Vol. 147: 243–256, 1997 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published February 27

Photophysiology and photoacclimation in surface sea ice algae from McMurdo Sound, Antarctica

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ABSTRACT: Microalgal absorption, pigment concentrations, photophysiology and the efficiency for energy conversion at photosystem II (*Fv/Fm*) were measured for surface ice algal communities freshly collected from saline ponds overlying fast ice in McMurdo Sound, Antarctica, during austral spring and summer 1989-90. These parameters also were measured for surface ice algae exposed in the laboratory to irradiances from 4 to 600 µmol photons m^{-2} s^{-1}. Freshly collected algae exhibited a pigment composition consistent with acclimation to high irradiance, which included low intracellular chlorophyll (chl) *a* concentrations (0.19 to 0.50 kg m^{-3}), low accessory photosynthetic pigments relative to chl *a* (chl *c*: chl *a* = 0.16 to 0.25 mol mol^{-1}; fucoxanthin: chl *a* = 0.53 to 0.77 mol mol^{-1}), and high photoprotective pigments relative to chl *a* (diatoxanthin+diadinoxanthin: chl *a* = 0.19 to 0.50 mol mol^{-1}). In contrast, the photoadaptive index for freshly collected algae (E_k = 37 to 45 µmol photons m^{-2} s^{-1}) was less than the daily average photosynthetically active radiation reaching the algal communities during the study (110 to 720 µmol photons m^{-2} s^{-1}), indicating that the algae were not acclimated to their high irradiance environment. No depression of photosynthesis was observed in the photosynthesis-irradiance curve at irradiances ≤250 µmol photons m^{-2} s^{-1} (4- to 8-fold greater than E_k). However, *Fv/Fm* (0.24 to 0.43) and the quantum yield of photosynthesis (ϕ_C, 0.018 to 0.037 mol C mol^{-1} absorbed photons) were low in freshly collected algae, which suggests that the algae were photoinhibited under natural illumination conditions. Within 32 h after shifting algae to low irradiance, a relaxation from high-light stress was observed. Photosynthetic efficiency (α^b), ϕ_C and *Fv/Fm* increased by 165, 170 and 67%, respectively, and E_k decreased by 60%. In addition, whereas total cellular concentrations of photosynthetic pigments were unchanged, diatoxanthin: chl *a* decreased by >75% due to the conversion of diatoxanthin to diadinoxanthin. The presence of xanthophyll cycling and an observed depression of relative maximum and minimum quantum yields of fluorescence in response to high irradiance indicate that algae employed the dissipation of absorbed energy from the pigment bed of photosystem II as a protection mechanism from high irradiance. Indications of additional photoprotection mechanisms and photoinhibitory damage were also observed. These results indicate that surface ice algae successfully inhabit the surface ice habitat by employing a strategy of low-light harvesting, absorbed energy dissipation, and tolerance to photoinhibitory damage.

KEY WORDS: Antarctic · Sea ice algae · Photoacclimation · Photoinhibition · Pump and probe fluorometry

INTRODUCTION

In ice covered regions of the Southern Ocean, rich microalgal communities develop at the surface of sea ice within shallow saline ponds and areas of submerged ice and snow that are infiltrated with sea water (Burkholder & Mandelli 1965, Ackley et al. 1979, Whitaker & Richardson 1980, Fritsen et al. 1994). Burkholder & Mandelli (1965) and Whitaker & Richardson (1980) reported biomass accumulations of over 100 mg chlorophyll (chl) *a* m^{-2} and 200 mg chl m^{-2}, respectively, for surface ice microalgal communities found near the Antarctic Peninsula. In addition, Fritsen et al. (1994) monitored the development of a bloom that reached 30 mg chl *a* m^{-2} in the upper 0.4 m of multi-

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year sea ice in the western Weddell Sea. The physical environment of surface ice habitats is characterized during the austral spring and summer by relatively high irradiance, a long photoperiod, and low temperature. For example, at the latitude of McMurdo Sound, Antarctica (77° 49' S) the 24 h photoperiod begins in late October and maximum surface irradiance may be greater than 1400 µmol photons m^{-2} s^{-1} by mid-summer (Arrigo et al. 1993). Where snow cover is thin or absent, a large portion of the irradiance incident at the surface may penetrate into the surface ice habitat. The temperature of liquid water associated with surface ice habitats is relatively stable at about -1.8°C.

Light and temperature conditions like those present in the surface ice habitats are known to promote photoinhibition in algae and other photosynthetic organisms (Neale 1987). Photoinhibition occurs when algae are exposed to irradiances that are significantly in excess of photosynthetic requirements (super-saturating irradiance), and is enhanced by longer exposures and by conditions such as low temperature and nutrient limitation that reduce photosynthesis. Phytoplankton that are near the sea surface may find relief from super-saturating irradiance and nutrient limitation when mixed deeper in the water column (Neale & Heaney 1991). Microalgae inhabiting the bottom of sea ice do not experience a mixing regime and are subjected to sub-freezing temperatures (Littlepage 1965), but they rarely experience super-saturating irradiance due to the strong attenuation of light by overlying ice and snow (Arrigo et al. 1991). In contrast, surface ice algae grow fixed in position in habitats overlying the sea ice where super-saturating irradiances are more common. Nevertheless, the growth and accumulation of algae within the surface ice habitats suggests that these algal species are able to acclimate to photoinhibitory conditions. Published reports examining the photosynthetic capabilities of surface ice algal communities are few (Lizotte & Sullivan 1991), presumably because the bulk of primary production in the sea ice has been attributed to bottom ice algal communities (Grossi & Sullivan 1985, Arrigo et al. 1991). Recently, Fritsen et al. (1994) have suggested that surface ice algae may contribute more substantially to production in the sea ice, particularly when snow and ice cover are thick. Consequently, the physiology of surface ice algae merits further investigation.

In this study, we investigated the photophysiology of surface pond communities associated with the fast ice in McMurdo Sound. Photosynthesis-irradiance characteristics, pigmentation, absorption characteristics and the efficiency of energy conversion at photosystem II (PSII) were examined for natural algal populations freshly collected from the field and those subjected to laboratory incubations under controlled light conditions. Our results indicate that surface ice algae employ mechanisms to dissipate excess excitation energy and that they have a high level of tolerance to photoinhibitory damage. These characteristics, however, offer only a limited acclimation to the high irradiance of the surface ice habitat.

METHODS

Sampling site. Algal samples were collected from saline surface ponds associated with tidal cracks in land-fast sea ice located near Dunlop Island, Granite Harbor, and Cape Evans in McMurdo Sound during austral spring and summer 1989-90. Algal material was cleared from a measured area of the surface ponds with a polypropylene ladle and placed in 4 l polypropylene containers. Filled containers were placed in insulated chests and transported rapidly by helicopter to Ekland Biological Laboratory at McMurdo Station. Throughout collection and subsequent manipulations care was taken to maintain sample temperature between -2 and 0°C. Upon arrival at the laboratory, algal samples were diluted to approximately 50 µg chl *a* l^{-1} using filtered (0.2 µm pore size) McMurdo Sound sea water. The total time elapsed from sample collection to the beginning of experimental work was less than 1 h.

On 4 occasions, algal samples collected from the surface ponds were incubated at either 2 or 5 different irradiance levels in the laboratory. Aliquots (1.5 l) of the diluted sample were put into 4 l wide-bottom glass flasks and placed in a Plexiglas incubator. Temperature was maintained at -2.0 ± 0.1°C using a flow of ethylene glycol cooled by a circulating water bath. Illumination, provided from below by a 500 W tungsten-halogen lamp, was passed through a 5 cm thick Plexiglas water jacket to absorb excess heat. Flasks were screened with acetate neutral density filters to provide the appropriate irradiances. For algal samples collected on 27 November and 14 December 1989, the algae were allowed to acclimate to 2 different irradiance levels: a low irradiance experimental treatment (4 µmol photons m^{-2} s^{-1}) and a high irradiance experimental treatment (600 µmol photons m^{-2} s^{-1}). At 6 to 12 h intervals for 80 h, subsamples were removed from each flask for photosynthesis-irradiance (P-E) determinations, high-performance liquid chromatography (HPLC) and fluorometric pigment measurements, particulate absorption measurements, and pump and probe fluorometry. These experiments will be referred to as the time-series experiments. For algal samples collected on 20 December 1989 and 16 January 1990, 5 irradiance treatments were used: 4, 17, 70, 200, and

600 µmol photons m^{-2} s^{-1}. Illumination was adjusted and incubation conditions were provided as described for the time-series experiments. The incubations were terminated after 24 h and subsamples were removed for P-E determinations, HPLC and fluorometric pigment measurements, particulate absorption measurements, and pump and probe fluorometry. These experiments will be referred to as the light-series experiments.

