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Comparison of the irradiance response of photosynthesis and nitrogen uptake by sea ice microalgae

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ABSTRACT: The response of photosynthesis, and of the uptake of NO_3^-, NH_4^+ and serine, to irradiance was measured in diatom-dominated sea ice microbial assemblages from bottom ice and surface ice of McMurdo Sound, Antarctica. Uptake responses for dissolved inorganic nitrogen (DIN; NO_3^- and NH_4^+) could be fitted to a standard model used for photosynthesis after the addition of a dark uptake parameter; serine uptake showed no dependence on irradiance. The derived uptake models were used to predict the patterns of photosynthesis and DIN uptake over diel irradiance cycles. According to model predictions, uptake rates in the bottom ice assemblage were always limited by irradiance; neither light saturation nor photoinhibition regulated photosynthesis or DIN utilization in this assemblage. Conversely, photosynthesis in the surface ice assemblage was nearly always light-saturated, whereas DIN uptake was photo-inhibited near midday and saturated at the minimum irradiance. Integrated daily C:DIN uptake ratios (g:g) in the bottom ice and surface ice assemblages were 8.6 and 9.7, respectively, corresponding to particulate C:N ratios (g:g) of 8.1 and 5.8 for these respective diatom-dominated communities. Our results indicate that information on diel patterns of photosynthesis and N uptake is required to evaluate accurately the stoichiometric balance of essential elements in sea ice microalgae.

INTRODUCTION

Antarctic sea ice microalgae live in a variety of habitats ranging from surface melt pools, infiltration layers and tide cracks to bottom platelet and congelation ice (see Horner 1985 and Garrison et al. 1986 for reviews). Organisms living in these disparate environments during the austral spring, summer and fall experience drastically different irradiances ranging from full sunlight (ca 1500 μmol quanta m^{-2} s^{-1}) in the surface communities to less than 10 μmol quanta m^{-2} s^{-1} in the bottom ice. Superimposed on these irradiance differences is the episodic regime typical of high latitude systems, i.e. continuous sunlight in the summer and continuous darkness in the winter.

Owing to the unique irradiance regime experienced by sea ice microalgae, numerous studies have addressed photosynthesis-irradiance (*P–I*) relationships in natural assemblages of microalgae from McMurdo Sound, Antarctica (e.g. Bunt 1964, Palmisano et al. 1985, Rivkin & Putt 1987a, b, Cota & Sullivan 1990). Most of the detailed investigations have concentrated on microalgae living in bottom-ice because of the high biomass levels they attain (Bunt & Lee 1970, Palmisano & Sullivan 1983) despite persistent low irradiance. No detailed comparisons of *P–I* relationships have been made between surface ice microalgae and bottom ice microalgae in Antarctic sea ice.

The uptake and assimilation of most nutrients by photoautotrophic microalgae is ultimately dependent on light as an energy source (Syrett 1981). Nutrient utilization can be considered a second order metabolic process with respect to irradiance, a relationship which lacks simple biochemical mechanisms (Miflin & Lea 1979, Syrett 1981). Unfortunately, few field studies have compared *P–I* characteristics with irradiance-dependent nutrient uptake by microalgae, despite its apparent ecological importance. Priscu (1984), working

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in a temperate-subalpine lake, showed that deep-living (low light) microbial populations could utilize dissolved inorganic nitrogen (DIN) compounds at lower irradiance levels than surface (high light) populations, allowing the former to fulfill their nitrogen requirements at low ambient irradiance. Priscu also showed that NO_3^- and NH_4^+ uptake in the dark was about 50 % of uptake at saturating irradiance levels, which would allow these assemblages to continue DIN uptake when photosynthesis ceased. Whalen & Alexander (1984) measured photosynthesis and the uptake of DIN under continuous but variable irradiance in an arctic lake; photosynthesis was found to track the irradiance pattern more closely than did the uptake of NO_3^- or NH_4^+. Whalen & Alexander's findings support those of Priscu (1984) indicating that the microalgae can take up DIN during the night when photosynthetic carbon uptake is negligible. A recent study by Dodds & Priscu (1989) showed that the irradiance dependence of both photosynthesis and nutrient uptake must be known for an understanding of cellular biochemical balance and, consequently, growth. Because of the extreme annual variation in irradiance at high latitudes, it seems particularly important to know the irradiance dependence of nutrient uptake and photosynthesis. This would provide essential information on the physiological state and ultimately the growth of microalgae in polar environments.

We used ^{15}N labeled compounds to measure uptake rates of NO_3^-, NH_4^+ and serine as a function of irradiance for algal assemblages from a surface tide crack and bottom congelation ice in McMurdo Sound, Antarctica. The irradiance dependence of uptake of these nitrogenous compounds was compared to photosynthesis-irradiance relationships and modeled over a diel irradiance pattern to simulate diel oscillations in C:N uptake ratios. The relative rates of C:N uptake were evaluated in terms of the particulate carbon (PC) and particulate nitrogen (PN) of these algal assemblages to test the idea that the cells were in balanced growth.

