

## Effects of four environmental variables on photosynthesis-irradiance relationships in Antarctic sea-ice microalgae

A. C. Palmisano<sup>1,\*</sup>, J. Beeler SooHoo<sup>1</sup> and C. W. Sullivan<sup>2</sup>

<sup>1</sup> Allan Hancock Foundation, University of Southern California; Los Angeles, California 90089-0371, USA

<sup>2</sup> Marine Biology Research Section, Department of Biological Sciences, University of Southern California; Los Angeles, California 90089-0371, USA

### Abstract

The effects of temperature, salinity, growth irradiance and diel periodicity of incident irradiance on photosynthesis-irradiance (*P-I*) relationships were examined in natural populations of sea-ice microalgae from McMurdo Sound in the austral spring of late 1984. Both  $P_m^b$  (photosynthetic rate at optimum irradiance) and  $a^b$  (initial slope of *P-I* curve) were temperature-dependent reaching optimal rates at approximately +6° and +2°C, respectively. *P-I* relationships showed little difference at 20 and 33‰ S; however, no measurable photosynthesis by sea-ice microalgae was detected in a 60‰ S solution of brine collected from the upper layers of congelation ice. Although diel periodicity characteristic of the under-ice light field appeared to have little effect on *P-I* relationships, changes in growth irradiance had a profound effect. An increase in growth irradiance from  $7 \mu\text{E m}^{-2} \text{s}^{-1}$  (ambient) to 35 or 160  $\mu\text{E m}^{-2} \text{s}^{-1}$  resulted in a transient three-fold increase in  $P_m^b$  and  $I_k$  (index of photoadaptation) during the first four days, followed by a sharp decline. The effects of these environmental factors on ice algal photosynthesis may influence the distribution of microalgae in sea-ice environments.

### Introduction

In McMurdo Sound, microalgal communities dominated by diatoms are found living in the brine pockets and channels that permeate the lower layers of hard, coarse-grained congelation ice (Palmisano and Sullivan, 1983). Such communities may extend up to 25 cm into the congelation ice, often occurring in discrete, golden-brown colored bands (Grossi and Sullivan, 1985). Microalgae

may also be found in the unconsolidated platelet-ice layer below congelation ice (Bunt and Wood, 1963).

Photosynthetic rates in microalgae are influenced by many environmental factors including (1) temperature (Bunt, 1964; Steeman-Nielsen and Jørgensen, 1968; Morris and Farrell, 1971; Li, 1980; Neori and Holm-Hansen, 1982), (2) salinity (Bunt, 1964), (3) nutrient status (Falkowski and Stone, 1975; Healey, 1979; Prézelin and Matlick, 1983), and (4) light history (Beardall and Morris, 1976; Perry *et al.*, 1981; Prézelin, 1981; Jacques, 1983; Hoepffner, 1984). Light history includes magnitude, diel periodicity, and spectral composition of irradiance.

Microalgae living in the bottom of annual sea ice are unique in their ability to photosynthesize under a set of extreme environmental conditions. Surface-water temperatures in McMurdo Sound are continually low, averaging  $-1.81^\circ\text{C} \pm 0.08^\circ\text{C}$  (Littlepage, 1965). Algae trapped in hypersaline brine pockets within the ice column may experience temperatures several degrees lower (Kottmeier *et al.*, 1986). Microalgae in the bottom of congelation ice are subject to fluctuations in salinity. As the ice forms, excluded salts are concentrated in microscopic (< 1 mm) brine pockets. However, as snow and surface ice melt in early summer, meltwater percolates through the porous sea ice, flushing the sea-ice microalgae with low-salinity water. Photosynthetically available radiation (PAR) beneath sea ice is typically < 1% of surface downwelling irradiance during the peak of the austral spring bloom of ice microalgae. Diel periodicity in surface downwelling irradiance is slight during the summer months. Low sun angle, however, results in a diel periodicity in irradiance beneath annual sea ice (Sullivan *et al.*, 1982), although such diel changes are not as great as those to which most temperate microalgae are exposed.

Here we examine the effects of temperature, salinity, growth irradiance and diel periodicity of irradiance on photosynthesis-irradiance relationships in sea-ice microalgae from McMurdo Sound. We then consider how physiological responses to these environmental variables

\* Present address: NASA-Ames Research Center, Mail Stop 239-4, Moffett Field, California 94035, USA

may affect the vertical distribution of microalgae in sea ice.

### Materials and methods

Microalgae were collected from sea ice in McMurdo Sound, Antarctica, the southernmost extension of the Ross Sea, in the austral spring of late 1984. Microalgae from congelation ice were collected using a SIPRE ice auger while microalgae from platelet ice were collected by SCUBA divers using 4-liter Nalgene containers. A small amount of ice crystals with attached microalgae were melted into 300 ml of 0°C seawater.

*P-I* relationships were determined by the uptake of  $\text{NaH}^{14}\text{CO}_3$  (ICN Pharmaceuticals) at 30 to 35 irradiances between 0 and  $506 \mu\text{E m}^{-2} \text{s}^{-1}$ , as described in Palmisano *et al.* (1985). One ml samples were incubated for 1 h using the small volume, short-term method of Lewis and Smith (1983), except that a 500 W tungsten halogen lamp was used and the counter-current heat filter was omitted. All incubations (except for the temperature experiments) were performed at  $-1.9^\circ\text{C} \pm 0.2^\circ\text{C}$ , the ambient surface-water temperature in McMurdo Sound (Littlepage, 1965; Kottmeier *et al.*, 1986). Chlorophyll *a* was extracted in 90% acetone and estimated fluorometrically by the method of Yentsch and Menzel (1963), as modified by Holm-Hansen *et al.* (1965). Photosynthetic rates normalized to chlorophyll *a* were fitted to the empirically derived equations of Platt *et al.* (1980) to estimate the parameters described in Table 1.

Standard deviations for the primary parameters ( $P_s^b$ ,  $\alpha^b$ , and  $\beta^b$ ) were determined by the linear approximation procedure which will be described elsewhere by Zimmerman *et al.* (in preparation). This method produces results comparable to a reiterative Monte Carlo approach.

