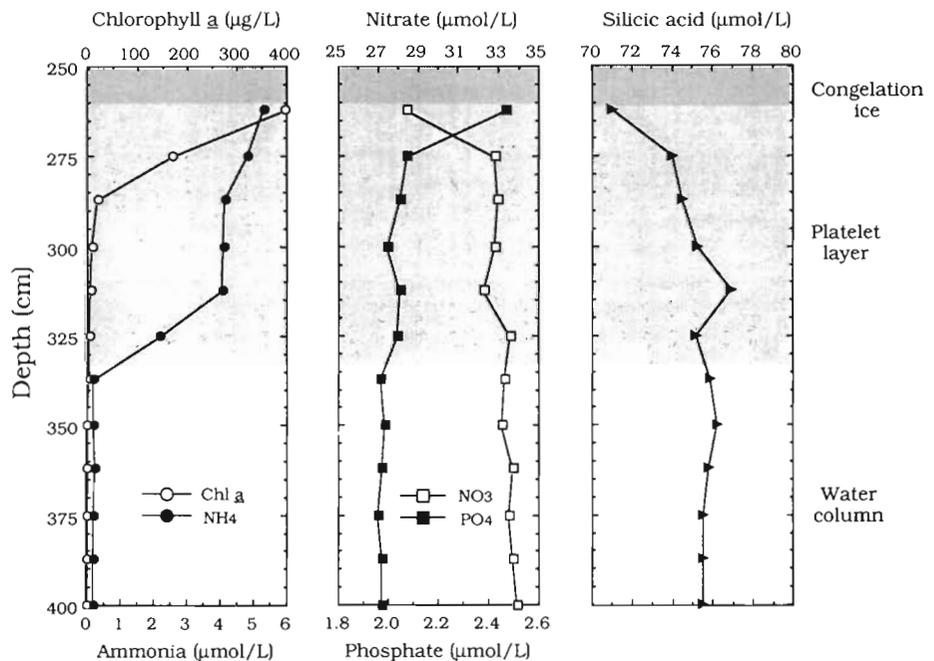


Fig. 4. Profiles of chlorophyll a and inorganic nutrients collected from the platelet layer and underlying water column at Stn 1 on 3 December 1989

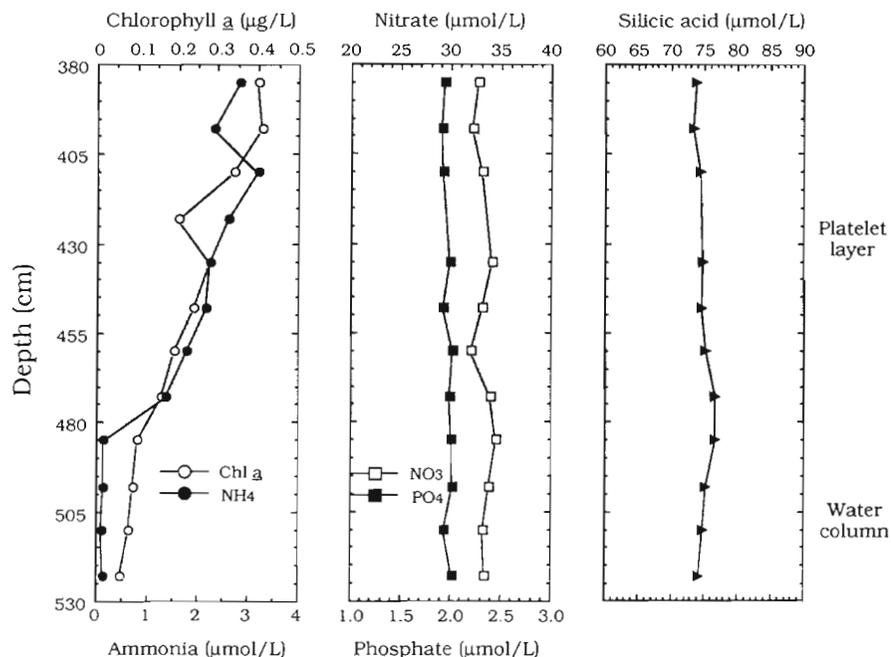


Fig. 5. Profiles of chlorophyll *a* and inorganic nutrients collected from the platelet layer and underlying water column at Stn 2 on 2 December 1989

ammonium (Fig. 3), although gradients were not as steep for these nutrients. After 19 November profiles of nitrate and silicic acid continued to follow this pattern, while ammonium and phosphate concentrations in the upper platelet ice increased (Fig. 4).