Photosynthesis vs irradiance incubations. P-E relationships were determined using a modification of the ^{14}C bicarbonate technique of Lewis & Smith (1983) as described by Robinson et al. (1995). Incubations were carried out within a photosynthetron incubator at 25 irradiances ranging from 0 to 250 µmol photons m^{-2} s^{-1}.

The photosynthetic parameters P^b_m (maximum realized photosynthetic rate, mg C mg^{-1} chl *a* h^{-1}), α^b_{inc} [photosynthetic efficiency, mg C mg^{-1} chl *a* h^{-1} (µmol photons m^{-2} $s^{-1})^{-1}$], and β^b [photoinhibition parameter, mg C mg^{-1} chl *a* h^{-1} (µmol photons m^{-2} s^{-1}) $^{-1}$] were estimated from a fit of P-E data to the equation of Platt et al. (1980) using the procedure of Zimmerman et al. (1987). The spectrally dependent parameter photosynthetic efficiency was corrected to approximate values occurring *in situ* according to the relationship (Arrigo et al. 1993):

$$\alpha^b = 43.2\, \phi_C\, \bar{a}^*_{in\,situ} \quad (1)$$

where α^b is the corrected photosynthetic efficiency, $\bar{a}^*_{in\,situ}$ is the mean specific absorption coefficient weighted to the *in situ* irradiance spectra, and 43.2 is a factor to convert to units of mol C fixed mol^{-1} photons absorbed. The quantum yield of photosynthesis (ϕ_C), calculated from Eq. (2), was assumed to be independent of variations in spectral irradiance. The photoadaptive index (E_k) was calculated as P^b_m/α^b. Quantum yield of photosynthesis was calculated using the equation:

$$\phi_C = \alpha^b_{inc}(43.2\, \bar{a}^*_{inc})^{-1} \quad (2)$$

where $\bar{a}^*_{inc}$ is the mean specific absorption coefficient weighted to the irradiance spectrum of the photosynthetron incubator. ϕ_C is defined as the ratio of the moles of carbon fixed to moles of photons absorbed.

Specific absorption coefficients. Microalgae and associated particles were collected on glass fiber filters (GF/F Whatman). The absorption coefficients ($a_{(\lambda)}$, m^{-1}) were determined by the method of Mitchell & Kiefer (1988) using the β-correction of Bricaud & Stramski (1990). Mean specific absorption coefficients ($\bar{a}^*$) were calculated as:

$$\bar{a}^* = [\text{chl } a]^{-1} \frac{\int_{700}^{400} a_{(\lambda)} E_{(\lambda)}\, d\lambda}{\int_{700}^{400} E_{(\lambda)}\, d\lambda} \quad (3)$$

where [chl *a*] is the chl *a* concentration and $E_{(\lambda)}$ is the spectral distribution of irradiance. Estimates of $\bar{a}^*_{in\,situ}$ and $\bar{a}^*_{inc}$ were determined by using $E_{(\lambda)}$ measured in the surface pond and in the photosynthetron, respectively. Estimates of $\bar{a}^*$ for the photosynthetic pigments chl *a*, chl *c*, fucoxanthin, and the photoprotective pigments (diadinoxanthin, diadoxanthin, and β-carotene) as a group were made as described by Robinson et al. (1995) using the absorption coefficients for each pigment (Bidigare et al. 1990) and $E_{(\lambda)}$ in the surface pond. These $\bar{a}^*$ were used to obtain an estimate of the percent of total pigment absorption attributable to each pigment or pigment group (%abs_i) using:

$$\%abs_i = \frac{\bar{a}^*_i \bar{R}_i}{\sum_{i=1}^{n} \bar{a}^*_i \bar{R}_i} \quad (4)$$

where $\bar{a}^*_i$ is the mean pigment specific absorption coefficient, $\bar{R}_i$ is the mean ratio of pigment to chl *a* from Table 1 (converted to mg:mg), and *i* is the pigment (chl *a*, chl *c*, fucoxanthin, or the photoprotective pigments).

Irradiance measurements. Photosynthetically active radiation (PAR, 400 to 700 nm wavelengths) within the incubators and photosynthetron was measured using a Biospherical Instruments QSL-100 PAR wand equipped with a 4π sensor. Measurements of $E_{(\lambda)}$ were made above the surface of the ice using a MER 1010 spectroradiometer (Biospherical Instruments, San Diego, CA, USA). Spectral bands were centered at 410, 441, 488, 507, 520, 540, 570, 589, 625, 656, 671, and 694 nm. Whenever possible, $E_{(\lambda)}$ was measured in the surface ponds above the algae at 0.3 m depth using a MER 1010 spectroradiometer. Continuous measurements of surface PAR were made from 9 November to 27 December using a Biospherical Instruments QSR-240 hemispherical radiometer. These data are presented as daily average PAR (µmol photons m^{-2} s^{-1}) calculated from total PAR per day (µmol photons m^{-2}) divided by seconds of daylight. To determine the fraction of surface PAR reaching algae in the surface pond, loss of PAR due to reflectance at the pond surface and attenuation in the pond was estimated from solar elevation, measurements of surface PAR, and daily observations of atmospheric conditions using the model of Arrigo et al. (1991). Daily measurements of surface PAR were discontinued after 27 December when ice conditions forced the closure of our field laboratory. After that date, PAR incident on surface ice algae was estimated using the model of Arrigo et al. (1991).

Pigments and biomass. Chl *a* was determined fluorometrically using the method of Parsons et al. (1984). Areal biomass was estimated from the total area of the surface ponds that was cleared of algae and the total chl *a* collected during each field sampling. Total pig-

ment composition was determined using HPLC. Algal cells collected on glass fiber filters (GF/F Whatman) were placed in cryovials and immediately frozen in liquid N_2. Filters were later stored at −70°C and transported to the University of Southern California for HPLC analysis within 6 mo of collection as described by Robinson et al. (1995). The intracellular chl *a* concentration (*Ci*) was determined by dividing the chl *a* concentration by the cell concentration measured in a water sample, then dividing by the average volume of an algal cell. Algal material was preserved in Lugol's iodine solution for later determination of cell number and species composition as described by Robinson et al. (1995). Cell volume was determined by measuring the linear dimensions of 30 cells per sample using a calibrated ocular micrometer.

Nutrients and salinity. Nitrate, phosphate, and silicate concentrations were determined as described by Dieckmann et al. (1992). Salinity was measured from refractive index using a refractometer (Bausch and Lomb).

