

A. McMinn · K. Ryan · R. Gademann

Diurnal changes in photosynthesis of Antarctic fast ice algal communities determined by pulse amplitude modulation fluorometry

Received: 25 July 2002 / Accepted: 9 February 2003 / Published online: 15 May 2003
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Abstract The aim of this project was to determine both the diurnal changes in photosynthetic activity of Antarctic sea ice algae and also the protective mechanisms they use to mitigate the effects of in situ UV radiation. Changes in the diurnal photosynthetic parameters of fast ice algal communities at McMurdo Sound were measured in situ, using a custom designed monitoring pulse amplitude modulation fluorometer. The sea ice microalgae were able to adapt rapidly to either increasing or decreasing ambient irradiances. $\Delta F/F_m'$ values were between 0.2 and 0.51, while E_k varied between 2.1 and 18 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. $\Delta F/F_m'$, E_k , and relative electron transfer rate (rETR) all varied sequentially over the course of a day. rETR and E_k were highest at midday at the highest irradiances, when there was apparent midday down regulation of photosynthesis, while $\Delta F/F_m'$ was highest at midnight. The effects of natural UV radiation on sea ice were examined, but it was not possible to detect the effect of either UVB or UVA and UVB on photosynthesis. This was considered to be largely because of the large spatial and temporal heterogeneity of the under ice community, changing irradiances throughout the day and the relatively small change caused by UV.

Introduction

In coastal areas of Antarctica, microalgal communities, comprising predominantly diatoms, colonise the bottom few centimetres of the annual fast ice. These bottom, or interstitial, communities can reach biomass levels of over 300 mg Chl *a* m^{-2} (Palmisano and Sullivan 1983, Kirst and Wiencke 1995) and make a major contribution to the primary production of the area (McMinn et al. 2000). Light attenuation through the sea ice can be high, with as little as 0.1% of surface irradiation reaching the undersurface (SooHoo et al. 1987). Sea ice algae grow well in these stable, low-light environments. However, the natural addition or removal of snow cover on the ice can change irradiance levels several fold (Lizotte and Sullivan 1991). Furthermore, when the sea ice melts in spring, the algal cells may be released into the water column, where they are also likely to experience elevated irradiances.

Sea ice algae are amongst the most shade-adapted plants on earth (Thomas and Dieckmann 2002). Most records of the shade adaption index, E_k , of sea ice algae are less than 15 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, with evidence of photoinhibition at as little as 20 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Palmisano et al. 1985; Kirst and Wiencke 1995). Photosynthesis has still been detected at irradiances of less than 1 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Palmisano and Sullivan 1983).

Like most other types of algae, sea ice algae are able to adapt to either increases or decreases in irradiance (Lizotte and Sullivan 1991). On time scales of minutes to hours this is achieved by down regulation of photosynthesis. On longer time scales, i.e. hours to days, it is achieved by adjusting the amount of chlorophyll *a* (Chl *a*) in each cell; increasing the concentration with a decrease in irradiance and decreasing the concentration with an increase in irradiance (Prezelin and Matlick 1980). These latter changes have been demonstrated experimentally (Lizotte and Sullivan 1991) and by field observation (Kudoh et al. 1997). The time scale for these

Communicated by M.S. Johnson, Crawley

A. McMinn (✉)
Institute of Antarctic and Southern Ocean Studies,
University of Tasmania, Box 252-77, 7001 Hobart,
Tasmania, Australia
E-mail: andrew.mcminn@utas.edu.au
Fax: +61-3-62262973

K. Ryan
Industrial Research Ltd., PO Box 31 310,
Lower Hutt, New Zealand

R. Gademann
Dürrbachtal 232, 97080 Würzburg, Germany

changes to be completed is approximately 2–5 days (Lizotte and Sullivan 1991). Here we investigate the effects of diurnal irradiance changes to determine whether sea ice algae are able to acclimate to these large but rapid changes in irradiance during the course of a day. We also investigate whether natural levels of UV radiation can affect photosynthesis on the same time scale. Antarctic microalgae are potentially adversely affected by UV radiation, because of the additional UV flux resulting from the ozone hole (Frederick and Lubin 1994). While UV is known to affect photosynthesis by disrupting photosystem II (Cullen et al. 1992; Schofield et al. 1995), measurements on sea ice algae have mostly been equivocal (Ryan and Beaglehole 1994; Schofield et al. 1995; McMinn et al. 1999; Ryan et al. 2002). Natural UVB appears to depress phytoplankton productivity by around 5–15% (Smith et al. 1992) and sea ice by around 5% (Ryan 1992; Ryan and Beaglehole 1994; Prezelin et al. 1994). In sea ice, this level of suppression is usually much less than the temporal and spatial heterogeneity of the biomass (Swadling et al. 2000).