The effect of temperature on *P-I* parameters was determined in samples of microalgae from congelation ice collected on 31 October at Hut Point, McMurdo Sound, and microalgae from platelet ice collected on 1 November from nearby Cape Armitage. At the time of sampling, congelation-ice communities at these sites were dominated by the diatoms *Berkeleya* sp., *Amphiprora* sp., *Pleurosigma* sp. and *Nitzschia stellata*, while platelet-ice communities were dominated by *Nitzschia kerguelensis* and centric diatoms. Samples were incubated with radiolabel at  $-2.0^\circ$ ,

$+2.0^\circ$ ,  $+6.0^\circ$ , or  $+10.0^\circ\text{C} \pm 0.2^\circ\text{C}$  after 1 h preincubation at the designated temperature.

In a second set of experiments, *P-I* parameters were estimated at three salinities: 20, 33, and 60‰. 33‰ S seawater was collected from Cape Armitage, McMurdo Sound, at 3 m depth by lowering a Kemmerer bottle through an ice hole. Subsamples were diluted with deionized, distilled water to 20‰ S. Despite this dilution, it is unlikely that nutrients became limiting; nutrient concentrations in McMurdo Sound are typically very high (e.g.  $\text{NO}_3 = 19.2$ ,  $\text{PO}_4 = 1.52$ ,  $\text{SiO}_4 = 58.0 \mu\text{g-at l}^{-1}$ ; Palmisano *et al.*, 1986). The 60‰ S seawater was derived by mixing 33‰ S seawater with brine collected from the upper layers of sea ice. Salinity was estimated with a refractometer. Microalgae in this experiment were collected from congelation ice at Granite Harbor, McMurdo Sound, on 18 November; the community was dominated by *Nitzschia stellata* and *Pleurosigma* sp.

Changes in *P-I* parameters in ice algae were followed during adaptation to three different growth irradiances. Initial parameters were determined in microalgae from congelation ice collected on 6 November from Cape Armitage. The sample was subdivided into three 250 ml volumes which were incubated at  $-2^\circ\text{C}$  in a laboratory cold room under cool-white fluorescent lights at  $7 \mu\text{E m}^{-2} \text{s}^{-1}$  (a light-limiting irradiance);  $35 \mu\text{E m}^{-2} \text{s}^{-1}$  (irradiance of maximum photosynthesis); and  $160 \mu\text{E m}^{-2} \text{s}^{-1}$  (saturating or photoinhibiting irradiance; Palmisano *et al.*, 1985). *P-I* parameters were estimated in subsamples from each irradiance after 1, 2, 4, 6, and 9 d of incubation.

To examine diel periodicity of *P-I* parameters, two types of experiments were performed on samples from Cape Armitage. First, individual cores of congelation ice were collected at 6 h intervals over a 24 h period on 12 November. Second, to eliminate variation resulting from spatial heterogeneity in microalgal communities, microalgae from a single core were suspended *in situ* beneath sea ice by divers and subsampled at 6 h intervals. Under-ice spectral irradiance was measured during the diel experiments with an underwater spectroradiometer with a cosine collector (MER 1000, Biospherical Instruments, San Diego, California, USA) attached to a mooring.

Vertical stratification of the ice algal community was evident in samples from Granite Harbor, Hut Point, and the ice edge in which two or three distinct, golden-brown bands were found. Individual bands, 2 to 5 cm in width,

**Table 1.** Photosynthetic parameters estimated for microalgae from antarctic sea ice, together with abbreviations used throughout text

$P_s^b$	– Maximum photosynthetic rate in absence of photoinhibition	$(\text{mg C mg}^{-1} \text{ chl } a \text{ h}^{-1})$
$\alpha^b$	– Photosynthetic efficiency, the initial slope of the <i>P-I</i> curve	$(\text{mg C mg}^{-1} \text{ chl } a \text{ h}^{-1} [\mu\text{E m}^{-2} \text{ s}^{-1}]^{-1})$
$\beta^b$	– An index of photoinhibition	$(\text{mg C mg}^{-1} \text{ chl } a \text{ h}^{-1} [\mu\text{E m}^{-2} \text{ s}^{-1}]^{-1})$
$P_m^b$	– Photosynthetic rate at optimal irradiance	$(\text{mg C mg}^{-1} \text{ chl } a \text{ h}^{-1})$
$I_k^b$	– $P_m^b/\alpha^b$ , an index of photoadaptation	$(\mu\text{E m}^{-2} \text{ s}^{-1})$
$I_m^b$	– Irradiance at which photosynthesis is maximal	$(\mu\text{E m}^{-2} \text{ s}^{-1})$
$I_0^b$	– Irradiance at which extrapolation of the slope of the inhibited portion of the curve intersects the irradiance axis	$(\mu\text{E m}^{-2} \text{ s}^{-1})$

were excised from an ice core with a stainless steel ice saw, melted into 0°C seawater, and examined for their *P-I* relationships.

**Results and discussion**

Temperature

The short-term physiological response of photosynthetic parameters to changes in temperature revealed that maximum photosynthetic rates ( $P_m^b$ ) increased more than two-fold in congelation ice microalgae (Fig. 1a) and three- to four-fold in platelet ice microalgae (Fig. 1b) between -2° and +6°C (Table 2).  $P_m^b$  decreased when incubated at +10°C in both types of microalgae, indicating that the optimum temperature for light-saturated photosynthesis

was around +6°C. Because incubations at each temperature lasted only 2 h, it is unlikely that we were selecting for the growth of certain species with higher temperature optima for photosynthesis. Our estimate of the optimum temperature for ice algal photosynthesis falls at the low end of such estimates for ice algae and antarctic phytoplankton. Bunt (1964) found that a natural population of microalgae from platelet ice in McMurdo Sound showed maximum carbon fixation between 10° and 15°C, with a rapid decline above 15°C, when incubated at 65 ft-c (about 14  $\mu E m^{-2} s^{-1}$ ). In antarctic phytoplankton, Jacques (1983) found a maximum rate of primary production near 12°C with a decline above 17.5°C, while Neori and Holm-Hansen (1982) found that 7°C was optimal for photosynthesis.