DISCUSSION

ADONIS performance

Determination of nutrient concentrations in interstitial water from the platelet ice layer collected with ADONIS does not suffer from the serious problems inherent in sampling nutrients within congelation ice that has to be melted prior to analysis, which results in disruption of organisms, the release of their internal nutrient pools and dilution of the samples (Garrison & Buck 1986, Smith et al. 1990, Dieckmann et al. 1991). However, because the ADONIS probe is deployed through a hole drilled in the congelation ice, it is necessary to assess the potential confounding effects of seawater displaced from the platelet layer and water column into the hole. If the volume of water displaced by the hole is large relative to the volume sampled by ADONIS, the samples would be unreliable. An analysis of this relationship is represented schematically in Fig. 6. The hole for ADONIS in the congelation ice is 5 cm in diameter and has a maximum depth of 4 m, which represents a volume of 7.8 l. When ADONIS is in place and the sampling tubes are fully extended, it samples a cylindrical area ca 58 cm in diameter and 60 cm in height, with a volume of 155 l. Thus, the

volume displaced by the hole for ADONIS is, at most, 5 % of the volume encompassed by the extended sampling tubes. In fact, since the platelet ice layer is not disturbed during the drilling of the hole water which enters the hole when the drill is removed must come from near the congelation/platelet ice interface (Fig. 6). This, and the fact that we find steep gradients

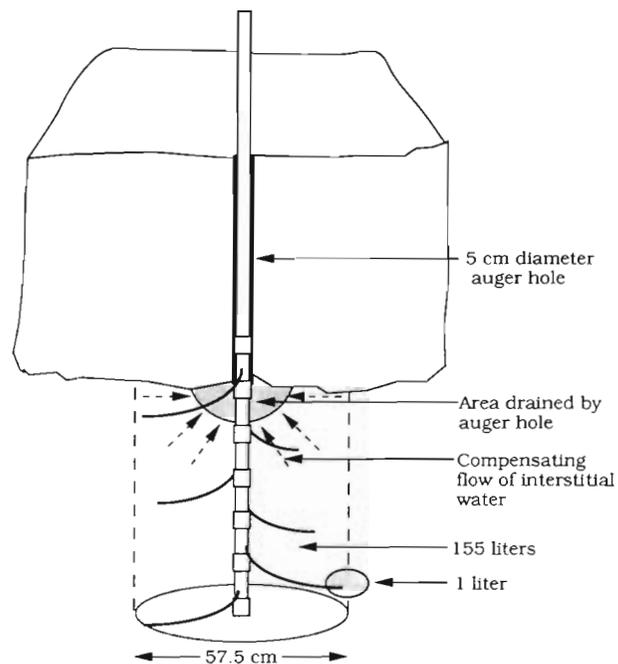


Fig. 6. Schematic diagram of the volume of seawater displaced by the ADONIS hole and the 'catchment area' when fully deployed in the platelet layer

in ammonium concentrations within the platelet layer and at the platelet layer/sea water interface, indicate that samples obtained with ADONIS are most likely accurate representations of conditions *in situ*.

Although ADONIS is effective in obtaining accurate profiles of inorganic nutrients and other parameters measurable in seawater (e.g. salinity, pH, alkalinity, dissolved organics, etc., not reported in this study), concentrations of chl *a* obtained by this method are likely to be underestimates of levels actually contained within the platelet layer. By separating ice crystals from the interstitial seawater collected from within the platelet ice layer, and comparing the chl *a* content of interstitial water and from melted ice platelets, it was determined that ca 47.2 % of the chl *a* was associated with platelet ice crystals (Table 1) and would not be sampled by ADONIS. However, this method does provide valuable qualitative information on microalgal distributions within the platelet layer, which can be coupled with estimates of biomass from bottom core sections and collections of ice platelet communities, to obtain vertical profiles of chl *a* concentration *in situ* (Arrigo et al. 1991). Sampling with ADONIS also will underestimate the abundance of particulates too large to be sampled or organisms which are able to escape. For example, antarctic krill *Euphausia superba* are known to forage in and around sea ice (Stretch et al. 1988), as are copepods of the genus *Pseudocalanus* (Conover et al. 1986). In addition, we observed the gammaridean amphipods *Cheirimedon fougneri* and *Paramoera walkeri* in bulk sea ice samples. Because of their large size and mobility, it is impossible to adequately sample these and other similar species given the small bore size of the ADONIS tubing.