Pump and probe fluorometric measurements. Fluorescence arising from chlorophyll associated with PSII (centered at 685 nm) provided a means of determining the photochemical efficiency of PSII and of assessing the extent of photoinhibition. According to the model of Butler (Kitajima & Butler 1975, Butler 1978) fluorescence emissions from algal cells where all reaction centers are open (*Fo*, dark-adapted cells) and where all reaction centers are closed by a saturating flash of light (*Fm*) can be described by:

$$Fo = E\bar{a}^{\bullet}\phi_{Fo} \quad (5)$$
$$Fm = E\bar{a}^{\bullet}\phi_{Fm} \quad (6)$$

where E is the incident PAR (photosynthetically available radiation), $\bar{a}^{\bullet}$ is the light absorption coefficient, and ϕ_{Fo} and ϕ_{Fm} are the quantum efficiencies of fluorescence for open and closed reaction centers, respectively. ϕ_{Fo}, ϕ_{Fm}, and the quantum efficiency for photochemical energy conversion by PSII (ϕ_{II}) can be described in terms of the rate constants of energy flow through photosystem II [photochemistry (k_p), fluorescence (k_f), thermal dissipation (k_d), and spillover to PSI (k_s)]:

$$\phi_{Fo} = k_f/(k_f + k_p + k_d + k_s) \quad (7)$$
$$\phi_{Fm} = k_f/(k_f + k_d + k_s) \quad (8)$$
$$\phi_{II} = k_p/(k_f + k_p + k_d + k_s) \quad (9)$$

Substituting Eqs. (5) through (8) into Eq. (9) yields:

$$\phi_{II} = (Fm - Fo)/Fm = Fv/Fm \quad (10)$$

where ϕ_{II} can be described by *Fv* (variable fluorescence, *Fm* − *Fo*) and *Fm*. In higher plants and algae, depression of ϕ_C and *Fv*/*Fm* is observed during supersaturating illumination. Changes in *Fv*/*Fm* and the quantum yield of photosynthesis are often proportional (Björkman & Demmig 1987, Greene et al. 1991) and the degree of *Fv*/*Fm* depression has been used as a measure of photoinhibition (Björkman 1987).

Fluorescence measurements were made using a custom-built fluorometer as described by Kolber et al. (1988). Algal samples were dark adapted for 20 min in an opaque glass reservoir cooled to −2.0°C. The dark-adapted sample was circulated through a 200 µl quartz flow-through cuvette positioned in the fluorometer sample chamber. Fluorescence resulting from a weak probe flash applied before (*Fo*) and 70 µs after (*Fm*) a strong saturating pump flash was measured. Each reported value of *Fo* and *Fm* was a mean of 25 to 30 separate determinations. Consequently, standard deviation from the mean was small (5 to 10%).

For the light-series experiments, the sensitivity of the fluorometer detector and the intensity of the probe flash (E_{pr}) were held constant, allowing determination of relative values for the quantum yield of fluorescence using the equation:

$$\phi_F = F\bar{a}^{\bullet}([\text{chl}]\,E_{pr})^{-1} \quad (11)$$

where ϕ_F is the quantum yield of fluorescence and [chl] is the chlorophyll concentration. The maximum (ϕ_{Fm}^{rel}) and minimum (ϕ_{Fo}^{rel}) relative ϕ_F are:

$$\phi_{Fm}^{rel} = Fm\,(\bar{a}^{\bullet}[\text{chl}])^{-1} \quad (12)$$
$$\phi_{Fo}^{rel} = Fo\,(\bar{a}^{\bullet}[\text{chl}])^{-1} \quad (13)$$

For presentation purposes, relative ϕ_F were normalized so that the highest values equaled 100.

By varying the intensity of the pump flash (E_{pu}) over a range of sub-saturating intensities, a flash-saturation curve was generated and fitted to a 1-hit Poisson function (Falkowski & Kolber 1993):

$$\frac{F - Fo}{Fo} = \frac{Fm - Fo}{Fo}(1 - e^{-E_{pu}\sigma_{PSII}}) \quad (14)$$

where F is the fluorescence resulting from a probe flash applied 70 µs after a sub-saturating pump flash and σ_{PSII} is the functional cross-sectional area of photosystem II. Because only relative intensity could be determined for the series of probe flashes, σ_{PSII} is a relative measure of the functional cross-sectional area of photosystem II. Equipment limitations allowed determination of σ_{PSII} only for the time-series experiments.

RESULTS

At each collection site, algal material was found in aggregates or mats approximately 2 to 5 mm in thickness lying in pits and depressions (<10 cm in diameter) at the bottom of the surface ponds. Areal chlorophyll biomass measured for all field samplings ranged from 10 to 51 mg chl *a* m^{-2}. The diatom *Navicula glaciei* van

Table 1. Intracellular chl *a* concentrations (*Ci*, kg m^{-3}) and molar pigment ratios of chl *c*, fucoxanthin (fucox), diadinoxanthin + diatoxanthin (dd+dt) and β-carotene (β-car) to chl *a* for surface ice algae collected on the specified dates during the 1989-1990 field season from surface ponds located near Dunlop Island (DI), Granite Harbor (GH), and Cape Evens (CE), McMurdo Sound, Antarctica. Values are the means of duplicate measurements and the range was <10% of the mean

Site	Date	chl *c* : chl *a*	fucox : chl *a*	dd+dt : chl *a*	β-car : chl *a*	*Ci*
DI	27 Nov	0.19	0.72	0.50	0.08	0.50
DI	14 Dec	0.16	0.53	0.25	0.05	0.19
GH	20 Dec	0.19	0.63	0.32	0.04	0.47
GH	16 Jan	0.20	0.60	0.19	0.07	0.33
CE	19 Jan	0.25	0.77	0.34	0.05	0.41
Mean		0.20	0.65	0.32	0.06	0.38

Heurck was the dominant algal species in all field samples (>99% of the cells present), supporting our assumption that the measurements reported in this study reflect the physiology and cellular composition of this single algal species. Mean cell volume and cell surface area were 1031 μm^3 and 762 μm^2, respectively, and did not differ significantly between collections.

In the ponds where collections were made, salinity ranged from 32 to 34‰ and temperature from −1.8 to −1.6°C. Nitrate, silicate, and phosphate concentrations were ≥28, 69, and 1.8 µmol l^{-1}, respectively. These high nutrient concentrations indicate that nutrients were not depleted in the surface ponds and that no nutrient limitation of algal physiology should be expected.

The pigment composition of the surface pond communities was characteristic of diatoms, and include the photosynthetic pigments chl *a*, chl *c*, and fucoxanthin (fucox), as well as the photoprotective pigments diatoxanthin (dd), diadinoxanthin (dt), and β-carotene (β-car) (Table 1). Molar ratios of chl *c*:chl *a* and fucox:chl *a* averaged 0.20 and 0.65, respectively, and were low when compared to literature values of 0.11 to 0.64, and 0.61 to 0.83, respectively, for sub-tropical diatom cultures (Stauber & Jeffrey 1988). Compared to polar diatom cultures (Sakshaug et al. 1991), chl *c*:chl *a* fell within the lower values and fucox:chl *a* within the middle values of the reported ranges of 0.10 to 0.89 and 0.43 to 0.63, respectively. Intercellular chl *a* concentrations (*Ci*) averaged 0.38 kg m^{-3} and also fell within the lower range of values reported for diatoms (0.2 to 10.2 kg m^{-3}; Morrow 1987). Photoprotective pigments comprised approximately 40% of the total carotenoid content of the algal cells. Mean pigment-specific absorption coefficients ($\bar{a}^*_i$) for chl *a*, chl *c*, and fucox were determined to be 0.006, 0.014, and 0.013 m^2 mg^{-1} pigment, respectively (Table 2). The photoprotective pigments dd, dt and β-car were grouped into a single $\bar{a}^*_i$ determined to be 0.017 m^2 mg^{-1} pigment. Using the mean pigment:chl *a* ratios presented in Table 1 it was estimated that approximately 70% of total absorption of PAR by pigment was attributable to the photosynthetic pigments (chl *a*, chl *c*, and fucox), whereas 30% was attributable to photoprotective pigments (Table 2). We note that absorption by photoprotective pigments did not significantly affect our estimates of ϕ_C (calculated from Eqs. 2 & 3) because the absorption spectra of these pigments do not strongly overlap the spectrum of the tungsten light source used in P-E incubations.