The temperature optima for  $P_m^b$  were very low, confirming the psychrophilic nature of ice algae; however,

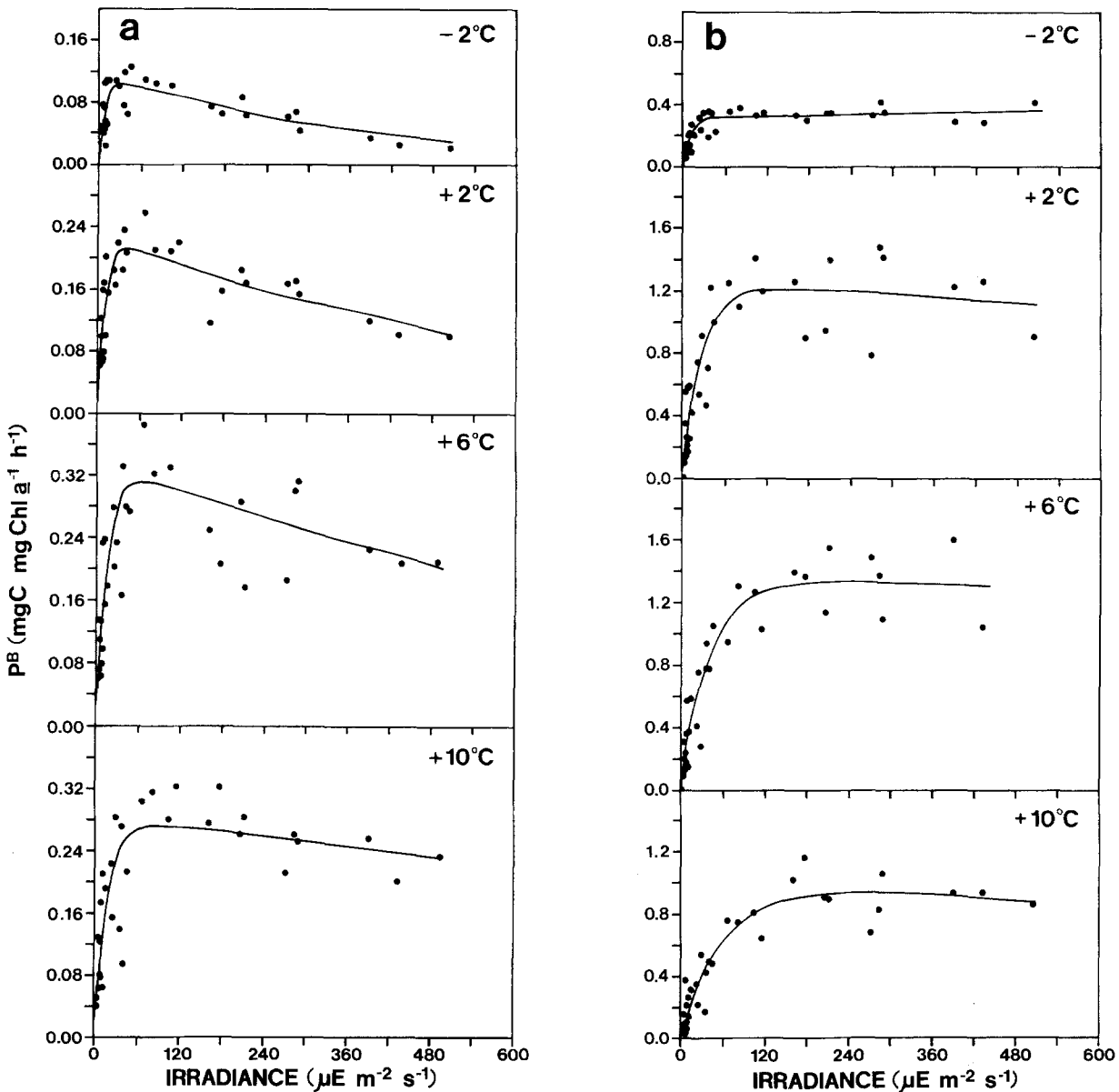


Fig. 1. Photosynthesis-irradiance relationships in microalgae from (a) congelation ice and (b) platelet ice at four incubation temperatures

**Table 2.** Photosynthetic parameters (see Table 1) of microalgae from congelation or platelet ice in McMurdo Sound, Antarctica, at four incubation temperatures (all  $\pm 0.2$  °C). Standard deviations are given

Temperature (°C)	$P_s^b$	$\alpha^b$	$\beta^b (\times 10^3)$	$P_m^b$	$I_k^b$	$I_m^b$	$I_b^b$
Congelation ice (31. Oct. 1984; Hut Point)							
- 2.0	0.117 $\pm$ 0.011	0.014 $\pm$ 0.002	0.319 $\pm$ 0.101	0.105	7.4	31.4	365
+ 2.0	0.233 $\pm$ 0.017	0.023 $\pm$ 0.003	0.375 $\pm$ 0.114	0.214	9.3	41.8	621
+ 6.0	0.327 $\pm$ 0.038	0.022 $\pm$ 0.004	0.305 $\pm$ 0.194	0.304	13.8	63.6	1 073
+ 10.0	0.265 $\pm$ 0.028	0.017 $\pm$ 0.003	0.051 $\pm$ 0.111	0.260	14.8	88.4	5 241
Platelet ice (1. Nov. 1984; Cape Armitage)							
- 2.0	0.320 $\pm$ 0.023	0.027 $\pm$ 0.004	0 $\pm$ 0.085	0.320	11.7	11.7	- <sup>a</sup>
+ 2.0	1.268 $\pm$ 0.153	0.044 $\pm$ 0.007	0.347 $\pm$ 0.572	1.21	27.4	139	3 646
+ 6.0	1.353 $\pm$ 0.174	0.034 $\pm$ 0.004	0.099 $\pm$ 0.627	1.33	38.7	230	13 611
+ 10.0	1.020 $\pm$ 0.163	0.017 $\pm$ 0.002	0.319 $\pm$ 0.520	0.930	54.3	238	3 193