METHODS

Sample collection. Bottom ice microalgae were collected in Erebus Bay, McMurdo Sound (see Fig. 1 of Priscu et al. 1990) on 16 December 1985. Samples were collected by removing the lower 10 to 20 cm from cores (ca 1.8 m long) obtained with a SIPRE coring device. This bottom layer of congelation ice typically contains more than 95 % of the microalgal biomass in McMurdo Sound sea ice (Palmisano & Sullivan 1983). Surface ice microalgae were collected on 14 December 1985 by gently scraping ice from an overflow region near a coastal tide crack in Wohlschlag Bay, McMurdo Sound. This surface assemblage, located in sea ice immediately above the seawater level, was exposed to direct sunlight in situ (see Whitaker & Richardson 1980 for details of this type of surface ice habitat). Samples of bottom ice and surface ice were placed in 4 l polyethylene carboys containing filtered (Whatman GF/C) seawater (FSW) for transport in darkness and near −1.9 °C (the ice did not melt appreciably) to the McMurdo Station laboratory. The microalgae contained in ice cores and ice collected from the tide crack were released by slow melting at 0.5 °C and an irradiance level of about 40 µmol quanta m^{-2} s^{-1}. Additional FSW was added if necessary to maintain the salinity between 30 and 34 ppt, thus avoiding osmotic stress. These cell suspensions were used for all experiments.

Chemical analyses. A 10 ml subsample of the cell suspension was collected before each incubation for determination of NH_4^+ (Solorzano 1969), NO_3^- (Parsons et al. 1984), phaeophytin-corrected chlorophyll *a* (Holm-Hansen et al. 1965) and particulate C and N (Carlo-Erba model 1106 elemental analyzer). Particulate material was collected on precombusted Whatman GF/C filters; inorganic nitrogen chemistry was determined on the filtrate which had been stored frozen before analysis.

Rate measurements. Irradiance dependence of nitrogen uptake was determined with a photosynthetron (Lewis & Smith 1983) using 10 ml cell suspensions in acid-cleaned scintillation vials. ^{15}N (99 atom-%) labeled NO_3^-, NH_4^+ or serine was added to each suspension to a final concentration of 28.6 µg-at. N l^{-1}. A separate series of experiments (Priscu unpubl.) showed that this concentration would saturate uptake for all compounds tested. Because the microalgae live in brine channels within the ice, the exact in situ concentrations of these nitrogen forms within ice microenvironments remains unknown. However, because McMurdo Sound seawater contains high levels of inorganic nitrogen which can infiltrate brine channels within the ice, we assume that the microalgae are exposed to near-saturating levels of NO_3^- and NH_4^+ in their ambient microenvironment. Intracellular NO_3^- and NH_4^+ pools were also found to be high (order of mM; J. C. Priscu unpubl.) corroborating our contention of high inorganic N levels in situ. Hence, our $^{15}NO_3^-$ and $^{15}NH_4^+$ enrichments should not influence significantly the biological uptake rates. However, serine concentrations in bottom congelation ice are generally less than 1.0 µM (Manahan & Sullivan unpubl.), a level below the half-saturation constants for uptake (K_s = ca 3.5 µM; Priscu unpubl.). Therefore, our serine uptake rates in bottom ice assemblages, measured at 28.6 µM enrichment, overestimate in situ uptake rates. No information exists on serine levels in surface ice assemblages.

Following 11 to 16 h incubations at −1.9 °C (seawater temperature), the cell suspensions were filtered onto precombusted Whatman GF/C filters and rinsed with artificial seawater lacking DIN. The filters were air-dried at room temperature and stored frozen until analysis. The ^{15}N content of the microalgae was determined by emission spectrometry following Dumas combustion (Timperly & Priscu 1986). Uptake rates were computed according to the equations of Neess et al. (1962) and Dugdale & Goering (1967) using particulate N (PN), NO_3^- and NH_4^+ levels measured at the beginning of the experiment. An ambient serine concentration of 0.4 nM was assumed in the rate calculations for this compound. Corrections were not made for isotopic dilution during the incubation (e.g. Glibert et al. 1982). Such a correction would probably be negligible given the large amount of ^{15}N added to each experimental vessel. Time-course measurements showed that uptake of both NO_3^- and NH_4^+ was linear over the time period and DIN concentrations used in these experiments.

Photosynthesis-irradiance relationships were determined with a photosynthetron using ^{14}C-HCO_3^- on 2 ml cell suspensions as described by Palmisano et al. (1985). Biological activity was terminated by acidification with 2N HCl following 1 to 2 h incubations at −1.9 °C. The samples were dried, scintillation cocktail was added and ^{14}C activity was determined by standard liquid scintillation spectrometry. Dissolved inorganic carbon concentration was derived from alkalinity titrations (Parsons et al. 1984). Self-shading was not a problem at the chlorophyll *a* concentrations used in our experiments (Bates & Cota 1986).

Inhibitor experiments. Replicate (5) 10 ml subsamples of sample from the surface and bottom ice microbial assemblages were inoculated with 3-(3,4-dichlorophenyl)-1,1-dimethyl-urea (DCMU), a specific inhibitor of non-cyclic photophosphorylation, at a final concentration of 10^{-5} M and the samples were incubated for 24 h at 40 µmol quanta m^{-2} s^{-1} and −1.9 °C along with unamended control samples; a second set of unamended samples was incubated in the dark for the same period. Legendre et al. (1983) have shown that DCMU effectively inhibits photosynthesis in marine microalgae. All samples were inoculated with 28.6 µM $^{15}NH_4^+$ or $^{15}NO_3^-$ at the beginning of the experiment. Incubation was terminated by filtration and the ^{15}N enrichment of the concentrated microalgae was determined as described above.