Fv/Fm and ϕ_C for freshly collected algal samples (Table 3) were low relative to the values of 0.65 and 0.1 mg C mg^{-1} chl *a* (µmol photons m^{-2} s^{-1})$^{-1}$, respectively, thought to be maximal for these 2 parameters. *Fv/Fm* ranged from 37 to 66% of the maximum value while ϕ_C ranged from 18 to 37% of the maximum value. P^b_m, α^b, and E_k were high when compared with bottom ice algae, but similar to values reported by Lizotte & Sullivan (1991) for *Navicula glaciei*-dominated surface communities from McMurdo Sound. No inhibition of photosynthetic rate was observed at saturating irradiances as great as 250 µmol photons m^{-2} s^{-1}. E_k ranged from 37 to 45 µmol photons m^{-2} s^{-1} and was low relative to average PAR reaching the surface ponds communities, which indicates that for most of the day ambient irradiance was super-saturating for photosynthesis. During our study, the light period was 24 h but total PAR reaching the surface of the tidal cracks varied with diurnal and seasonal changes in

Table 2. Mean pigment specific absorption coefficients ($\bar{a}^*_i$, m^2 mg^{-1} pigment) determined for chl *a*, chl *c*, and fucoxanthin. $\bar{a}^*_i$ for the photoprotective pigments (diadinoxanthin, diatoxanthin, and β-carotene) are lumped into a single coefficient. The percentage of total absorption by pigments that is attributed to each pigment or pigment group (%Abs) is also presented. Abbreviations as in Table 1

	chl *a*	chl *c*	fucox	dd+dt+β-car
$\bar{a}^*_i$	0.0056	0.014	0.013	0.017
%Abs	17	13	40	30

Table 3. P_m^b (mg C mg^{-1} chl *a* h^{-1}), α^b [mg C mg^{-1} chl *a* h^{-1} (µmol photons m^{-2}s^{-1})$^{-1}$], E_k (µmol photons m^{-2}s^{-1}), ϕ_C (mol C mol^{-1} photons), and *Fv/Fm* (dimensionless) for surface ice algae collected on the specified dates during the 1989-90 field season from surface ponds located near Dunlop Island (DI), Granite Harbor (GH), and Cape Evens (CE). Abbreviations as in Fig. 1

Site	Date	P_m^b	α^b	E_k	ϕ_C	*Fv/Fm*
DI	27 Nov	1.02	0.027	38	0.037	0.43
DI	14 Dec	0.82	0.022	37	0.033	0.33
GH	20 Dec	1.20	0.032	38	0.029	0.31
GH	16 Jan	0.50	0.011	45	0.018	0.24
CE	19 Jan	1.10	0.026	42	0.025	0.35

solar elevation and changes in cloud cover. Daily averaged PAR incident on the algal aggregates ranged from 110 to 720 µmol photons m^{-2} s^{-1} from 9 November to 27 December. Over the same time period maximum daily PAR ranged from 340 to 1200 µmol photons m^{-2} s^{-1}. Daily measurements of surface PAR were discontinued after 27 December when ice conditions forced the closure of our field laboratory. Modeled estimates of average PAR for 28 December to 20 January generated using cloud cover data from historical records ranged from 150 to 700 µmol photons m^{-2} s^{-1}.

Time-series incubations

The temporal responses of phytoplankton that were shifted to 4 µmol photons m^{-2} s^{-1} can be divided into 2 phases: an early phase (0 to 32 h after the light shift) representing relaxation from high irradiance stress and a late phase (32 to 80 h after the light shift) representing acclimation to low irradiance. During the first 32 h after high-light stress was relieved by incubating the algae under low irradiance (4 µmol photons m^{-2} s^{-1}), dt:chl *a* decreased rapidly, falling to <25% of initial values (Fig. 1a). Over the same time period, *Ci* and dd+dt:chl *a* remained relatively unchanged (Fig. 1b), which indicates that the decrease in dt:chl *a* resulted from a conversion of dt to dd. The mean ± SD for chl *c*:chl *a* and fucox:chl *a* were 0.18 ± 0.03 and 0.56 ± 0.05 and did not exhibit any temporal trends. Coinciding with the decrease in dt:chl *a* were a 67% increase in *Fv/Fm* (Fig. 1c) and a 170% increase in ϕ_C (Fig. 1d). During the early phase the mean specific absorption coefficient ($\bar{a}^*$) was relatively invariant (Fig. 2a), which indicates that the 165% increase in α^b (Fig. 2b) resulted primarily from changes in ϕ_C. P_m^b increased and E_k decreased by 15 and 60%, respectively (Fig. 2b, c).

The late phase (32 to 80 h after the light shift) was characterized by a sharp increase in *Ci* (Fig. 1b) and sharp decreases in $\bar{a}^*$, α^b, and P_m^b (Fig. 2a, b). The lower values for $\bar{a}^*$ were likely due to greater pigment packaging (Morel & Bricaud 1981) resulting from the 6- to 7-fold increase in *Ci*. The chl *a*-specific parameters P_m^b and α^b decrease nearly proportionally during the late phase of the time-series (Fig. 2b), thereby producing only a small temporal decrease in E_k (Fig. 2c). The decrease in dd+dt:chl *a* and dt:chl *a* which was observed between 32 and 80 h after the light shift also coincided with the increase in *Ci* (Fig. 1b) and, therefore, was the result of an increase in chl *a* rather than a decrease in dd or dt. Significant increases in cell-specific saturated photosynthetic rate (P_m^{cell}) and photosynthetic efficiency (α^{cell}) were observed during the early and late phase, illustrating the increased photosynthetic capabilities of the cell in response to a low-light shift.

For time-series incubations where light stress was kept high (600 µmol photons m^{-2} s^{-1}), pigment ratios and photosynthetic parameters showed similar but smaller changes than those observed in the early phase when high-light stress was relieved (4 µmol photons m^{-2} s^{-1}). Immediately after the incubations began, dt:chl *a* decreased steadily, stabilizing at 80% of its initial value by Hour 32 (Fig. 3a). Coinciding with the decrease in dt:chl *a*, *Fv/Fm* (Fig. 3c) increased by 15%. ϕ_C increased by 85% from its initial value during the first 18 h after the light shift (Fig 3d), then decreased slightly by Hour 32. *Ci* and dd+dt:chl *a* (Fig. 3b) remained stable for the early time points (until 18 to 32 h). Later in the time-series, *Ci* exhibited a slight increasing trend and dd+dt:chl *a* exhibited a slight decreasing trend. The data for α^b, P_m^b, and $\bar{a}^*$ are not shown but are summarized as follows. Changes in α^b mimicked those of ϕ_C, increasing by 75% during the first 18 h after the light shift from an initial value of 0.020 mg C mg^{-1} chl *a* (µmol photons m^{-2} s^{-1})$^{-1}$. P_m^b (0.90 ± 0.05) and $\bar{a}^*$ (0.0138 ± 0.0006) were relatively unchanged during the time-course.

Light-series incubations

The results from the time-series experiments showed that most of the rapid responses related to a relaxation from high-light stress (i.e. changes in dt:chl *a*, *Fv/Fm*,

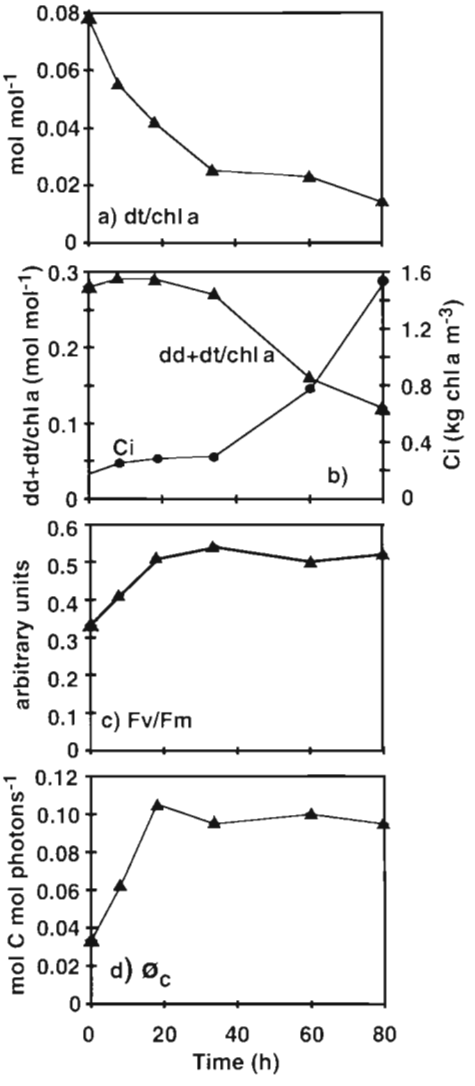

Fig. 1. A time-series of (a) the molar ratio of diatoxanthin : chl *a* (dt : chl *a*), (b) the molar ratio of diadinoxanthin+diatoxanthin : chl *a* (dd+dt : chl *a*) and the intracellular chl *a* concentration (*Ci*), (c) the efficiency for energy conversion at photosystem II (*Fv/Fm*), and (d) the quantum yield of photosynthesis ($ø_C$), for surface ice algal collected on 14 December 1989 and incubated in the laboratory at an irradiance of 4 µmol photons m^{-2} s^{-1} Pigment ratios are the means of duplicate measurements and the range was < 10% of the mean