There have only been limited attempts to investigate sea ice algae using fluorescent techniques. Schofield et al. (1995) used a pulse amplitude modulation fluorometer (PAM) 101 to measure the fluorescence of incubated frazil samples extracted onto filters. Incubated, dark-adapted samples of platelet ice algae from McMurdo Sound were analysed with a fast repetition rate fluorometer (FRRF) by Robinson et al. (1998). The first and only other in situ measurements of sea ice algal photosynthesis were made by Kühl et al. (2001) from summer fast ice in Greenland using a Diving PAM (Waltz). They found that the in situ effective quantum yields of PSII of the under ice microalgae were between 0.3 and 0.7. Rapid light curves on these communities showed an E_k of $7.9 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. All communities were found to be well adapted to the low under ice light climate and able to adapt to moderate changes in irradiance within minutes.

The aim of our work was to determine both the diurnal changes in photosynthetic activity of Antarctic sea ice algae and the protective mechanisms they use to mitigate the effects of in situ UVA and UVB radiation.

Materials and methods

Field work was undertaken at Cape Evans, McMurdo Sound (Fig. 1) from 15 October to 16 November 2001. Ice cores were collected by augering to 1.7 m with a Jiffy Drill and then extracting the remaining ice with a 13-cm diameter SIPRE Corer. Extreme care was taken at all times to ensure that the cores had a minimal exposure to surface light. Surface light levels were measured with a Biospherical QSP 200 2π PAR sensor. Under ice irradiance was measured with QSP 200 4π PAR sensor mounted on a flexible arm to position the sensor 2 m away from the hole in the ice. Surface UV levels were measured with an International Light (IL) broadband UVB radiometer (Ryan and Beaglehole 1994). Under ice UV levels were measured with a Biospherical PUV500 multi channel radiometer measured at 305 nm, 320 340 380 and PAR 400–600 nm. This instrument was also mounted on a flexible arm, so



Fig. 1 Location of field site at Cape Evans, McMurdo Sound, Antarctica

that UV measurements could be measured directly under the ice away from the influence of the deployment hole. All data are presented as percentage transmission through the sea ice.

Sea ice algal biomass was determined by Chl *a* analysis on a Turner 10AU Fluorometer using the standard methodology of Holm-Hansen and Riemann (1978). Ice cores, 13 cm in diameter, were taken with a SIPRE corer, and the lower 10 cm was melted in 2 l of filtered seawater. 100 ml of the sample was filtered on to a 42-mm GF/F filter and extracted for 8 h in 90% methanol prior to measurement.

Chlorophyll fluorescence has become a widely accepted method of measuring the photophysiology of terrestrial plants. The development of the FRRF and Diving PAM in the 1980s allowed the in situ measurement of photosynthesis in marine plants without using chambers (Falkowski and Kolber 1993; Schreiber et al. 1994). PAM fluorometers are able to measure quantum yield ($\Delta F/F_m$), photosynthetic efficiency (F_v/F_m) and electron transfer rate (ETR) of photosystem II (PSII) in photosynthesis. Using rapid light curves (RLC), it is also possible to gain an insight of the photoadaptive state of the plant and to measure the photoadaptive index, E_k . The PAM method is based on the supply of weak, modulated light pulses (the measuring light) that allows chlorophyll fluorescence to be monitored without inducing photosynthesis. In the dark-adapted state, a minimum fluorescence (F_0) is determined when the measuring light is turned on. This mostly results from emissions from the antenna pigments. When the sample is exposed to actinic light, i.e. light that induces photosynthesis, a much higher fluorescence results. This fluorescence rapidly peaks and then declines till an equilibrium level, F , is attained. This characteristic behaviour is referred to as the Kautsky curve (Schreiber et al. 1995). Maximum fluorescence (F_m) is achieved by exposing the dark-adapted sample to a pulse of very intense light. The maximum quantum yield of PSII is defined as