Irradiance response models. The response of C uptake as a function of irradiance was modeled by the equation of Platt et al. (1980):

$$P^B = P_s^B (1 - e^{-a}) e^{-b} \quad (1)$$

where P^B = photosynthetic rate per unit chlorophyll (mg C mg chl^{-1} h^{-1}); P_s^B = light-saturated photosynthesis in the absence of photoinhibition (i.e. $\beta = 0$) (same units as P^B); $a = I/P_s^B$ where α = slope of the initial light-limited portion of the curve [(mg C mg chl^{-1} h^{-1})/(µmol quanta m^{-2} s^{-1})]; I = irradiance (µmol quanta m^{-2} s^{-1}); $b = \beta/P_s^B$, where β = slope of the curve showing light inhibition (same units as α). Platt et al. (1980) also discuss several derived parameters which can be used to characterize the *P–I* relationship:

$$P_m^B = P_s^B (\alpha/\alpha + \beta) (\beta/\alpha + \beta)^{\beta/\alpha} \quad (2)$$

where P_m^B = chlorophyll-specific rate at optimal irradiance. It has the same units as P_s^B;

$$I_k = P_m^B/\alpha \quad (3)$$

where I_k = irradiance level where extrapolations of α and P_m^B intersect;

$$I_s = P_s^B/\alpha \quad (4)$$

where I_s = a parameter similar to I_k which is based on P_s^B rather than P_m^B;

$$I_b = P_s^B/\beta \quad (5)$$

where irradiance level I_b = an index of photoinhibition; and

$$I_m = (P_s^B/\alpha) \ln((\alpha + \beta)/\beta) \quad (6)$$

where I_m = irradiance at which maximum uptake occurs.

Eqs. (1) to (6) were also used to model nitrogen uptake. It should be noted that many of the parameters used in these equations do not directly relate to nitrogen uptake. For example, α implies chloroplast activity and is proportional to the quantum yield of photosynthesis. Because nitrogen is a second order process with respect to irradiance (i.e. some of the immediate energy may come from intermediary metabolism; Priscu 1984), the exact meaning of α for DIN uptake is obscured. With these reservations, we use the model and derived parameters in a comparative sense only. To avoid undue introduction of symbols, we applied the symbols used to describe *P–I* characteristics to nitrogen uptake.

Visual inspection of the N uptake curves indicated a significant dark uptake component. Consequently, a dark uptake parameter (D^B = chlorophyll-specific dark uptake; *y*-intercept) was added to the right hand side of Eqs. (1) and (2) (see Priscu 1989). Eq. (1) was fitted using Marquardt's algorithm. The addition of D^B in Eq. (1) requires that the predicted D^B value be added to the predicted P_s^B to obtain the true value of P_s^B.

All of the rates used in these models were normalized to chlorophyll *a* concentration at the beginning of the experiment because chlorophyll *a* is the primary compound which absorbs the photons required for photosynthesis and because most published *P–I* parameters

Table 1. Parameters characterizing the irradiance response of photosynthesis, and uptake of NO_3^-, NH_4^+ and serine by microbial assemblages from bottom ice and surface ice in McMurdo Sound, Antarctica. Row headings denote photosynthesis ($^{14}CO_2$), and the uptake of $^{15}NO_3^-$, $^{15}NH_4^+$ and ^{15}N-serine, respectively. UD: mathematically undefined; —: parameters could not be generated with the models used. Units for all parameters are given in 'Methods'

	P_s^B ($\times 10^{-3}$)	α ($\times 10^{-3}$)	β ($\times 10^{-5}$)	D^B ($\times 10^{-3}$)	P_m^B ($\times 10^{-3}$)	I_k	I_s	I_b	I_m
Bottom ice microalgae									
$^{14}CO_2$	310.0	20.0	57.0	0.0	270.0	13.4	15.3	535	55.0
$^{15}NO_3^-$	3.4	0.2	0.7	0.8	2.9	18.0	21.8	473	68.1
$^{15}NH_4^+$	4.1	0.1	1.8	1.4	2.8	19.7	29.3	229	63.6
^{15}N-serine	—	—	—	1.2	1.2	—	—	—	—
Surface ice microalgae									
$^{14}CO_2$	419.0	10.4	0.0	0.0	419.0	40.0	40.0	UD	UD
$^{15}NO_3^-$	29.6	2.5	1.5	0.7	28.5	11.5	11.9	2,000	61.2
$^{15}NH_4^+$	16.8	0.7	0.7	8.6	16.0	22.4	23.5	2,560	110.0
^{15}N-serine	—	—	—	14.3	14.3	—	—	—	—

are given in terms of chlorophyll *a*. We chose to express all of our nitrogen uptake rates on a mass (rather than molar) basis to facilitate comparison with the large body of published material on *P–I* relationships in other systems.

Photosynthetically available radiation (PAR) incident at the surface was measured on 10 December 1989 with a LI–COR 192 quantum sensor coupled with a LI–COR LI–1000 data logger. The detector was located in the Taylor Valley at Lake Bonney, about 80 km from the sea ice sampling sites. Under-ice PAR was measured with a Biospherical Instruments MER–1000 spectroradiometer beneath ca 1.8 m of sea ice near Cape Armitage, McMurdo Sound (about 10 km from the sampling site) on 4 December 1984. Under-ice PAR between 04:00 and 12:00 h was smoothed to eliminate variability associated with intermittent cloud cover during this period.