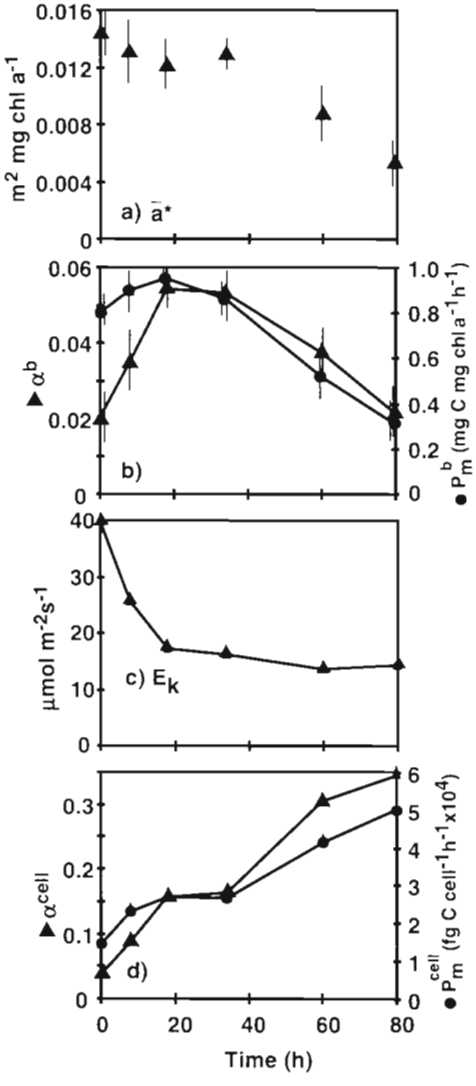

Fig. 2. A time-series of (a) mean specific absorption coefficient ($\bar{a}^*$), (b) maximum photosynthetic rate normalized to chlorophyll (P_m^b) and maximum photosynthetic rate normalized to chlorophyll (α^b), (c) photoadaptive index (E_k), and (d) maximum photosynthetic rate normalized to cell number (P_m^{cell}) and maximum photosynthetic rate normalized to chlorophyll (α^{cell}), for surface ice algae collected on 14 December 1989 and incubated in the laboratory at an irradiance of 4 µmol photons m^{-2} s^{-1}. Units for α^b are mg C mg chl a^{-1} h^{-1} (µmol photons m^{-2} $s^{-1})^{-1}$ and α^{cell} are fg C cell^{-1} h^{-1} × 10^4 (µmol photons m^{-2} $s^{-1})^{-1}$ Error bars indicate (a) range of duplicate measurements and (b) standard deviation

and $ø_C$) occurred during the first ca 24 h following the light shift and that responses related to acclimation to low irradiance (i.e. increases in *Ci*) were most strongly developed after the first ca 24 h following the light shift. Therefore, an incubation period of 24 h was chosen for the light-series experiments to focus on responses due to relaxation from high-light stress while minimizing the responses due to acclimation to low irradiance. At the end of the 24 h light-series incubations, no appreciable differences in *Ci*, chl *c* : chl *a*, and fucox : chl *a* (means ± SD for the 5 light treatments were 0.38 ± 0.04, 0.18 ± 0.02, and 0.63 ± 0.05 kg chl *a* m^{-3}, respectively) were observed among the 5 light treatments, which suggests that few changes due to acclimation to low irradiance had occurred.

The ratio dt : chl *a* progressively increased with increased incubation irradiance (Fig. 4a). In contrast, dd+dt : chl *a* did not change greatly among light treat-

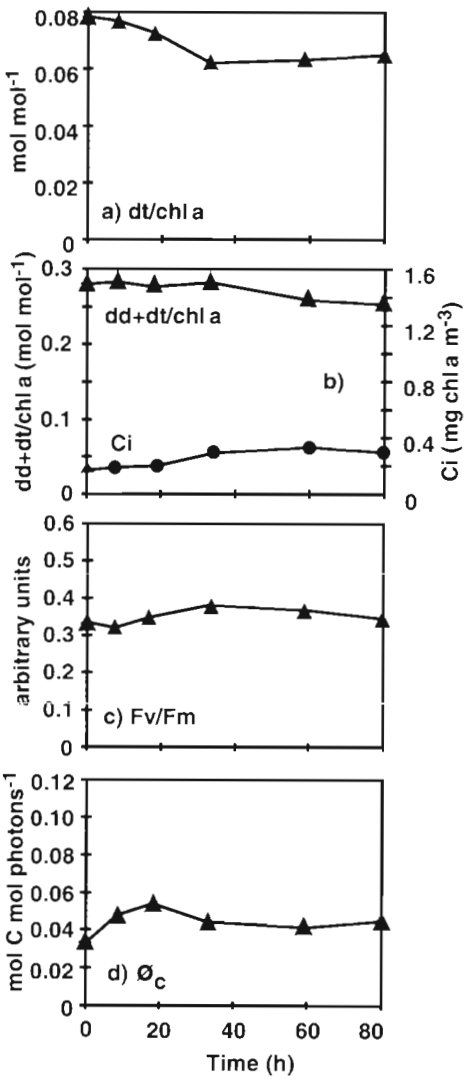

Fig. 3. A time-series of (a) dt:chl *a*, (b) dd+dt:chl *a*, *Ci*, (c) *Fv/Fm*, and (d) $\varnothing_C$, for surface ice algal collected on 14 December 1989 and incubated in the laboratory at an irradiance of 600 µmol photons m^{-2} s^{-1}. Abbreviations as in Fig. 1. Pigment ratios are the means of duplicate measurements and the range was < 10% of the mean

ments (Fig. 4b), indicating that the changes in dt resulted from interconversion between dd and dt. P^b_m was relatively unchanged among irradiance treatments (mean ± SD for the 5 light treatments = 1.32 ± 0.12 mg C mg^{-1} chl *a*) and α^b became smaller as incubation irradiance increased (Fig. 4c), which resulted in larger E_k with higher irradiance (Fig. 4d). Values for $\varnothing_C$ (Fig. 4e) and *Fv/Fm* (Fig. 4f) also became smaller with higher irradiance. Because $\bar{a}^*$ showed little variation among irradiance treatments (mean ± SD for the 5 light treatments = 0.013 ±0 .002 m^2 mg^{-1} chl *a*), the changes in α^b were primarily attributed to the changes in $\varnothing_C$. In contrast, σ_{PSII} became progressively smaller as incubation irradiance increased (Fig. 4g). For the light-series experiments, reductions in *Fv/Fm* in response to higher irradiance were accompanied by large reductions in the relative $\varnothing_{Fm}$ ($\varnothing^{rel}_{Fm}$) and comparatively small reductions in the relative $\varnothing_{Fo}$ ($\varnothing^{rel}_{Fo}$) (Fig. 5). For example, *Fv/Fm* was 47% lower in algae incubated at 600 µmol photons m^{-2} s^{-1} than in those incubated at 4 µmol photons m^{-2} s^{-1}. Similarly, $\varnothing^{rel}_{Fm}$ was 40% lower whereas $\varnothing^{rel}_{Fo}$ was 8% lower.