<sup>a</sup> Undefined for  $\beta=0$

**Table 3.** Photosynthetic parameters (see Table 1) of microalgae from congelation ice collected on 18 November 1984 from Granite Harbor, McMurdo Sound, at two salinities; no photosynthetic activity was measurable at 60‰ S

Salinity (‰)	$P_s^b$	$\alpha^b$	$\beta^b (\times 10^3)$	$P_m^b$	$I_k^b$	$I_m^b$	$I_b^b$
20	0.235 $\pm$ 0.023	0.031 $\pm$ 0.007	0.139 $\pm$ 0.121	0.228	7.33	40.86	1 687
33	0.183 $\pm$ 0.020	0.031 $\pm$ 0.009	0 $\pm$ 0.087	0.183	6.01	6.01	- <sup>a</sup>

<sup>a</sup> Undefined for  $\beta=0$

temperature optima were about 8 °C higher than ambient surface-water temperatures. Our data conform to a generalization made by Li (1980) that temperature optima for photosynthesis are usually somewhat higher than the growth temperature. Natural populations of sea-ice algae might possibly experience *in situ* temperatures as high as 5 °C, if carried by surface currents toward the Antarctic convergence upon release from sea ice.

A temperature effect on photosynthetic efficiency ( $\alpha^b$ ) was also evident (Table 2). The  $\alpha^b$  reached a peak value at +2 °C, then declined in both congelation- and platelet-ice microalgae. Similarly, Verity (1981) found that  $\alpha^b$  was not constant in the marine diatom *Leptocylindrus danicus* Cleve, but changed with environmental variables such as temperature. He pointed out that his results are contrary to the view that  $\alpha^b$  represents the rate of photochemical reactions which are independent of temperature. Furthermore, photosynthetic efficiency in our study had a lower temperature optimum than did the  $P_m^b$ , which is thought to represent the enzymatic dark reactions of carbon fixation (Rabinowitch and Govindjee, 1969).

The  $I_k^b$  increased steadily with temperature from 7.4 to 14.8  $\mu\text{E m}^{-2} \text{s}^{-1}$  in congelation-ice microalgae, and from 11.7 to 54.3  $\mu\text{E m}^{-2} \text{s}^{-1}$  in platelet-ice microalgae (Table 2). Even greater increases were seen in  $I_m^b$ , which changed from 31.4 to 88.4  $\mu\text{E m}^{-2} \text{s}^{-1}$  in congelation-ice microalgae and from 11.7 to 238  $\mu\text{E m}^{-2} \text{s}^{-1}$  in platelet-ice microalgae. Verity (1981) also found that higher temperatures resulted in an increase in  $I_k$  in *Leptocylindrus danicus* from 2  $\text{ly h}^{-1}$  (about 116  $\mu\text{E m}^{-2} \text{s}^{-1}$ ) at 5 °C to 3.5  $\text{ly h}^{-1}$  (about 203  $\mu\text{E}$

$\text{m}^{-2} \text{s}^{-1}$ ) at 20 °C. In the low-temperature-adapted sea-ice microalgae, even relatively small changes in temperature have a significant effect on photosynthesis-irradiance relationships.

### Salinity

Ice algae were actively photosynthetic at 20 to 33‰ S, with  $P_m^b$  slightly higher at the lower salinity (Table 3). By contrast, Bunt (1964) found that the photosynthetic activity of platelet ice algae was maximal at 7.5 to 10‰ S. Bunt collected his samples in late December, however, when algae may have been preconditioned by low-salinity meltwater. We were not able to detect photosynthetic activity at 60‰ S. Brine collected from 1.5 m depth in sea ice is often as high as 113‰ S (Kottmeier, unpublished data). High brine salinities may be a factor limiting the vertical distribution of algae within the ice column. Dilution of the high-salinity brine with seawater in the lower few centimeters of sea ice (Reeburgh, 1984) may be essential for algal growth, and may partially explain why algal growth is primarily confined to the bottom 5 to 20 cm of congelation ice in McMurdo Sound (Palmisano and Sullivan, 1983).

### Growth irradiance

Antarctic ice algae are often cited as shade-adapted (Bunt, 1964; Palmisano *et al.*, 1985). To determine whether sea-

**Table 4.** Changes in photosynthetic parameters (see Table 1) of microalgae from congelation ice collected on 6 November from Cape Armitage during low-to-mid and low-to-high light adaptation