RESULTS

More than 99% of the algal biomass in the surface ice assemblage used in our experiments was comprised of the pennate diatom *Navicula glaciei* van Huerck. The bottom ice assemblage was dominated by the pennate diatoms *Nitzschia stellata* Manguin and *Amphiprora* spp. Past studies on McMurdo Sound sea ice have shown that this latter assemblage receives less than 10% of incident PAR (Palmisano et al. 1987). The particulate C:N (PC:PN) ratios (g:g) for the surface and bottom ice communities at the time of the experiments were 5.8 and 8.1, respectively.

Photosynthesis-irradiance characteristics in the bottom ice assemblage showed evidence of shade adaptation relative to the surface assemblage (Table 1). Perhaps the strongest indication was the much lower I_k value for the bottom ice assemblage. In addition, β and I_b for the bottom ice assemblage were 57.0×10^{-5} [(mg C mg chl^{-1} h^{-1})/(µmol quanta m^{-2} s^{-1})] and 535 µmol quanta m^{-2} s^{-1}, respectively, while the surface ice assemblage exhibited no photoinhibition of photosynthesis at irradiance reaching 900 µmol quanta m^{-2} s^{-1}.

Bottom ice and surface ice algal communities showed similar dissolved inorganic nitrogen (DIN) uptake responses to irradiance and, after the addition of a term for dark uptake, could be fitted by the Platt et al. (1980) model for photosynthesis (Figs. 1 & 2). The parameters derived from this model (Table 1) indicate that DIN uptake by the bottom ice assemblage was adapted to lower irradiances relative to the surface ice assemblage; i.e. lower P_s^B, P_m^B and I_b values for DIN were exhibited by the bottom ice algae.

No clear trends were evident in β, the slope of the light-inhibited portion of the DIN uptake curves. However, because β is scaled by P_s^B, β is not as consistent an index of photoinhibition as I_b (Platt et al. 1980). I_b values for NO_3^- and NH_4^+ uptake by the bottom ice assemblage were 4 and 11 times lower than that derived for the surface ice algae indicating stronger photoinhibition of DIN uptake in the bottom ice algae.

The major difference between DIN uptake and photosynthesis occurred in D^B, the dark uptake parameter. Dark uptake of NH_4^+ was about 50% of P_m^B in both communities whereas it ranged from 28% of P_m^B for NO_3^- uptake in the bottom ice assemblage to 2.4% of P_m^B for NO_3^- uptake in the surface ice assemblage. Carbon fixation was always negligible in the dark.

Differences in P_s^B, P_m^B and α between photosynthesis and DIN uptake reflect, to varying degrees, the stoichiometric requirements for C and N by microalgae. Serine uptake showed no light dependence over the range of irradiance levels used in our experiments. Maximum rates of serine uptake in the surface ice

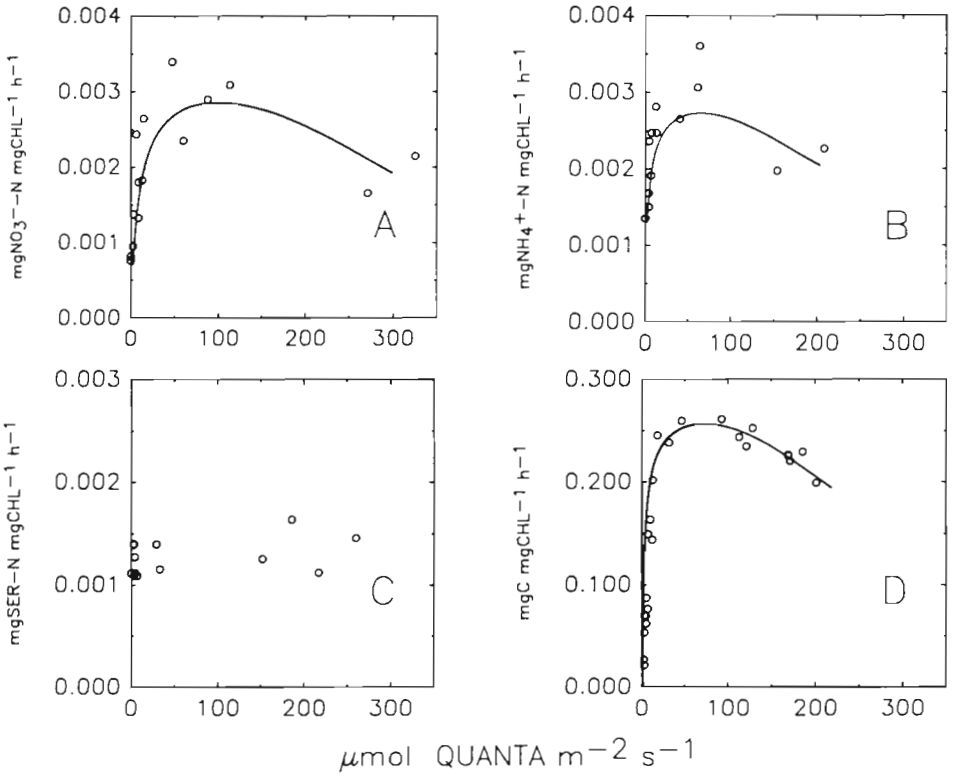

Fig. 1. Uptake of (A) NO_3^-, (B) NH_4^+, (C) serine and (D) inorganic carbon (photosynthesis) by a bottom ice microbial assemblage in response to irradiance