Photoinhibition

Our results provide evidence that *Navicula glaciei* was photoinhibited under the irradiance conditions prevailing in the tidal crack habitats. The limited output of the photosynthetron incubator available at the remote McMurdo Sound location prevented direct measurement of photosynthesis and potential photoinhibition over the entire range of irradiances found within the tidal crack environment. At irradiances up to 250 µmol photons m^{-2} s^{-1} (4- to 8-fold greater than E_k), no photoinhibition of photosynthesis was observed. However, surface ice algae exposed to high irradiance in the field and the laboratory exhibited a depression in *Fv/Fm* and $\varnothing_C$ (Table 3, Figs. 3c, d & 4e, f) characteristic of organisms experiencing photoinhibition (Björkman 1987). Furthermore, when high-light stress was relieved under laboratory conditions, both *Fv/Fm* and $\varnothing_C$ rapidly increased to values approaching the maximum obtainable values (Fig. 1c, d), indicating that depression of *Fv/Fm* and $\varnothing_C$ was in response to high irradiance. The strong correlation between *Fv/Fm* and $\varnothing_C$ obtained from field and laboratory data is consistent with the proportional relationship between these 2 parameters often observed during photoinhibition in higher plants (Björkman 1987). If *Fv/Fm* is used as a measure of photoinhibition, then at the time of our collections as much as 34 to 63% of PSII efficiency was lost in response to high irradiance (using *Fv/Fm* values from Table 3 and a maximum *Fv/Fm* from Fig. 1c).

DISCUSSION

Photosynthesis by the *Navicula glaciei*-dominated, surface ice algal communities was super-saturated with respect to incident PAR over most of the 24 h light period during this study. In photoacclimated microalgae, the onset of light-saturated photosynthesis (i.e. E_k) often occurs at irradiances similar to those of the ambient light field, thereby striking a balance between the energy absorbed by photosynthetic pigments and the ability to use that energy for photosynthetic carbon

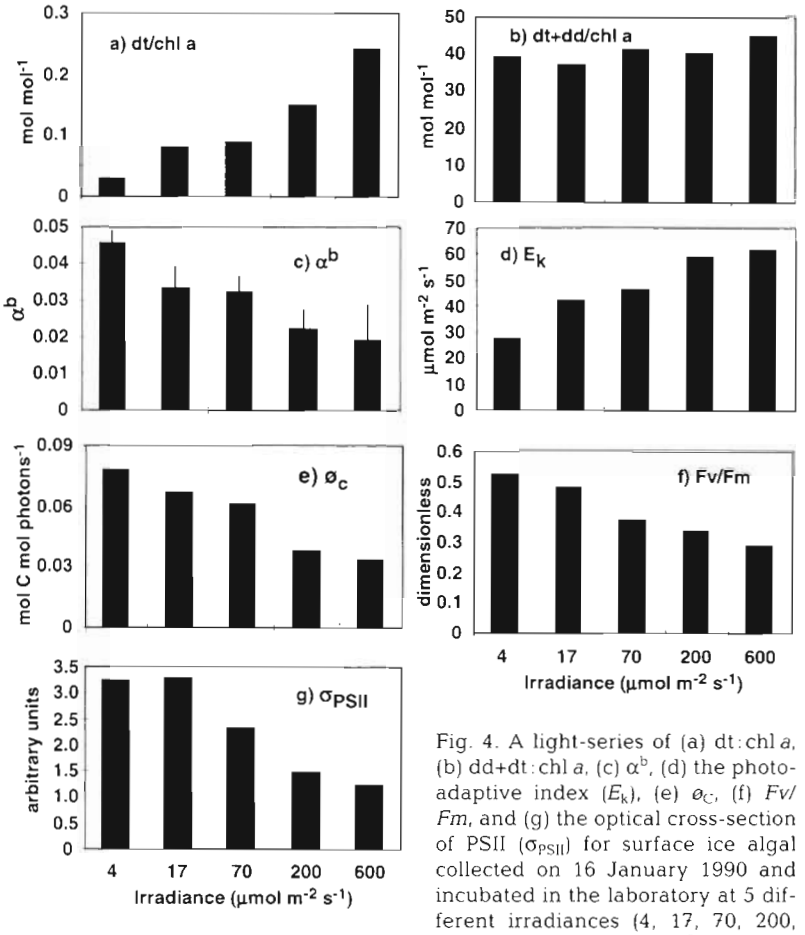

Fig. 4. A light-series of (a) dt:chl *a*, (b) dd+dt:chl *a*, (c) α^b, (d) the photoadaptive index (E_k), (e) ϕ_C, (f) *Fv/Fm*, and (g) the optical cross-section of PSII (σ_{PSII}) for surface ice algal collected on 16 January 1990 and incubated in the laboratory at 5 different irradiances (4, 17, 70, 200, and 600 µmol photons m^{-2} s^{-1}). Units for α^b are mg C mg^{-1} chl *a* h^{-1} (µmol photons m^{-2} $s^{-1})^{-1}$; and units for σ_{PSII} are arbitrary. Abbreviations as in Figs. 1 & 2. Error bars indicate standard deviation

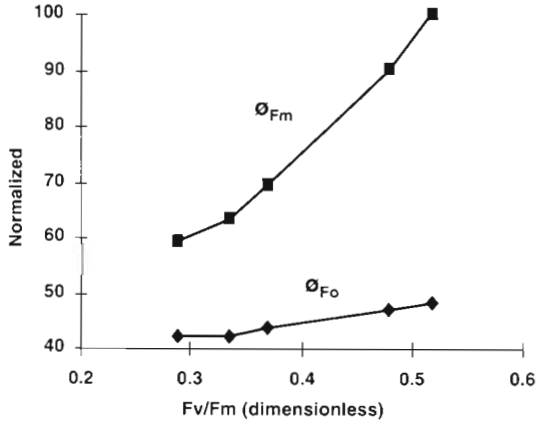

Fig. 5. Relative values for the maximum (ϕ_{Fm}^{rel}) and minimum (ϕ_{Fo}^{rel}) quantum yield of fluorescence determined for surface ice algae incubated at 5 different irradiances during the light-series experiments

assimilation (Richardson et al. 1983, Raven & Geider 1988). Daily average PAR incident on the algal aggregates was 2- to 20-fold in excess and daily maxima were 7- to 32-fold in excess of the capacity of the alga to use light energy (E_k; Table 3) for photosynthetic carbon assimilation. However, photoacclimation is the result of light history and, consequently, may not reflect acclimation to the light conditions at the time of sampling. At the latitude of McMurdo Sound (ca 78° S), daily light period, maximum PAR, and daily average PAR increase rapidly during the spring months (September to October; Sakshaug & Slagstad 1991). Therefore, the values for P_m^b, α^b, and E_k reported in the present study may reflect acclimation to the lower incident PAR that reached the tidal crack habitat earlier in the season. The length of our study spanned approximately 2 mo (November through mid-January), during which time daily average PAR ranged from 110 to 720 µmol photons m^{-2} s^{-1}. Assuming that *N. glaciei* shows a measurable response to a light shift in 3 to 4 d (Lizotte & Sullivan 1991), sufficient time had elapsed by the end of our study for at least partial acclimation to be observed. However, E_k values for algal communities collected in late-December and January were not significantly larger than for algal communities collected in November and early-December, and showed no increasing trend with time (Table 3). These observations indicate that the algal communities were not well acclimated to the irradiance conditions existing in the surface ice habitat.

Considering the aggregate growth habit of *Navicula glaciei*, one explanation for the apparent lack of acclimation to ambient irradiance may be that the bulk of the cells were actually experiencing much lower irradiance, due to self-shading within the aggregate (Vincent & Howard-Williams 1989): algal cells at the upper surface of the aggregate may have absorbed sufficient light to reduce to sub-saturating levels the light reaching cells lower in the aggregate. An estimate of light available to algae within the lower layers of the aggregate may be obtained using the Lambert-Beers relationship:

$$E_0 = E_z e^{(-\bar{a} \cdot Cb)} \quad (15)$$

where E_0 is the spectral irradiance reaching the top of the aggregate, E_z is the spectral irradiance emerging from the bottom of the aggregate, and *Cb* is the areal biomass accumulation in the mat. *Cb* at the sampling sites ranged between 10 to 50 mg chl *a* m^{-2}. Using an average specific absorption coefficient ($\bar{a}^*$, 0.012 m^2 mg^{-1} chl *a*) for surface ice algae from our results and assuming negligible attenuation by water within the 5 mm thickness of the aggregate, then PAR remaining after passing through the aggregate (49 to 86% of PAR incident on the aggregate surface) would still be saturating for photosynthesis, even when the degradation of spectral light quality is considered. Therefore, it is unlikely that the density of cells within the aggregates was sufficient to reduce irradiance to sub-saturating levels, although self-shading may play a role in reducing irradiance where standing crops of algae are greater (e.g. >100 mg chl *a* m^{-2}; Burkholder & Mandelli 1965, Whitaker & Richardson 1980).