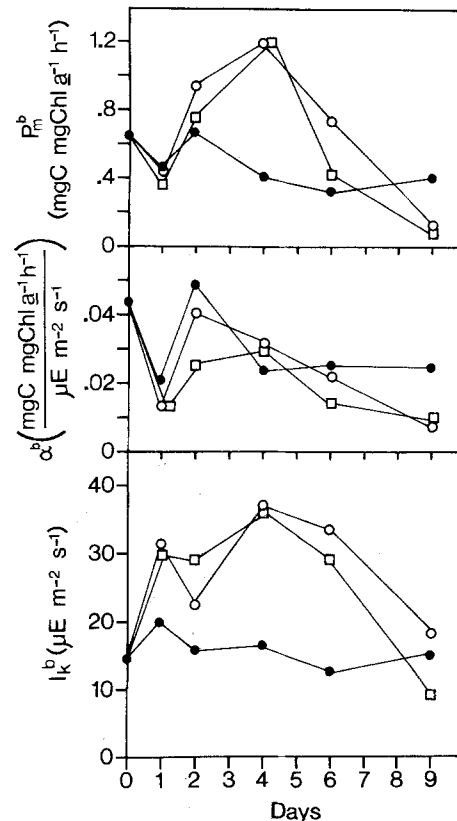
Incubation irradiance + period	$P_s^b$	$\alpha^b$	$\beta^b$ ( $\times 10^3$ )	$P_m^b$	$I_k^b$	$I_m^b$	$I_b^b$
0	$0.634 \pm 0.053$	$0.042 \pm 0.007$	$0 \pm 0.197$	0.634	14.9	14.9	— <sup>a</sup>
7 $\mu\text{E m}^{-2} \text{s}^{-1}$ (control)							
1d	$0.465 \pm 0.047$	$0.021 \pm 0.003$	$0.185 \pm 0.194$	0.442	20.9	104	2 509
2d	$0.748 \pm 0.078$	$0.047 \pm 0.009$	$0 \pm 0.243$	0.748	16.0	16.0	— <sup>a</sup>
4d	$0.406 \pm 0.035$	$0.024 \pm 0.003$	$0 \pm 0.124$	0.406	16.9	16.9	— <sup>a</sup>
6d	$0.319 \pm 0.037$	$0.026 \pm 0.007$	$0 \pm 0.101$	0.319	12.3	12.3	— <sup>a</sup>
9d	$0.401 \pm 0.032$	$0.025 \pm 0.004$	$0.083 \pm 0.129$	0.393	15.4	90.1	4 852
35 $\mu\text{E m}^{-2} \text{s}^{-1}$							
1d	$0.433 \pm 0.070$	$0.013 \pm 0.002$	$0.154 \pm 0.253$	0.406	31.7	150	2 858
2d	$0.938 \pm 0.094$	$0.041 \pm 0.006$	$0.021 \pm 0.324$	0.934	22.7	172	44 380
4d	$1.410 \pm 0.262$	$0.032 \pm 0.006$	$1.283 \pm 1.100$	1.192	36.8	142	1 099
6d	$0.909 \pm 0.086$	$0.022 \pm 0.003$	$0.465 \pm 0.340$	0.728	33.6	144	1 738
9d	$0.139 \pm 0.017$	$0.007 \pm 0.002$	$0.029 \pm 0.069$	0.135	18.1	1 035	4 824
160 $\mu\text{E m}^{-2} \text{s}^{-1}$							
1d	$0.408 \pm 0.066$	$0.012 \pm 0.002$	$0.129 \pm 0.266$	0.385	30.6	149	3 140
2d	$0.811 \pm 0.084$	$0.025 \pm 0.003$	$0.322 \pm 0.314$	0.758	29.6	139	2 514
4d	$1.686 \pm 0.331$	$0.029 \pm 0.004$	$2.154 \pm 1.420$	1.292	43.7	153	782
6d	$0.417 \pm 0.058$	$0.014 \pm 0.003$	$0.079 \pm 0.209$	0.403	29.1	156	5 289
9d	$0.096 \pm 0.042$	$0.010 \pm 0.005$	$0 \pm 0.157$	0.097	9.1	9.1	— <sup>a</sup>

<sup>a</sup> Undefined for  $\beta=0$

ice algae are obligately shade-adapted as proposed by Cota (1985) for arctic ice algae, cells were incubated at higher irradiances than are typically found during the peak of the ice algal bloom in November. The higher irradiances tested (35 and 160  $\mu\text{E m}^{-2} \text{s}^{-1}$ ) were not, however, unrealistic for *in situ* conditions for bottom-ice algae. Sullivan *et al.* (1983) reported an irradiance of 165  $\mu\text{E m}^{-2} \text{s}^{-1}$  beneath snow-free congelation ice. Thus, microalgae colonizing the sea ice prior to the algal bloom, microalgae located at the top of the bloom within the ice column, or microalgae remaining in the sea ice after snow and ice melt in late December may be subjected to relatively high irradiance.

In a control sample incubated at 7  $\mu\text{E m}^{-2} \text{s}^{-1}$ ,  $P_m^b$  showed little change over the 9 d incubation period, averaging  $0.462 \pm 0.166$  SD mg C mg<sup>-1</sup> chl *a* h<sup>-1</sup> (Table 4; Fig. 2). At 35 and 160  $\mu\text{E m}^{-2} \text{s}^{-1}$ , however,  $P_m^b$  increased from 0.4 to 1.3 in four days, then declined to a value less than half that of the control. It is unlikely that the decline was due to self-shading or nutrient limitation. Throughout the incubation period, chlorophyll *a* concentrations in each flask increased logarithmically at rates of 0.22, 0.23, and 0.13 doublings d<sup>-1</sup> at 7, 35, and 160  $\mu\text{E m}^{-2} \text{s}^{-1}$ , respectively.

Changes in  $\alpha^b$  at higher irradiances initially followed the control, but then steadily decreased after four days of incubation.  $I_k^b$ , however, increased sharply during the first four days, then declined.  $I_k^b$  at 160  $\mu\text{E m}^{-2} \text{s}^{-1}$  was similar to  $I_k^b$  at 35  $\mu\text{E m}^{-2} \text{s}^{-1}$ . This contrasts with the findings of Jacques (1983), who reported that  $I_k^b$  increased in ant-



**Fig. 2.** Changes in photosynthetic parameters ( $\alpha^b$ ,  $P_m^b$ ,  $I_k^b$ ) at three growth irradiances. ●: 7  $\mu\text{E m}^{-2} \text{s}^{-1}$ ; ○: 35  $\mu\text{E m}^{-2} \text{s}^{-1}$ ; □: 160  $\mu\text{E m}^{-2} \text{s}^{-1}$

arctic phytoplankton from 22 to 114  $\mu\text{E m}^{-2} \text{s}^{-1}$  when growth irradiance increased from 2.2 to 132  $\mu\text{E m}^{-2} \text{s}^{-1}$ . Our results indicate that despite an initial enhancement of photosynthesis, higher growth irradiance ultimately resulted in a decline in photophysiological state.

Data in Fig. 2 also illustrate the importance of considering the dynamics of photoadaptation over time rather than drawing conclusions from an endpoint. A single sample taken after four days where photosynthesis was transiently-enhanced would have produced the opposite conclusions to a sample taken after nine days where photosynthesis was ultimately depressed. Cota (1985) concluded that arctic ice algae were obligately shade-adapted, using a single endpoint of 6 to 7 wk; he may, however, have missed the dramatic short-term enhancement that we found in antarctic ice algae.