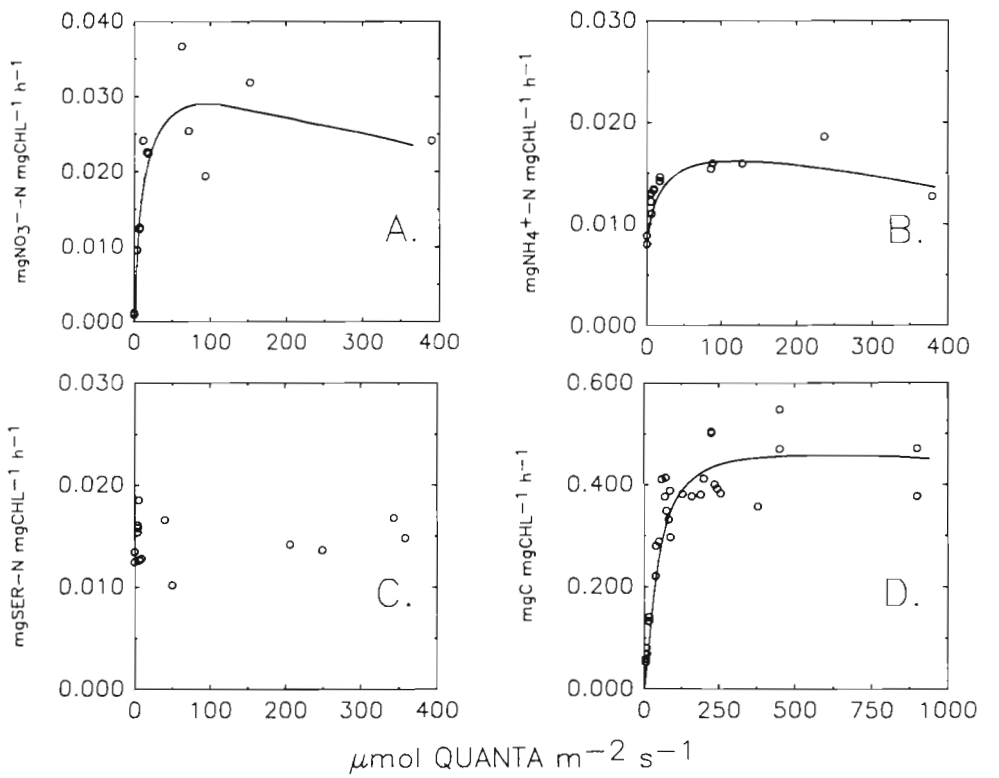

Fig. 2. Uptake of (A) NO_3^-, (B) NH_4^+, (C) serine and (D) inorganic carbon (photosynthesis) by a surface ice microbial assemblage in response to irradiance

assemblage were more than 10 times those in the bottom ice assemblage.

Experiments on a surface ice assemblage dominated by *Navicula glaciei* and a bottom ice assemblage dominated by *Nitzschia stellata* and *Amphiprora* sp. showed that the addition of DCMU usually reduced DIN uptake to the level of dark uptake (Table 2). An exception occurred in the surface ice assemblage where NO_3^- uptake was 40 % higher in the presence of DCMU than in the dark.

A recording of surface irradiance for a mid-December day with little cloud cover shows a diel oscillation ranging from about 100 μmol quanta m^{-2} s^{-1} between local midnight and 02:00 h to about 1300 μmol quanta m^{-2} s^{-1} near local noon (Fig. 3A). A similar oscillation in under-ice irradiance ranged from about 0.4 to 2.1 μmol quanta m^{-2} s^{-1} (Fig. 3B). Photosynthesis and DIN uptake parameters (Table 1) were used together with these diel irradiance profiles to model daily patterns in inorganic C and DIN uptake rates. Uptake rates for inorganic C, NO_3^- and NH_4^+ in the bottom ice algae were all maximal when irradiance was highest (Fig. 4B). Despite low light adaptation by this bottom-ice assemblage, the maximum daily rates predicted for photosynthesis, NO_3^- uptake and NH_4^+ uptake reached only about 14, 41, and 60 %, respectively, of P_m^B. Hence, inorganic C and DIN utilization would be limited by irradiance over the entire day and neither light-saturation nor photoinhibition would play a role in regulating inorganic C or DIN uptake in this assemblage.

The modeled pattern of daily photosynthesis and DIN uptake in the surface ice assemblage (Fig. 4B) was different from that in the bottom ice assemblage. Photosynthesis occurred at the maximum rate (i.e. P_m^B) for most of the day (from 04:00 to 23:00 h) and only dropped by about 10 % of P_m^B during the period of lowest irradiance. The lowest irradiance measured (ca 93 μmol quanta m^{-2} s^{-1}) was more than twice the I_k value for photosynthesis (40 μmol quanta m^{-2} s^{-1}). The highest irradiance used in the model was 1364 μmol quanta m^{-2} s^{-1} which exceeded the highest irradiance used in the photosynthesis-irradiance (*P–I*) experiment (900 μmol quanta m^{-2} s^{-1}). We caution that modeled rates in the regions above 900 μmol quanta m^{-2} s^{-1} are based on the assumption that photoinhibition does not occur between 900 and 1364 μmol quanta m^{-2} s^{-1}.

Modeled daily uptake of NO_3^- and NH_4^+ by the surface assemblage was maximal at the lowest daily irradiance, a pattern opposite that shown for photosynthesis in either ice assemblage or for DIN uptake in the bottom congelation ice assemblage. The predicted uptake patterns for both NO_3^- and NH_4^+ are almost entirely a function of photoinhibition of DIN uptake; only the irradiance between 24:00 and 02:00 h is below inhibitory levels. DIN uptake would operate at maximum levels between local midnight and 02:00 h, never dropping to light-limited rates.