Under high irradiance conditions, such as those experienced by algae in the surface ice habitat, photoacclimation may be manifested as low light-harvesting capacity and high photosynthetic capacity (Richardson et al. 1983). As noted above, photosynthesis in surface ice communities was super-saturated at ambient irradiance, which indicates that light-harvesting capacity was apparently in excess and/or photosynthetic capacity was insufficient to effectively use the ambient light for photosynthesis. However, the *Navicula glaciei*-dominated algal assemblages collected from tidal cracks exhibited a cellular pigment composition, which was low in chl *a* and accessory pigments and high in photoprotective pigments, consistent with a strategy of low light-harvest capacity. Low cellular content of photosynthetic pigments is commonly reported for algae acclimated to high irradiance (Falkowski 1980). For example, Kolber et al. (1988) observed that microalgae acclimated to an irradiance of 1000 µmol photons m^{-2} s^{-1} had 50% less chl *a* per cell and 30% less chl *c*:chl *a* than microalgae grown at 7 µmol photons m^{-2} s^{-1}. In addition, non-photosynthetic pigments present in high concentrations within the cell may absorb a significant portion of incident irradiance, thereby reducing that which is available for absorption by photosynthetic pigments (Dubinsky et al. 1986). Bidigare et al. (1993) reported that high cellular content of the carotenoid astaxanthin within snow algae *Chlamydomonas* sp. restricted irradiance available for photosynthesis to wavelengths >550 nm. Robinson et al. (1995), working with *N. glaciei* from tidal crack habitats, observed a decrease in the efficiency of energy transfer to PSII for wavelengths between 450 to 550 nm that they attributed to absorption by photoprotective pigments. In the present study, the cellular content of the photoprotective pigments diadinoxanthin (dd), diatoxanthin (dt), and β-carotene (β-car) also was high, representing 40% of the carotenoid content (Table 1). We calculate that absorption by photoprotective pigments accounted for approximately 30% of total absorption of incident PAR by all pigments (Table 2), making this portion of the absorbed energy unavailable for photosynthesis. Furthermore, dd and dt also may function to mediate excess energy dissipation from the pigment bed, thereby providing additional protection from excess incident irradiance. These observations indicate that the surface ice algae harvested light energy for use in photosynthesis with low efficiency. This conclusion is supported by absorption efficiency measurements of individual *N. glaciei* cells collected from a surface ice habitat (Robinson et al. 1995) that show that at the red absorption peak (676 nm, a wavelength of low absorption by non-photosynthetic pigments) less than 15% of irradiance incident on cells was absorbed.

Accepting that the efficiency of light harvest was low for surface ice communities, the implication is that photosynthetic capacity was constrained, possibly by environmental conditions that were present within the surface ice, thereby restricting the ability of surface ice algae to acclimate to high irradiance. One possibility is that the low temperature of the tidal crack habitat imposed an upper limit on photosynthetic capacity and that this restriction, in combination with high irradiance, lead to the observed super-saturation of photosynthesis. It is well established that short-term decreases in temperature inhibit photosynthesis (reviewed by Davison 1991) and growth (Eppley 1972). Given sufficient time these short-term effects of temperature may be partially or fully overcome as algae employ mechanisms that allow acclimation to the lower temperature (Christopherson 1973). However, Eppley (1972) presented evidence that maximal growth rate for temperate algae is controlled by temperature and, therefore, does not compensate for temperature inhibition. Similarly, it has been suggested that polar microalgae do not compensate for the inhibitory effects of the low temperatures on photosynthesis (Neori & Holm-Hanson 1982, Li et al. 1984). For example, photosynthetic capacity typically ranges from 2 to 15 mg C mg^{-1} chl *a* h^{-1} for temperate microalgae (Falkowski 1981), whereas the range is much lower for polar microalgae, falling between 0.3 to 2.0 mg C mg^{-1} chl *a* h^{-1} (Sakshaug & Slagstad 1991), indicating that full compensation for low temperature is not attained by polar microalgae. Li et al. (1984) reported that photosynthetic capacities for polar microalgae are often less that those predicted for temperate algae grown at the same low temperature. The factors responsible for the apparent lack of acclimation to low temperature are not fully understood. Li et al.

(1984) suggested that polar microalgae may lack the genetic ability to overcome low temperature limitation. Berry & Björkman (1980) have suggested that low temperatures limit photosynthesis by lowering the activity of carbon fixation enzymes and that the energetic expense of producing the quantity of enzyme necessary to overcome this limitation is too great. In the present study, photosynthetic capacity (Table 3) was within the range typically reported for polar microalgae from variety of habitats, suggesting that temperature may limit photosynthetic capacity surface ice algae.

The prolonged exposure to super-saturating irradiance experienced by *Navicula glaciei* in the tidal crack habitat may have lead to photoinhibition (Neale 1987). At low irradiance, photosynthetic rate increases linearly with increasing irradiance over the light-limited portion of the photosynthesis-irradiance curve. Here the capacity to process excitation energy exceeds the rate at which energy is absorbed, and most of the energy of absorbed photons is used for photochemistry (Demmig-Adams 1990). At super-saturating irradiances, the capacity to process the energy of absorbed photons is exceeded, leading to an accumulation of excess excitation energy (Osmond 1981). The reduction in photosynthetic rate and the maximum quantum yield of photosynthesis characteristic of photoinhibition may result from the damaging effect that excess excitation energy has on PSII and from cell-mediated processes that dissipate excess energy through non-photochemical pathways, thereby reducing the possibility of photoinhibitory damage.

The surface pond algae were photoinhibited under *in situ* environmental conditions as indicated by the depression of *Fv/Fm* and ϕ_C in fresh field collections and the response of both parameters to changes in irradiance in the laboratory (Table 3, Figs. 1c, d & 4e, f) Some insight as to whether the depression of ϕ_C and ϕ_{II} observed in this study was the result of damage to PSII or cell-mediated dissipation of excess energy through non-photochemical pathways may be obtained by examining ϕ_{Fo}^{rel} and ϕ_{Fm}^{rel} as high-light stress was relieved in the low-light incubation studies. It is believed that the rate constant for photochemistry (k_p) is reduced as a result of damage to PSII (Kitajima & Butler 1975, Butler 1978, Demmig-Adams 1990). A reduction of k_p is observed in the fluorescence signal as an increase in ϕ_{Fo} and a reduction in *Fv/Fm* (Eqs. 7 to 9). The major source of changes in non-photochemical energy dissipation within the pigment bed is through thermal pathways (increased k_d), assuming that changes in k_s and k_f are negligible (Butler 1978). An increase in k_d is observed in the fluorescence signal as reductions in ϕ_{Fo}, ϕ_{Fm}, and *Fv/Fm*. The reductions in ϕ_{Fo} should be comparatively smaller than those of ϕ_{Fm}, as can be seen from Eqs. (7) & (8). In the present study, ϕ_{Fo}^{rel} was 8% less and ϕ_{Fm}^{rel} was 40% less in algae incubated at 600 µmol photons m^{-2} s^{-1} than those incubated at 4 µmol photons m^{-2} s^{-1} (Fig. 5). It must be kept in mind that changes in ϕ_{Fo}^{rel} and ϕ_{Fm}^{rel} may result from a combination of changes in k_p and k_d, and from other processes that alter chlorophyll cyclic electron flow around PSII and energy dissipation within the PSII antenna (Bonaventura & Myers 1969, Falkowski et al. 1986, 1988, Weis & Berry 1987, Rees & Horton 1990). Consequently, the magnitude of thermal dissipation or the degree of protection provided from high irradiance is difficult to evaluate. However, our observations are consistent with a change in thermal dissipation (decreased k_d). Furthermore, larger thermal dissipation of absorbed energy could explain the lower σ_{PSII} observed in the light-series experiment as incubation irradiance increased (Fig. 4g). Genty et al. (1990) reported that in several species of higher plants an increase in non-photochemical quenching resulted in a decrease in σ_{PSII}. We propose, therefore, that dissipatory processes were in operation within the pigment bed of *Navicula glaciei* and that at least a portion of the initial increase in *Fv/Fm* and ϕ_C observed in the time-series experiments (Fig. 1c, d) resulted from a relaxation of these protective processes.