Our findings may have implications for ice-edge algal communities as well. Smith and Nelson (1985) suggested that algal blooms at ice-edge zones may be seeded by bottom-ice algal communities. Our data indicate that bottom-ice algae would experience a significant yet transient enhancement of photosynthesis in the relatively high surface-light conditions at the ice edge.

#### Diel periodicity

Temperate phytoplankton have exhibited maxima in  $P_m^b$  and  $\alpha^b$  during the light period (morning, midday, or afternoon) and minima during the dark (Prézelin and Ley, 1980). The amplitude of daily variation in these parameters has been on the order of 3 to 9 for  $P_m^b$  and 2 to 8 for  $\alpha^b$  (Harding *et al.*, 1982).

In sea-ice microalgae sampled in November, we were unable to detect any such changes in photosynthetic parameters that were consistent with diel changes in irradiance (Table 5). Furthermore, changes in amplitude within each 24 h experiment were usually less than two-fold. Manifestation of this biological rhythm may require (1) a larger difference between light and "dark" periods, or

(2) longer periods of reduced irradiance. Algae trapped in sea ice during the late winter months, when more dramatic diel changes in surface downwelling irradiance occur, may exhibit transient diel rhythms in photosynthesis.

#### Vertical stratification

In comparing *P-I* parameters in three stratified-ice algal communities (Table 6; Fig. 3), algae in the bottom few centimeters of ice appeared to be somewhat more sensitive to photoinhibition, as indicated by a higher  $\beta^b$  than those algae higher in the ice column. This suggests the possibility that bottom algae became more shade-adapted due to lower growth irradiance. The upper algal layers act as a filter, absorbing wavelengths critical to photosynthesis (Sullivan *et al.*, 1984).

Grossi and Sullivan (1985) estimated gradients for temperature, salinity, and irradiance within the ice column (Fig. 4). Such vertical gradients may be responsible for both (1) the concentration of the algal community in the lower part of the ice column, and (2) the vertical stratification within the ice algal community. Palmisano and Sullivan (1983) found 99% of the total chlorophyll *a* in the lower 20 cm of sea ice at McMurdo Sound. As shown in Fig. 4, algae living higher in the ice column may experience salinities > 60‰, which may be prohibitive to photosynthesis. Moreover, rates of photosynthesis, which were very temperature-sensitive, would be reduced as temperatures decrease higher in the ice column. Higher growth irradiances, such as would be available higher in the ice column, could ultimately have a deleterious effect on photosynthesis by certain ice algal species. Grossi and Sullivan (1985) found that the species in the lower 10 cm of ice were distinct from those growing higher in the ice column. The higher assemblage included *Navicula glaciei*, a diatom that has also been found in high-light ice environments such as surface-melt pools (Whitaker and Richardson, 1980).

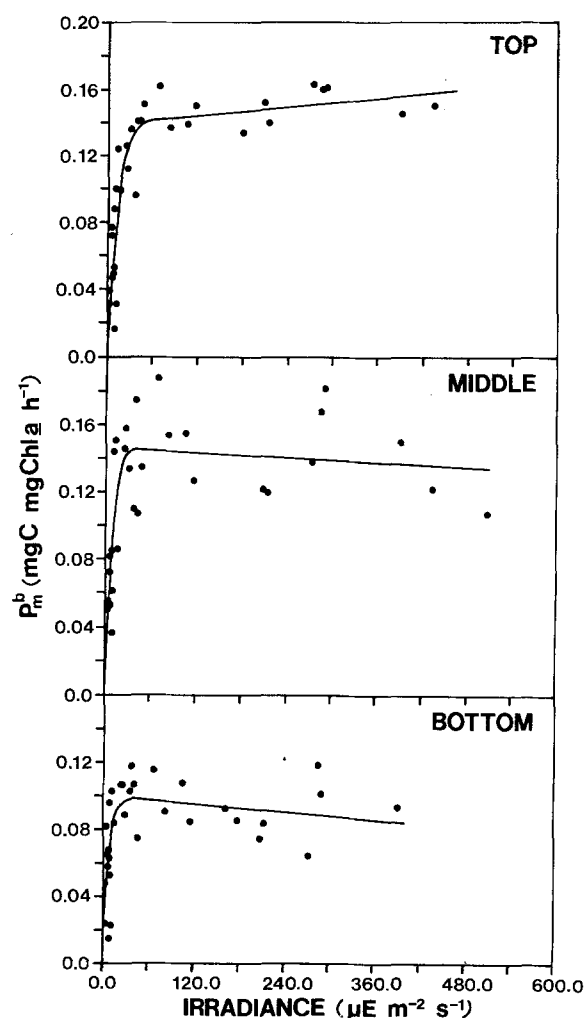
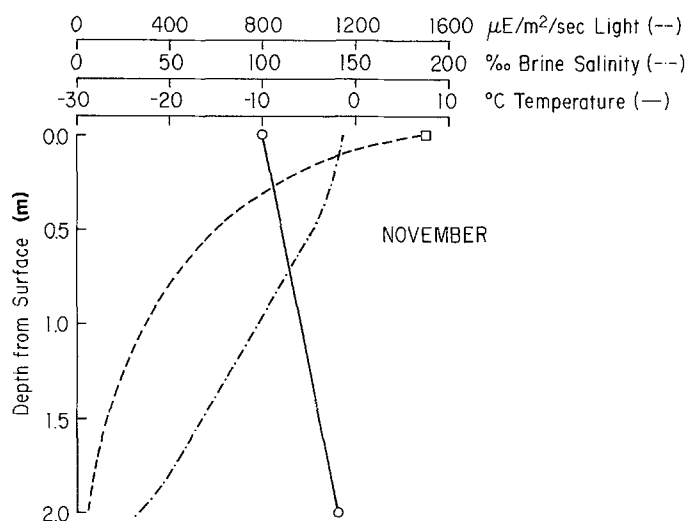
**Table 5.** Diel periodicity of photosynthetic parameters (see Table 1) in microalgae from congelation-ice from Armitage