The physiological consequences of daily inorganic C and DIN uptake patterns can be expressed as C:N uptake ratios. These ratios varied considerably over a diel cycle in the bottom ice assemblage with estimates of C:NO_3^-, C:NH_4^+ and C:DIN (g:g) ranging from 8.4 to 32.6, 5.1 to 23.2 and 3.2 to 13.6, respectively. The

Table 2. Influence of 10^{-5} M DCMU and dark incubation on uptake of NO_3^- and NH_4^+ in microbial assemblages from bottom ice and surface ice. Mean (± SD) is given for each treatment. Uptake rates have been normalized to particulate N concentration

Sample	Nitrogen uptake (h^{-1} $\times 10^{-4}$) (mean ± SD)		
	Control	DCMU	Dark
Bottom ice			
NH_4^+ uptake	11.40 (1.54)	2.73 (0.86)	1.34 (0.40)
NO_3^- uptake	5.38 (0.61)	2.52 (0.73)	2.61 (0.85)
Surface ice			
NH_4^+ uptake	49.08 (2.47)	28.97 (0.71)	27.77 (0.76)
NO_3^- uptake	47.36 (1.46)	17.36 (1.59)	10.35 (1.52)

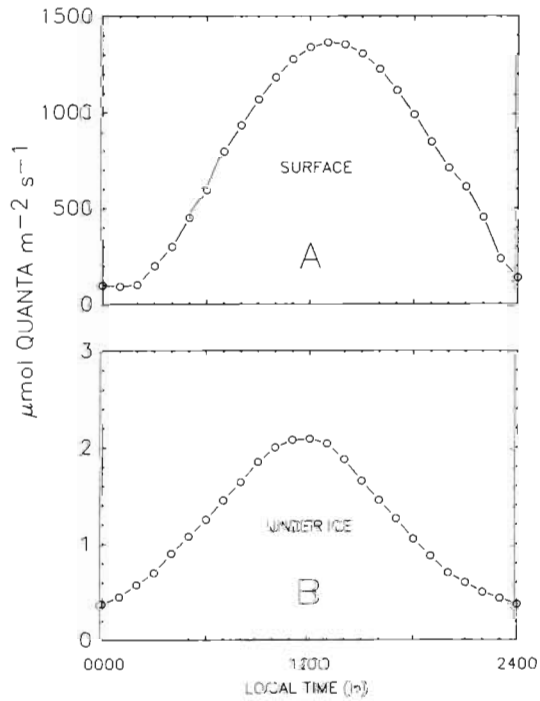

Fig. 3. Daily oscillation in (A) surface irradiance measured on 10 December 1989, and (B) under-ice irradiance measured on 4 December 1984 in the McMurdo sound area

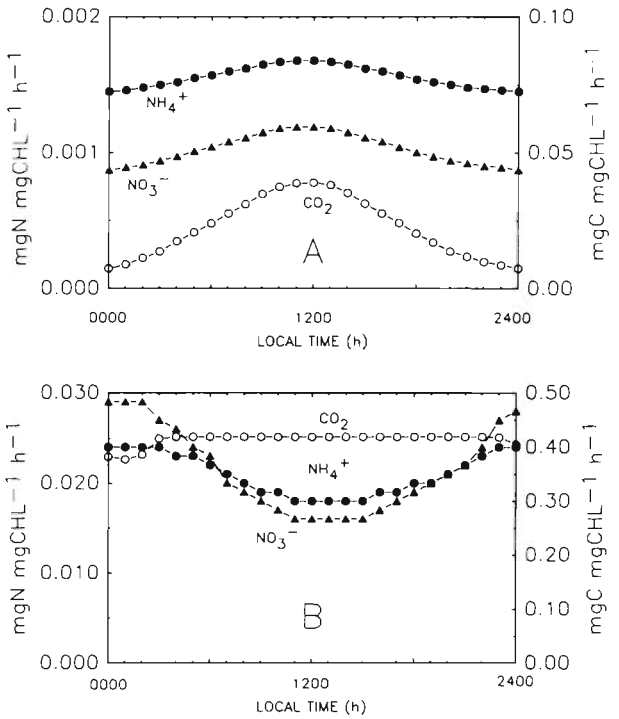

Fig. 4. Modeled diel patterns of photosynthesis and inorganic N uptake predicted for (A) bottom ice and (B) surface ice microbial assemblages. Models are based on the data presented in Figs. 1, 2 & 3

lowest ratios always coincided with the lowest irradiance (around midnight) whereas the highest ratios corresponded to the period of highest irradiance (around local noon) and were determined primarily by differences in α and dark uptake rates. Relative C:N uptake rates in the surface ice assemblage were also positively correlated to incident irradiance with C:NO_3^-, C:NH_4^+ and C:DIN ratios ranging from 13.1 to 27.0, 15.5 to 23.1 and 7.1 to 12.5, respectively, but were determined primarily by differences in the modeled photoinhibition parameter β. Daily integrated C:NO_3^- C:NH_4^+ and C:DIN (g:g) for the bottom ice and surface ice communities were 21.8, 14.3 and 8.6, and 19.3, 19.6, and 9.7, respectively.