Our observations that a xanthophyll cycle was present and functioning in surface ice algae provides further evidence that a thermal dissipation process was operating in the algae. Xanthophyll cycles involve reversible light-driven conversions of xanthophyll epoxides into epoxide-free forms. The presence of the epoxide-free form is thought to mediate the dissipation of excitation energy from the pigment bed, thereby providing protection from photoinhibitory damage (Demmig-Adams 1990). Higher plants and microalgae growing under higher irradiance are found to have an elevated content of xanthophyll cycle pigments relative to those growing under lower irradiance (Mandelli 1972, Thayer & Björkman 1990, Sakshaug et al. 1991). A sudden shift to a higher irradiance results in a rapid conversion of the epoxide forms to the epoxide-free forms (Demmig et al. 1987, Demmers et al. 1991). Increases in zeaxanthin, the epoxide-free form in higher plants, have been correlated to increases in fluorescence quenching and decreases in *Fv/Fm* attributable to increased thermal dissipation of absorbed light energy in the antenna of PSII (Demmig-Adams 1990). Recently, the ratio of diatoxanthin (epoxide-free form in diatoms) to chl *a* has been linearly correlated to non-photochemical quenching in the diatom *Chaetoceros muelleri* Lemm. (Olaizola & Yamamoto 1994), indicating that the diadinoxanthin/diatoxanthin cycle operating in diatoms has a photoprotective role similar to that proposed for the violaxanthin/antheraxanthin/zeaxanthin cycle in higher plants.

Despite the strong correlation between *Fv/Fm* and ϕ_C, suppression of the efficiency of PSII photochemistry in response to super-saturating irradiances cannot completely account for the depression of ϕ_C observed for *Navicula glaciei* from tidal crack habitats. When high irradiance stress was relieved by incubating *N. glaciei* collected from the field under low irradiance laboratory conditions, *Fv/Fm* increased by 62% during the first 16 h of incubation (Fig. 1c). During the same time period, ϕ_C increased by over 150% (Fig. 1d). Assuming that changes in *Fv/Fm* produce proportional changes in ϕ_C, then less than half of the change in ϕ_C can be attributed to *Fv/Fm*. One possible explanation is that diadinoxanthin transfers absorbed energy to chl *a* with higher efficiency than does diatoxanthin. As conversion of diatoxanthin to diadinoxanthin proceeds following a shift to lower irradiance (Fig. 1a), the overall efficiency of energy transfer would then increase, thereby increasing the measured values of ϕ_C. Since *Fv/Fm* would be unaffected by changes in the energy transfer of photoprotective pigments, changes in *Fv/Fm* and ϕ_C would be uncoupled. However, because the energy transfer efficiency for both photoprotective pigments is low and because the absorption spectra of dd and dt do not greatly overlap the spectral distribution of irradiance used for P-E determinations, it is unlikely that interconversions between diatoxanthin and diadinoxanthin would strongly affect ϕ_C. Alternately, it has been suggested that cyclic electron flow around PSII may occur in algae exposed to super-saturating irradiance (Falkowski et al. 1986, 1988, Rees & Horton 1990), possibly acting as a sink for excess excitation energy. By this mechanism the linearity between fluorescence-based estimates of *Fv/Fm* and carbon-based estimates of the quantum yield of photosynthesis may be altered: closed reaction centers are re-oxidized without passing electrons onto the electron transport chain, thereby maintaining some variable fluorescence even as ϕ_C approaches zero. Falkowski et al. (1988), working with a chlorophyte and a diatom species, estimated cyclic electron flow around PSII to be 15 to 28% of linear electron flow at super-saturating irradiance. We have no means to assess the extent of cyclic electron flow around PSII for algae examined in this study. Nevertheless, the regression of ϕ_C vs *Fv/Fm* for all measurements made on freshly collected field samples and laboratory-incubated samples (Fig. 6) has a positive intercept of the *Fv/Fm* axis of 0.21, which indicates that when ϕ_C approaches 0 about 30% of maximum variable fluorescence would remain (assuming a maximum *Fv/Fm* of 0.65, Kolber et al. 1990).

To conclude, in the *Navicula glaciei*-dominated surface ice community, the algal inhabitants enact a suite of acclimative measures that reduce or offset the damaging effects of high irradiance. Cellular light harvesting efficiency was low. Nevertheless, low E_k relative to ambient PAR indicates that the algae were not able to adjust E_k to the irradiance conditions of their habitat. To survive in a habitat where further adjustments of E_k are no longer an option for coping with high irradiance, the surface ice algae employ energy dissipation to divert excess energy that would otherwise damage labile photosynthetic components. Our results indicate that a portion of the excess energy is dissipated through pathways mediated by the dd/dt-xanthophyll cycle and suggest that additional dissipatory processes may be in operation. Under these circumstances, the dissipatory processes are not implemented as a temporary response to transient high irradiance, but as part of a strategy to manage the super-saturating irradiance that is typically incident upon the algae. Even with all of these protective mechanisms in place they do not offer full protection from photoinhibitory damage under irradiances 20-fold greater than of photosynthetic requirements. We note that when high irradiance stress was relieved in laboratory experiments, the time scale of recovery to maximal values for *Fv/Fm* and ϕ_C (ca 1 d; Fig. 1c, d) was slower than typically reported for xanthophyll cycle transitions (minutes to hours; Demmig-Adams 1990) but similar to time scales for synthetic processes such as protein synthesis (hours to days), suggesting that repair processes may be involved in recovery.

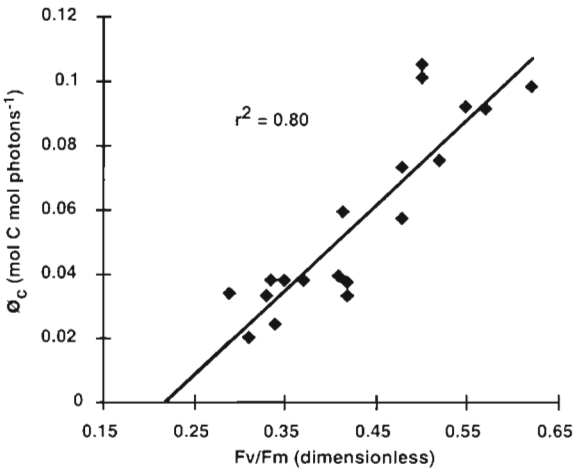

Fig. 6. A plot of all measurements of ϕ_C vs *Fv/Fm* made on freshly collected and laboratory-incubated algal samples. The solid line represents the linear regression of the 2 parameters (r^2 = 0.80, *x*-intercept = 0.21). Abbreviations as in Fig. 1

Acknowledgements. The authors thank Michel Gosselin and Gerhard Dieckmann for assistance in the field. We also thank Kevin Arrigo and 3 anonymous reviewers for critiquing this manuscript. We are grateful to Paul Falkowski for his advice and the use of the Pump and Probe Fluorometer. This work was supported by NSF grants DPP-8717237 and DPP-8717692 to C.W.S.

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This article was presented by O. Holm-Hansen, La Jolla, California, USA

Manuscript first received: August 24, 1996
Revised version accepted: December 11, 1996