Time (hrs)	Under-ice irradiance ( $\mu\text{E m}^{-2} \text{s}^{-1}$ )	$P_s^b$	$\alpha^b$	$\beta^b (\times 10^3)$	$P_m^b$	$I_k^b$	$I_m^b$	$I_b^b$
(A) Collected as 4 separate cores (12 Nov. 1984)								
06.30	2.05	0.831 ± 0.109	0.029 ± 0.006	0 ± 0.338	0.831	28.2	28.2	— <sup>a</sup>
12.00	5.34	0.279 ± 0.026	0.010 ± 0.002	0 ± 0.085	0.279	26.9	26.9	— <sup>a</sup>
17.30	3.78	0.551 ± 0.044	0.018 ± 0.002	0.042 ± 0.150	0.542	30.8	189	13 150
00.30	0.64	0.605 ± 0.056	0.021 ± 0.003	0.140 ± 0.206	0.581	28.3	147	4 315
(B) One core subsampled at 4 times (23 Nov. 1984)								
06.00	1.23	0.124 ± 0.018	0.009 ± 0.003	0 ± 0.030	0.124	13.6	13.6	— <sup>a</sup>
12.00	2.77	0.161 ± 0.019	0.008 ± 0.002	0 ± 0.058	0.166	19.9	19.9	— <sup>a</sup>
18.00	1.46	0.119 ± 0.019	0.007 ± 0.002	0.047 ± 0.079	0.114	16.9	87.7	2 529
24.00	0.49	0.130 ± 0.016	0.009 ± 0.002	0 ± 0.056	0.130	14.2	14.2	— <sup>a</sup>

<sup>a</sup> Undefined for  $\beta=0$

**Table 6.** Photosynthetic parameters (see Table 1) for microalgae in vertical strata in McMurdo Sound

Site and strata <sup>a</sup>	Dominant species	$P_s^b$	$\alpha^b$	$\beta^b$ ( $\times 10^3$ )	$P_m^b$	$I_k^b$	$I_m^b$	$I_b^b$
<b>Granite Harbor</b>								
4.5–8 cm	<i>Berkeleya</i> sp.	$0.137 \pm 0.011$	$0.013 \pm 0.002$	$0 \pm 0.039$	0.137	10.4	10.4	—*
2–4.5 cm	<i>Amphiprora</i> sp.	$0.147 \pm 0.012$	$0.019 \pm 0.004$	$0.029 \pm 0.052$	0.145	7.5	49.2	5 001
0–2 cm	<i>Pleurosigma</i> sp., <i>Nitzschia stellata</i>	$0.102 \pm 0.006$	$0.020 \pm 0.004$	$0.049 \pm 0.031$	0.100	4.9	30.2	2 078
<b>Hut Point</b>								
2–6 cm	<i>Amphiprora</i> sp.	$0.157 \pm 0.013$	$0.012 \pm 0.002$	$0.092 \pm 0.632$	0.150	12.5	63.8	1 708
0–2 cm	<i>Pleurosigma</i> sp., <i>Nitzschia stellata</i>	$0.129 \pm 0.014$	$0.011 \pm 0.002$	$0.216 \pm 0.091$	0.118	10.4	45.6	599
<b>Ice edge</b>								
20–22 cm	<i>Berkeleya</i> sp. <i>Amphiprora</i> sp.	$0.063 \pm 0.010$	$0.004 \pm 0.001$	$0.111 \pm 0.060$	0.055	13.5	55.8	571
12–15 cm	<i>Pleurosigma</i> sp., <i>Nitzschia stellata</i>	$0.111 \pm 0.009$	$0.038 \pm 0.012$	$0.108 \pm 0.059$	0.108	2.8	16.8	1 021

<sup>a</sup> Distance from bottom of the congelation ice\* Undefined for  $\beta = 0$ **Fig. 3.** Photosynthesis-irradiance relationships in three vertical strata of sea-ice microalgae**Fig. 4.** Theoretical gradients of temperature, salinity and irradiance. (Reprinted from Grossi and Sullivan, 1985)

### Conclusions

Photosynthesis in antarctic sea ice microalgae is very sensitive to environmental factors, especially temperature, high salinities, and growth irradiance. Gradients in temperature, salinity, and irradiance exist within the ice column as well as at areas such as ice-edge zones. The effects of these factors on photosynthesis may determine, in part, the distribution of microalgae in sea-ice environments.

*Acknowledgements.* The authors thank Dr. S. Kottmeier for supplying irradiance data, M. Lizotte for laboratory and field assistance, and M. Miller and B. Marinovich for dive support. This research was supported by National Science Foundation Grants DPP 83-04985 and 81-17237.