A 12 cm sampling resolution was chosen for the present study, mainly for technical reasons concerning the construction of ADONIS and because we assumed that closer spacing of the sampling depths could result in an overlap in sampling volume. For example, the numerous analyses performed during this study (chl *a*, nutrients, salinity, pH, alkalinity, etc.) required ca 1 l of seawater per sampling depth.

The use of ADONIS samples for analyses of oxygen or other dissolved gases is of questionable value because samples are collected under vacuum and any gases at concentrations above saturation are likely to be rapidly released during sampling.

Biological considerations

In Antarctic waters, macronutrient concentrations are high compared to other oceanic regions and thus generally are considered to be non-limiting for algal growth (e.g. Jacques 1983, Sakshaug & Skjoldal 1989).

However, recent studies on fast ice, pack ice and the platelet ice layer under fast and pack ice of the Weddell Sea (Cota & Sullivan 1990, Garrison et al. 1990, Dieckmann et al. 1991, Smetacek et al. 1992) indicate that the nutrient concentrations in these environments can differ considerably from those in the underlying water column. One reason for this is a restricted seawater exchange between sea ice and the underlying water column, concomitant with enhanced biological activity. Based upon chl *a* and inorganic nutrient profiles reported here, however, distributions of algae in the platelet layer appear to be controlled predominantly by light, not nutrient availability, since at no time during the sampling season did the concentration of any measured major nutrient fall to levels that might be expected to be limiting. This also is substantiated by the difference in chl *a* concentrations measured in the platelet layers of Stn 1 and 2, which showed that very little algal biomass had accumulated under 3.8 m of congelation ice covered by 0.4 m of snow. Because surface irradiance potentially available to the platelet ice community is rapidly attenuated by snow, sea ice and particulates (including microalgae) present in the congelation ice (Iturriaga & Sullivan 1989, Arrigo et al. 1991), irradiance at the top of the platelet layer is low (0 to 50 $\mu\text{E m}^{-2} \text{s}^{-1}$) depending upon congelation ice thickness, snow cover and particle concentration. Also, a steep light gradient exists in the platelet layer due to high concentrations of algae present there (Arrigo, Robinson and Sullivan unpubl.). The result is that light available to microalgae growing in the lower portion of the platelet layer 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 presumably is optimized (Arrigo, Robinson and Sullivan unpubl.).

The observed nutrient profiles imply that a rich and highly regenerative community develops in the platelet ice layer. Concentrations of ammonium far in excess of that in the water column indicate that this nutrient is regenerated in the platelet layer throughout the season, although some depletion is evident early on, presumably due to algal uptake at the top of the platelet layer. In the latter half of the season, however, regenerative ammonium production appears to exceed ammonium uptake even in the upper layers of the platelet ice as concentrations there increase relative to the layers below. A parallel regeneration of phosphate in excess of uptake and concentrations in the platelet layer below is apparent only toward the end of the season and may represent the first signs of a declining algal community. However, the fact that there is not always a concomitant increase of phosphate with an

increase in ammonium earlier in the season has yet to be explained. The high ammonium concentrations observed in the absence of high chl *a* concentrations (Fig. 5) are difficult to explain, and we have not succeeded in clarifying an enigma which has baffled several authors, i.e. explaining the exceptionally high ammonium concentrations often associated with sea ice (Oradovskiy 1974, Garrison et al. 1990, Dieckmann unpubl.). The likely cause of high ammonium concentrations is the activity of microheterotrophs and larger metazoan grazers, such as krill, copepods, and amphipods which are occasionally associated with platelet ice. Alternatively, Oradovskiy (1974) proposed that physical processes associated with ice formation such as snow precipitation and diffusion from the water could lead to ammonium enrichment within sea ice. We do not consider this a valid explanation for the platelet layer, since ammonium concentrations in the congelation ice meltwater above it are less than in the platelet layer (C. Sullivan, unpubl. obs.).