$$\Phi_{\text{PSII}} = (F_m - F_0)/F_m = F_v/F_m$$

If the sample is experiencing additional in situ actinic light, a similar, saturating pulse will lead to a lower maximum fluorescence, $F_{m'}$, which is the maximal fluorescence yield of an illuminated sample. There is a strong relationship between photosynthetic charge separation and oxygen production. The effective quantum yield of charge separation in PSII, ϕ_{PSII} is defined as

$$\Phi_{PSII} = (F_{m'} - F)/F_{m'} \quad \text{or} \quad \Delta F/F_{m'}$$

The relative electron transfer rate (rETR) can be calculated from

$$rETR = \Phi_{PSII} \times E$$

where E is the irradiance.

Photochemical quenching (q_P) is dependent on the redox state of the primary electron acceptor (Q_A) and measures the photosynthetic energy flow. Non-photochemical quenching (q_N) is affected by the proton gradient on the thylakoid membrane and energy dissipation processes, primarily heat (Schreiber et al. 1994). Here

$$q_P = (F_{m'} - F)/(F_{m'} - F_0), \quad q_N = (F_m - F_{m'})/(F_m - F_0) \quad \text{and} \\ q_N = (F_m - F_{m'})/F_{m'}$$

For the in situ under ice measurements the microalgal mats were not dark adapted. In this situation estimations of F_0 and F_m were made, i.e. $F_0 = F - 10\%$ and $F_m = F_{m'} + 10\%$. Fluorometric measurements were made with a custom-built Monitoring PAM (Gademann Instruments, Wurzburg, Germany) with a 1-mm-diameter plastic fibre-optic strand. The instrument was basically a Junior PAM (Walz) with a blue LED (470 nm) in a submersible case. For laboratory measurements ice cores were dark adapted for 15 min before measurements were taken. The ice cores were floated upside down in an ice/water bath so the algal mat was at the surface. Replicate measurements were then taken with the fibre placed manually on the ice surface. F_v/F_m measurements were taken under software control using WinControl (Walz Effeltrich Germany).

For in situ use, the Monitoring PAM was attached to an extendable arm that allowed deployment through a 30-cm diameter auger hole and placement 2 m away from the hole. Data collection was either under software control at the surface or pre-programmed prior to deployment. Rapid light curves (RLC) were all collected under software control (WinControl, Walz). Actinic light levels for the RLCs were preset to 6, 12, 18, 30, 48, 84 and 138 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. In situ light measurements were made simultaneously, using a Biospherical Instruments QSP 200 4π PAR radiometer. Actinic light levels produced by the PAM were subsequently corrected by adding the in situ light levels recorded by the radiometer.

The photosynthetic parameters, E_k , $rETR_{\text{max}}$ and ϕ_{PSII} were estimated for each RLC by following a similar approach to determining photosynthetic parameters from a P versus E curve (Jassby and Platt 1976) and undertaking a non-linear regression to the function

$$rETR = rETR_{\text{max}} * e^{(-\phi E/rETR_{\text{max}})},$$

where E = irradiance. E_k is derived by dividing $rETR_{\text{max}}$ by ϕ_{PSII} (Schofield et al. 1998). The RLCs were measured at approximately hourly intervals throughout the day and night.

Four 6x8-m areas of sea ice were selected for study of the effects of UV radiation. One was covered with mylar, which screens out UVB radiation, another with polycarbonate, which screens out UVA and UVB radiation, and a third was covered with polyvinyl chloride (PVC), which transmits all UV radiation (Ryan et al. 2002). The PVC screen was added as a control because it has similar albedo properties to the other plastics, reflecting approximately 9% of the light. A fourth area, with no plastic added, was monitored for comparison. Replicate ice cores were taken from randomly selected sites beneath the plastic coverings after 12 days of cover. Ten F_v/F_m measurements were made on each of the dark-adapted cores.

For in situ measurements of the effect of UVA and UVB, the fibre tip of the Monitoring PAM was first deployed beneath the ice

and measurements made of ϕ_{PSII} and RLCs. Polycarbonate or Mylar sheets (4x4 m) were placed over the ice above the deployed Monitoring PAM measuring fibre, and the response was measured over 1 h. The plastic cover was then removed, and measurements were made in the following hour.