## Literature cited

- Beardall, J. and I. Morris: The concept of light intensity adaptation in marine phytoplankton: some experiments with *Phaeodactylum tricoratum*. *Mar. Biol.* 37, 377–387 (1976)
- Bunt, J. S.: Primary productivity under sea ice in Antarctic waters. Influence of light and other factors on photosynthetic activities of Antarctic marine microalgae. *Antarctic Res. Ser.* 1, 27–31 (1964)
- Bunt, J. S. and E. J. F. Wood: Microalgae and antarctic sea ice. *Nature, Lond.* 199, 1254–1255 (1963)
- Cota, G. F.: Photoadaptation of high Arctic ice algae. *Nature, Lond.* 315, 219–222 (1985)
- Falkowski, P. G. and D. P. Stone: Nitrate uptake in marine phytoplankton: energy sources and the interaction with carbon fixation. *Mar. Biol.* 32, 77–84 (1975)
- Grossi, S. M. and C. W. Sullivan: Sea ice microbial communities. V. The vertical zonation of diatoms in an Antarctic fast ice community. *J. Phycol.* 21, 401–409 (1985)
- Harding, L. W., Jr., B. B. Prézelin, B. M. Sweeney and J. L. Cox: Diel oscillations of the photosynthesis-irradiance (*P-I*) relationship in natural assemblages of phytoplankton. *Mar. Biol.* 67, 176–178 (1982)
- Healey, F. P.: Short term responses of nutrient deficient algae to nutrient addition. *J. Phycol.* 15, 289–299 (1979)
- Hoepffner, N.: Strategies d'adaptation photosynthétique chez des diatomées de l'Océan Antarctique: variations du nombre et de la taille des unités photosynthétiques. *J. Plankton Res.* 6, 881–895 (1984)
- Holm-Hansen, O., C. J. Lorenzen, R. W. Holmes and J. D. H. Strickland: Fluorometric determination of chlorophyll. *J. Cons. perm. int. Explor. Mer* 30, 3–15 (1965)
- Jacques, G.: Some ecophysiological aspects of the Antarctic phytoplankton. *Polar Biol.* 2, 27–33 (1983)
- Kottmeier, S. T., M. A. Miller, M. P. Lizotte, L. L. Craft, B. Gulliksen and C. W. Sullivan: Ecology of sea ice microbial communities during the 1984 winter-to-summer transition in McMurdo Sound, Antarctica. *Antarctic J. U.S.* 20, 128–130 (1986)
- Lewis, M. R. and J. C. Smith: A small volume, short-term incubation time method for measurement of photosynthesis as a function of incident irradiance. *Mar. Ecol. Prog. Ser.* 13, 99–102 (1983)
- Li, W. K. W.: Temperature adaptation in phytoplankton: cellular and photosynthetic characteristics. *In: Primary production in the sea*, pp 259–279. Ed. by P. Falkowski. New York: Plenum Press 1980
- Littlepage, J. L.: Oceanographic investigations in McMurdo Sound, Antarctica. *Antarctica Res. Ser.* 5, 1–37 (1965)
- Morris, I. and K. Farrell: Photosynthetic rates, gross patterns of carbon dioxide assimilation and activities of ribulose diphosphate carboxylase in marine algae grown at different temperatures. *Physiologia Pl.* 25, 372–377 (1971)
- Neori, A. and O. Holm-Hansen: Effect of temperature on rate of photosynthesis in Antarctic phytoplankton. *Polar Biol.* 1, 33–38 (1982)
- Palmisano, A. C., J. Beeler SooHoo, S. L. SooHoo, S. T. Kottmeier, L. L. Craft and C. W. Sullivan: Photoadaptation in *Phaeocystis pouchetii* advected beneath annual sea ice in McMurdo Sound, Antarctica. *J. Plankton Res.* 8, 891–906 (1986)
- Palmisano, A. C., J. Beeler SooHoo and C. W. Sullivan: Photosynthesis-irradiance relationships in sea ice microalgae from McMurdo Sound, Antarctica. *J. Phycol.* 21, 341–346 (1985)
- Palmisano, A. C. and C. W. Sullivan: Sea ice microbial communities (SIMCOs) I. Distribution, abundance and primary production of ice microalgae in McMurdo Sound in 1980. *Polar Biol.* 2, 171–177 (1983)
- Perry, M. J., M. C. Talbot and R. S. Alberte: Photoadaptation in marine phytoplankton: response of the photosynthetic unit. *Mar. Biol.* 62, 91–101 (1981)
- Platt, T., C. L. Gallegos and W. G. Harrison: Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. *J. mar. Res.* 38, 687–701 (1980)
- Prézelin, B. B.: Light reactions in photosynthesis. *Can. Bull. Fish. aquat. Sciences* 210, 1–43 (1981)
- Prézelin, B. B. and A. C. Ley: Photosynthesis and chlorophyll *a* fluorescence rhythms of marine phytoplankton. *Mar. Biol.* 55, 295–307 (1980)
- Prézelin, B. B. and H. A. Matlick: Nutrient-dependent low-light adaptation in the dinoflagellate *Gonyaulax polyedra*. *Mar. Biol.* 74, 141–150 (1983)
- Rabinowitch, E. and Govindjee: *Photosynthesis*, 273 pp. New York: Wiley 1969
- Reeburgh, W. S.: Fluxes associated with brine motion in growing sea ice. *Polar Biol.* 3, 29–33 (1984)
- Smith, W. O. and D. M. Nelson: Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with the density field. *Science, N.Y.* 227, 163–166 (1985)
- Steeman Nielsen, E. and E. G. Jørgensen: The adaptation of plankton algae. I. The general part. *Physiologia Pl.* 21, 401–413 (1968)
- Sullivan, C. W., A. C. Palmisano and J. Beeler SooHoo: Influence of sea ice and sea ice biota on downwelling irradiance and spectral composition of light in McMurdo Sound. *Proc. Soc. photo-opt. Instrmn Engrs* 489, 159–165 (1984)
- Sullivan, C. W., A. C. Palmisano, S. Kottmeier, S. McGrath Grossi, R. Moe and G. T. Taylor: The influence of light on development and growth of sea-ice microbial communities in McMurdo Sound. *Antarctic J. U.S.* 28, 177–179 (1983)
- Sullivan, C. W., A. C. Palmisano, S. Kottmeier and R. Moe: Development of the sea ice microbial community in McMurdo Sound. *Antarctic J. U.S.* 17, 155–157 (1982)
- Verity, P. G.: Effects of temperature, irradiance, and daylength on the marine diatom *Leptocylindrus danicus* Cleve, I. Photosynthesis and cellular composition. *J. exp. mar. Biol. Ecol.* 55, 79–91 (1981)
- Whitaker, T. M. and M. G. Richardson: Morphology and chemical composition of a natural population of an ice-associated antarctic diatom *Navicula glaciei*. *J. Phycol.* 16, 250–257 (1980)
- Yentsch, C. W. and D. W. Menzel: A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. *Deep-Sea Res.* 10, 221–231 (1963)
- Zimmerman, R. C., J. Beeler SooHoo, J. N. Kremer and D. Z. D'Argenio: An evaluation of variance approximation techniques for non-linear photosynthesis-irradiance models. (In preparation)

Date of final manuscript acceptance: October 1, 1986.  
Communicated by R. S. Carney, Baton Rouge