DISCUSSION

There have been a number of reports on the light dependence of NO_3^- and NH_4^+ uptake in natural phytoplankton communities in both marine and freshwater environments (e.g. MacIsaac & Dugdale 1972, Bates 1976, Nelson & Conway 1979, Terry 1982, Priscu 1984, Dodds & Priscu 1989, Kanda et al. 1989, Priscu 1989). Many of these studies indicated inconsistencies in the degree of light adaptation between high and low light assemblages. For example, Bates (1976) found that a shade-adapted population had a lower half-saturation constant for NO_3^- uptake than a sun-adapted population of chlorophytes, but he observed no such trend in diatom cultures. Priscu (1984) showed that NO_3^- uptake by phytoplankton forming the deep-chlorophyll maximum in a temperate subalpine lake generally had shade-adapted characteristics (i.e. lower half-saturation constants for irradiance than surface populations whereas NH_4^+ uptake by these populations showed no such distinction). In a more recent study on a permanently ice-covered Antarctic lake, no differences in the light dependence of NO_3^- or NH_4^+ uptake were observed between shallow and deep assemblages, both of which were subjected to limiting irradiance levels (Priscu 1989). Present results indicate that DIN uptake, like photosynthesis, is more shade-adapted in assemblages of sea ice microalgae growing in a lower light environment.

DIN uptake is not a first order reaction with respect to light absorption by the cells; a portion of the energy and reductant is derived from intermediary metabolism (Syrett 1981, Guerrero et al. 1981, Priscu 1984). We attempted to determine the contribution of energy and reductant from non-cyclic photophosphorylation by comparing DIN uptake in the dark with uptake in DCMU-inhibited samples. That uptake measured in the presence of DCMU was usually about the same as dark uptake implies that non-cyclic photophosphorylation supplied most of the energy required for light-mediated uptake, a result supported by other studies (e.g. Arnon 1961, Falkowski & Stone 1975).

Despite the ultimate requirement for light-derived energy, DIN uptake suppressed by darkness and DCMU still ranged from 12 to 57% of that at P_m^B indicating that a significant amount of energy required for DIN uptake comes from intermediary metabolism, at least over the time scales of our experiments. Dark uptake of NO_3^- has been interpreted as a reflection of the degree of nitrogen deficiency by a phytoplankton assemblage (Kanda et al. 1989). Dark NO_3^- uptake in our experiments was 3 and 28% of P_m^B in sea ice microalgal populations which showed no apparent indication of nitrogen deficiency when our experiments were conducted (Priscu unpubl. nutrient bioassay data). Others have also shown significant dark NO_3^- uptake in phytoplankton thought to be nitrogen-sufficient (e.g. Priscu 1984, 1989, Paasche et al. 1984). The degree of dark NO_3^- and NH_4^+ uptake is probably related to the general physiological state of the cells, specifically internal energy stores, which can be governed by factors other than nitrogen supply. The results of Bates (1976) further indicate that a certain degree of species specificity may exist in the ability of phytoplankton to utilize DIN in the dark.

Regardless of the physiological mechanisms involved

with light-mediated DIN uptake, the relationships among DIN uptake, photosynthesis and irradiance may delimit patterns by which algae incorporate C and N into their cellular biomass. These patterns may be particularly important in polar environments because extreme variations in irradiance occur, particularly on a seasonal scale. Our models of diel trends for sea ice microalgae from surface ice and bottom ice in McMurdo Sound show that distinctly different daily patterns can exist in C and N uptake during the spring bloom (Fig. 4A, B). Based on these diel models, integrated daily photosynthesis (mg C mg chl^{-1} d^{-1}), NO_3^- uptake (mg NO_3^--N mg chl^{-1} d^{-1}) and NH_4^+ uptake (mg NH_4^+-N mg chl^{-1} d^{-1}) would be 0.5, 0.03 and 0.04 for the bottom ice assemblage, and 9.9, 0.52 and 0.51 for the surface ice assemblage. Higher chlorophyll-specific rates in the surface (high-irradiance) assemblage is consistent with other reports comparing shade- with sun-adapted phytoplankton for DIN uptake (e.g. Bates 1976, Priscu 1989) and photosynthesis (e.g. Palmisano et al. 1986).

The daily patterns of C and N uptake can also be interpreted in terms of balanced growth if expressed as C:N uptake ratios. Daily integrated C:DIN (g:g) uptake by the bottom ice and surface ice assemblages were 8.6 and 9.7, respectively. The modeled C:DIN uptake ratio of the bottom ice assemblage was virtually identical to the measured PC:PN ratio (8.1), whereas the C:DIN uptake ratio of the surface ice assemblage exceeded the measured PC:PN ratio (5.8) by 67%. Microscopic examination (Lizotte 1989, Kottmeier et al. 1987) has shown that relatively little detritus or bacterial biomass is observed in these microbial communities, hence, PC:PN ratios should reflect closely the composition of the algae. It should be noted that β, the photoinhibition parameter, which regulates modeled DIN uptake over most of the day for the surface community, was predicted on relatively few data points (see Fig. 2) yielding a relatively high variance associated with this term (coefficient of variation >100%). Consequently, β is not statistically different from zero. If β is set to zero and the uptake model for the surface ice assemblage is rerun, the modeled C:DIN uptake ratio is reduced to 7.4, which is closer to the measured PC:PN value for this assemblage. The modeled C:DIN uptake ratio is not changed if β is set to zero in the model for the bottom ice assemblage. Our measured PC:PN ratios and modeled C:DIN uptake ratios (assuming $\beta = 0$ for the surface community) are within about 20% of the cellular C:N ratio of 5.7 (g:g) which is approached in balanced growth by phytoplankton (Redfield 1958).