We have no direct measurements of nutrient or seawater exchange rates between the platelet layer and underlying water column. However, on the grounds that there is very little depletion of nutrients in the platelet layer, despite an exceptionally high algal biomass, we assume that an adequate exchange exists. This means that since ammonium is able to accumulate relative to the water column it must be regenerated within the platelet layer at a rate which exceeds the dilution rate expected from a continuous or tidally pulsed replenishment of seawater from below the platelet layer. A difference between our observations and those of Smetacek et al. (1992) may lie in the fact that the interstitial water in the platelet layer of drifting pack ice is stagnant, because pack ice follows water movements and so can be regarded as a parcel floating with the currents. Under fast ice, however, the platelet layer is stationary relative to water movement such as tidal currents; this is expected to create shear and cause turbulence, which increases the rates of eddy diffusion across the ice/water boundary. Alternatively, the physical arrangement of platelets may differ between the alternative processes of platelet layer formation under sea ice, i.e. platelets may either drift up under the ice and form loose aggregations or may grow *in situ* into a more rigid layer. Finally, it may be a question of the depth of the platelet ice layer, as indicated by Arrigo, Robinson and Sullivan (unpubl.), who found that a platelet layer 0.65 m in thickness permits a greater rate of water exchange than one of 1 m thickness.

It is interesting to note that in the upper platelet layer, nitrate is slightly depleted in the presence of high ammonium concentrations. This is contrary to findings that nitrate uptake by phytoplankton is inhibi-

ted when ambient ammonium concentrations exceed a threshold level of 0.5 to 1 mg-at. N m⁻³ (Eppley et al. 1969, MacIsaac & Dugdale 1969, Olson 1980). It agrees very well, however, with reports that oyster pond algae, a group of diatom species which inhabit an environment similarly high in ammonium and nitrate, have higher ammonium threshold levels than similar pelagic species, so that alternative N sources may be assimilated when ammonium is high (Collos et al. 1989). Also, Harrison et al. (1990) found that sea ice algal communities in Barrow Strait, Canada, utilized ammonium preferentially to other nitrogen sources, but since ammonium did not inhibit nitrate reductase activity, parallel uptake of nitrate was possible. The interaction between ammonium uptake and nitrate uptake is thus still unclear, and since it is evidently affected by several factors such as low light levels and species composition (Dortsch 1990), it is difficult to advance an explanation at this stage. However, algae in the ice platelet habitat may in fact have a fundamentally different nitrogen metabolism than phytoplankton and therefore are worthy of further study.

CONCLUSIONS

Similarly to observations made previously for congelation ice, steep gradients of macronutrients, rapid light attenuation due to high concentrations of algal pigments and highly non-uniform distributions of chl *a* characterize the stratified yet dynamic nature of the very productive platelet ice habitat. In contrast to congelation ice, salinity and temperature remain relatively constant throughout this environment. Moreover, the platelet ice layer acts as an interface between the congelation ice and the water column, and appears to have the characteristics necessary for optimal algal growth and accumulation. These include constant temperature and salinity, high structural stability resulting in a large surface area for algal attachment, and high nutrient concentrations due to an obviously adequate seawater exchange and yet a relatively more stable physical environment in the interstitial water of the platelet layer as compared to the water column. Smetacek et al. (1992) attributed the stability of the interstitial water within the platelet layer observed under pack ice to a salinity gradient, which was due to melting and which in turn resulted in the manifestation of a strong nutrient gradient. Clearly a different mechanism, presumably one driven by biological features, is operative in the present study of platelet ice in McMurdo Sound.

With our newly acquired ability to adequately sample this environment, the platelet ice appears to be an ideal habitat for studying microbial processes *in*

situ. In previous studies this habitat has been represented by individual bulk measurements (Palmisano & Sullivan 1985b, Palmisano et al. 1985a, b, Grossi et al. 1987, Palmisano et al. 1987a, b, SooHoo et al. 1987) which may not always have accurately reflected conditions *in situ*. Certainly, prior to profiling with ADONIS there was no indication of the high degree of stratification present within this important and conspicuous sea ice environment.

The high production or regeneration of ammonium within the platelet layer is still enigmatic, and we anticipate a clearer understanding of the system following our evaluation of nitrogen uptake and regeneration experiments as well as data on elemental composition of the microbial community. However, preliminary microscopic analyses of the platelet ice community did not reveal extraordinarily high numbers of bacteria and other microheterotrophs. Zooplankton too were almost entirely absent from samples collected by bucket or nets and therefore cannot be considered a likely source of the high ammonium concentrations.