Results

The sea ice at Cape Evans, McMurdo Sound, in late October 2001 was 2.15 m thick, with a 2- to 5-cm-thick snow cover. The under ice water temperature was consistently -1.9°C , and the salinity was 34.4 psu. Surface PAR levels ranged between 2 and 2,196 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. In situ under ice light levels varied between 0.1 and 18.0 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. Transmission was consistently between 0.55% and 0.60%. UV data were collected in four band widths in the UVA and UVB; these were centred on 305, 320, 340 and 380 nm. The percentage transmission of the UVA, UVB and PAR radiation beneath each of the experimental treatments is presented in Fig. 2. There was no transmission of UVB radiation beneath the mylar and polycarbonate-covered treatments, but a 0.18% transmission beneath the cellulose acetate-covered treatment. There was no transmission of UVA radiation beneath the polycarbonate-covered treatment, but a 0.08% transmission beneath the mylar-covered treatment, and a 0.24% transmission beneath the cellulose acetate-covered treatment. The values for PAR transmission presented in Fig. 2 differ from those documented above. The data in Fig. 2 are based on values for PAR derived from the Biospherical PUV500 multi channel radiometer, which has a non-standard PAR bandwidth of 400–600 nm. The values presented here, i.e. 0.56% transmission, were measured with a Biospherical QSP 200 PAR sensor with a 400–700 nm bandwidth.

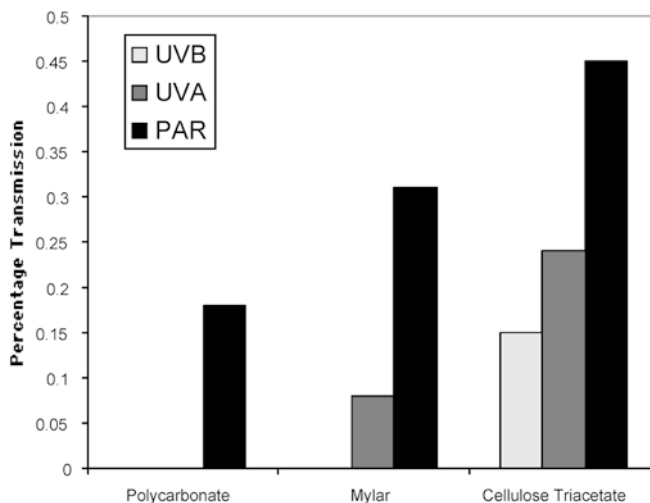


Fig. 2 Percentage transmission of UVA, UVB and PAR beneath the mylar, polycarbonate and cellulose acetate-covered experimental blocks

The microalgal community comprised mainly the diatoms *Entomoneis kjellmannii* (29%), *Fragilariopsis curta* (11%), *Nitzschia stellata* (26%) and *Navicula glaciei* (11%). Algal biomass (\pm standard error) on 30 October was 28.7 ± 7.7 mg Chl *a* m⁻².

Dark-adapted samples

One hundred F_v/F_m measurements were made of dark-adapted sea ice algal samples. These had an average (\pm standard error) value of 0.45 ± 0.15 , with a minimum of 0.20 and a maximum of 0.75. The length of dark adaptation seemed to have little effect beyond 10 min.

In situ diurnal changes in fluorescent parameters

ϕ_{PSII} : ϕ_{PSII} values varied between 0.24 and 0.51 on 26/27 October (Fig. 3A) and between 0.28 and 0.41 on 29/30 October (Fig. 3B, C). There is a clearly discernible diurnal pattern, with maximum values occurring close to midnight and minimum values occurring in the middle of the day.

$rETR_{max}$, E_k : Values of $rETR_{max}$ and E_k show clearly discernible diurnal trends. Both $rETR_{max}$ and E_k values were at their maximum towards the middle of the day, and at their minimum at midnight (Fig. 4A–C). $rETR_{max}$ values were between 0.22 and 4.57. Maximum $rETR_{max}$ values occurred between 1500 and 1800 hours and between 0900 and 1100 hours on 26/27 October, and between 0900 and 1500 hours on 29/30 October. The diurnal decline in $rETR_{max}$ and the relationship with E_k can be seen in the RLCs (Fig. 4A–C). On average, midnight $rETR_{max}$ values were between 30.4% and 33.2% of midday values. Evidence for a dip in values at midday is inconclusive. E_k values were between 2.1 and 18 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ with maximum and minimum values following the trends of $rETR_{max}$.