It should be noted that our daily uptake models are based on irradiance measured under relatively little cloud cover (integrated surface irradiance = 65 mol quanta m^{-2} d^{-1}; integrated under ice irradiance = 0.1 mol quanta m^{-2} d^{-1}), a condition which does not prevail for long periods during the austral summer in McMurdo Sound area (see Cota & Sullivan 1990, Fig. 5). Furthermore, all measurements were conducted in mid-December when solar angle is highest (i.e. the period of greatest solar flux). Given lower irradiance levels, the daily uptake trends (Fig. 4A, B) and ultimately the C:N uptake ratios (Fig. 5A, B) would change considerably. Based on modeled physiological parameters (Table 1), daily under-ice irradiance of 0.09 mol quanta m^{-2} d^{-1} (93% of measured under-ice irradiance on a cloudless day; Fig. 3B) and daily surface irradiance of 5 mol quanta m^{-2} d^{-1} (7.5% of measured incident irradiance on a cloudless day; Fig. 3A) would be required for the modeled C:DIN uptake ratios to balance measured PC:PN in the bottom and surface ice assemblages, respectively. A daily surface irradiance of 5.5 mol quanta m^{-1} d^{-1} would be required to balance these ratios for the surface ice assemblage if β is set to zero in the irradiance-response models (Fig. 2, Table 1). These lower irradiance levels may exist in the bottom ice and the surface ice environments given the variable effects of atmospheric conditions, snow cover, and shading. Shading may result from attenuation of light by the organisms themselves and, in the case of the surface ice communities, shadows from land, icebergs, or pressure ridges which are associated with this habitat.

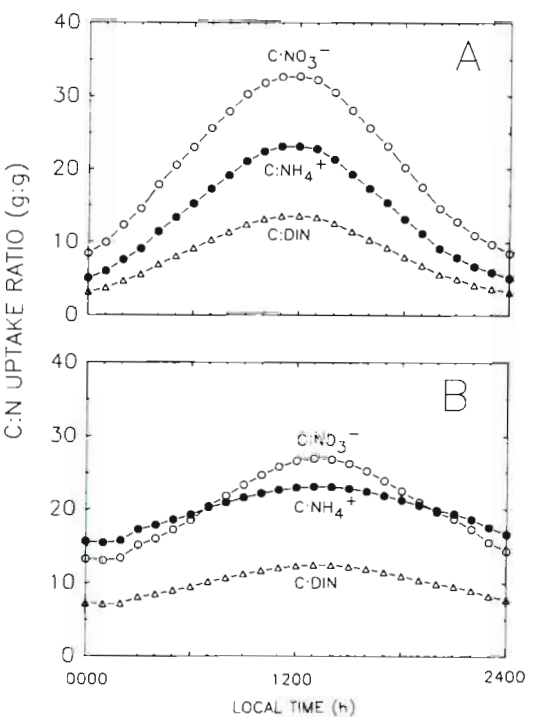

Fig. 5. Modeled C:N uptake ratios (g:g) predicted over a daily irradiance cycle for (A) bottom ice and (B) surface ice microbial assemblages. Uptake ratios were predicted from the modeled uptake rates presented in Fig. 4A, B

Discrepancies between modeled daily C:DIN uptake and measured PC:PN may be compensated for by uptake of organic nitrogen. Palmisano & Sullivan (1985), using ^{14}C-labeled serine and microautoradiography, found that certain species of bottom ice microalgae from McMurdo Sound exhibited light-independent serine uptake which supports our results with ^{15}N- labeled serine. Another study on heterotrophy in bottom ice microalgae from McMurdo Sound showed no consistent trends in light-mediated uptake for leucine, glutamate, glycine or an amino acid mixture (Rivkin & Putt 1987b). If daily serine uptake is added to modeled daily DIN uptake, the C:N uptake ratios (g:g) become 6.2 and 7.3 (5.8 if $\beta = 0$) for the bottom ice and surface ice assemblages, respectively. The resulting (i.e. with the addition of serine uptake) C:N uptake ratio for the bottom ice assemblage diverges from the measured PC:PN in the bottom ice assemblage whereas the C:N ratio in the surface ice assemblage converges on measured PC:PN implying that organic nitrogen uptake may be an important N source to the latter assemblage. More data on organic nitrogen concentrations and organic nitrogen uptake within surface ice is required to verify this contention. We emphasize that comparisons between C:N uptake and PC:PN of cell material assumes that there are no cellular losses of these elements. High rates of C excretion or respiration from cells could yield lower PC:PN ratios, despite relatively high C:N uptake ratios.

Our results indicate that nitrogen uptake in sea ice microalgae responds to changes in irradiance, but that light-mediated rates are not proportional to photosynthetic rates. Differences in light-mediated rates of uptake cannot be discerned in short-term, single-irradiance measurements, and may be misleading with respect to the physiological state of the algae. Full day (i.e. 24 h) incubations or a modeled approach using data from irradiance-response experiments and diel PAR measurements may be required to determine the stoichiometric balance of essential elements and ultimately the growth rate of the organisms. Irradiance-response characteristics of microalgae may be especially important in polar environments where large annual variations in irradiance and photoperiod occur. Our experimental and modeling efforts indicate that surface ice and bottom ice microalgal populations acquire inorganic carbon and nitrogen at different rates and during different periods of the diel irradiance cycle. This differential response may play an important role in the timing of blooms in these physiologically distinct communities.

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