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LITERATURE CITED

- Arrigo, K. R., Sullivan, C. W., Kremer, J. N. (1991). A bio-optical model of Antarctic sea ice. *J. geophys. Res.* 96: 10581–10592
- Barry, J. P. (1988). Hydrographic patterns in McMurdo Sound, Antarctica and their relationship to local benthic communities. *Polar Biol.* 8: 377–391
- Bunt, J. S. (1968). Microalgae of the Antarctic pack ice zone. In: Currie, R. I. (ed.) *Antarctic oceanography*. Scott Polar Res Inst., Cambridge, p. 198–218
- Bunt, J. S., Lee, C. C. (1970). Seasonal primary production in Antarctic sea ice at McMurdo Sound in 1967. *J. mar. Res.* 28: 204–220
- Collos, Y., Maestrini, S. Y., Robert, J.-M. (1989). High long-term nitrate uptake by oyster-pond microalgae in the presence of high ammonium concentrations. *Limnol. Oceanogr.* 34: 957–964
- Conover, R. J., Herman, A. W., Prinsenberg, S. J., Harris, L. R. (1986). Distribution of and feeding by the copepod *Pseudocalanus* under fast ice during the Arctic spring. *Science* 232: 1245–1247
- Cota, G. F., Sullivan, C. W. (1990). Photoadaptation, growth and production of bottom ice algae in the Antarctic. *J. Phycol.* 26: 399–411
- Dayton, P. K., Robilliard, G. A., DeVries, A. L. (1969). Anchor ice formation in McMurdo Sound, Antarctica, and its biological effects. *Science* 163: 273–274
- Dieckmann, G. S., Lange, M. A., Ackley, S. F., Jennings, J. C. Jr (1991). The nutrient status in sea ice of the Weddell Sea during winter: effects of sea ice texture and algae. *Polar Biol.* 11: 449–456
- Dieckmann, G. S., Rohardt, G., Hellmer, H., Kipfstuhl, J. (1986). The occurrence of ice platelets at 250 m depth near Filchner Ice Shelf and its significance for sea ice biology. *Deep Sea Res.* 33: 141–148
- Dortsch, Q. (1990). The interaction between ammonium and nitrate uptake in phytoplankton. *Mar. Ecol. Prog. Ser.* 61: 183–201
- Engelhardt, H., Determann, J. (1987). Borehole evidence for a thick layer of basal ice in the central Ronne Ice Shelf. *Nature, Lond.* 327: 318–319
- Eppley, R. W., Coatsworth, J. L., Solarzano, L. (1969). Studies on nitrate reductase in marine phytoplankton. *Limnol. Oceanogr.* 14: 194–205
- Foldvik, A., Kvinge, T. (1974). Conditional instability of sea water at the freezing point. *Deep Sea Res.* 21: 169–174
- Garrison, D. L., Buck, K. R. (1986). Organism losses during ice melting: a serious bias in sea ice community studies. *Polar Biol.* 6: 237–239
- Garrison, D. L., Close, A. R., Gordon, L. I. (1990). Nutrient concentrations in Antarctic pack ice during winter. In: Ackley, S. F., Weeks, W. F. (eds.) *Sea ice properties and processes*. Proceedings of the W. F. Weeks Sea Ice Symposium, CRREL Monograph 90-1, American Society for Testing and Materials, Philadelphia, p. 35–40
- Garrison, D. L., Sullivan, C. W., Ackley, S. F. (1986). Sea ice microbial communities in Antarctica. *BioSci.* 36 (4): 243–250
- Grossi, S. M., Kottmeier, S. T., Moe, R. L., Taylor, G. T., Sullivan, C. W. (1987). Sea ice microbial communities. VI. Growth and production in bottom ice under graded snow cover. *Mar. Ecol. Prog. Ser.* 35: 153–164
- Harrison, W. G., Cota, G. F., Smith, R. E. H. (1990). Nitrogen utilization in ice algal communities of Barrow Strait, Northwest Territories, Canada. *Mar. Ecol. Prog. Ser.* 67: 275–283
- Iturriaga, R., Sullivan, C. W. (1989). Spectral light absorption characteristics of individual sea ice microalgae from McMurdo Sound, Antarctica. *Antarctic J. U.S.* 24: 188–190
- Jacques, G. (1983). Some ecophysiological aspects of the Antarctic phytoplankton. *Polar Biol.* 2: 27–33
- Kipfstuhl, J. (1991). Zur Entstehung von Unterwassereis und das Wachstum und die Energiebilanz des Meereises in der Atka Bucht, Antarktis. *Ber. Polarforsch.* 85: 89
- MacIsaac, J. J., Dugdale, R. C. (1969). The kinetics of nitrate and ammonia uptake by natural populations of marine phytoplankton. *Deep Sea Res.* 16: 45–57
- Moretskiy, V. N. (1965). Underwater sea ice. *Problemy Arkt. Antarkt.* 19: 32–38 (translated by D.R.B. Canada. Report No. T497R, April 1968)
- Olson, R. J. (1980). Nitrate and ammonium uptake in Antarctic waters. *Limnol. Oceanogr.* 25: 1064–1074
- Oradovskiy, S. G. (1974). Investigations of the chemical composition of Antarctic sea ice. *Oceanology (Moscow)* 14: 50–54 (English translation)
- Palmisano, A. C., Beeler SooHoo, J., Moe, R. L., Sullivan, C. W. (1987a). Sea ice microbial communities VII. Changes in under-ice spectral irradiance during the development of Antarctic sea ice microalgal communities. *Mar. Ecol. Prog. Ser.* 35: 165–173
- Palmisano, A. C., Beeler SooHoo, J., Sullivan, C. W. (1985a). Photosynthesis-irradiance relationships in sea ice microalgae from McMurdo Sound, Antarctica. *J. Phycol.* 21: 341–346

- Palmisano, A. C., Beeler SooHoo, J., Sullivan, C. W. (1987b). Effects of four environmental variables on photosynthesis-irradiance relationships in Antarctic sea-ice microalgae. *Mar. Biol.* 94: 299–306
- Palmisano, A. C., Kottmeier, S. T., Moe, R. L., Sullivan, C. W. (1985b). Sea ice microbial communities. IV. The effect of light perturbation on microalgae at the ice-seawater interface in McMurdo Sound, Antarctica. *Mar. Ecol. Prog. Ser.* 21: 37–45
- Palmisano, A. C., Sullivan, C. W. (1985a). Pathways of photosynthetic carbon assimilation in sea-ice microalgae from McMurdo Sound, Antarctica. *Limnol. Oceanogr.* 30: 674–678
- Palmisano, A. C., Sullivan, C. W. (1985b). Physiological response of micro-algae in the ice-platelet layer to low-light conditions. In: Siegfried, W. R., Condy, P. R., Laws, R. M. (eds.) *Antarctic nutrient cycles and food webs*. Springer-Verlag, Berlin, p. 84–88
- Parsons, T. R., Miata, Y., Lalli, C. M. (1984). *A manual of chemical and biological methods for sea water analysis*. Pergamon Press, New York
- Sakshaug, E., Skjoldal, H. R. (1989). Life at the ice edge. *Ambio* 18(1): 60–67
- SooHoo, J., Palmisano, A. C., Kottmeier, S. T., Lizotte, M. P., SooHoo, S. L., Sullivan, C. W. (1987). Spectral light absorption and quantum yield of photosynthesis of sea ice micro-algae and a bloom of *Phaeocystis pouchetii* from McMurdo Sound, Antarctica. *Mar. Ecol. Prog. Ser.* 39: 175–189
- Smetacek, V., Scharek, R., Gordon, L. I., Eicken, H., Fahrback, E., Rohardt, G., Moore, S. (1992). Early spring phytoplankton blooms in ice platelet layers of the southern Weddell Sea, Antarctica. *Deep Sea Res.* 39 (in press)
- Smith, R. E. H., Harrison, W. G., Harris, L. R., Herman, A. W. (1990). Vertical fine structure of particulate matter and nutrients in sea ice of the high Arctic. *Can. J. Fish. Aquat. Sci.* 47: 1348–1355
- Stretch, J. J., Hamner, P. P., Hamner, W. M., Michel, W. C., Cook, J., Sullivan, C. W. (1988). Foraging behaviour of Antarctic krill *Euphausia superba* on sea ice microalgae. *Mar. Ecol. Prog. Ser.* 39: 175–189
- Sullivan, C. W., Palmisano, A. C. (1984). Sea ice microbial communities: distribution, abundance, and diversity of ice bacteria in McMurdo Sound, Antarctica, in 1980. *Appl. environ. Microbiol.* 47: 788–795

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