There was a clearly detectable drop in both $rETR$ and ϕ_{PSII} values when the same site was measured over a long period of time, i.e. greater than 15 h. When ϕ_{PSII} or $rETR$ values dropped to less than 10% of the maximum values, measurements were generally stopped. This was seen on the mornings of the 27, 30 and 31 October when ϕ_{PSII} (Fig. 3) and $rETR_{max}$ (Fig. 4) values failed to increase with increasing morning irradiances.

Initial yield measurements in RLCs were mostly between 0.44 and 0.48. Values were stable to approximately 20 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ and then dropped sharply (Figs. 5, 6). The light level at which the yield started to decline dropped sequentially through the evening as ambient light levels dropped. Unlike profiles

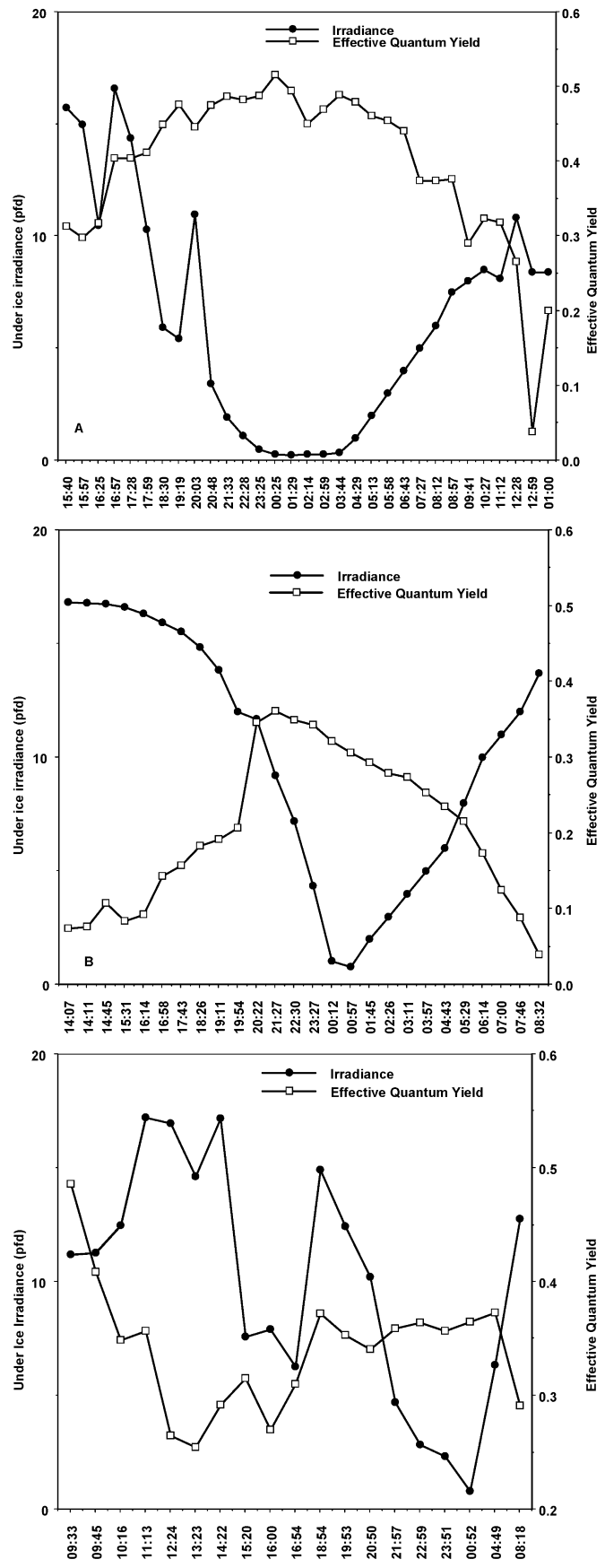
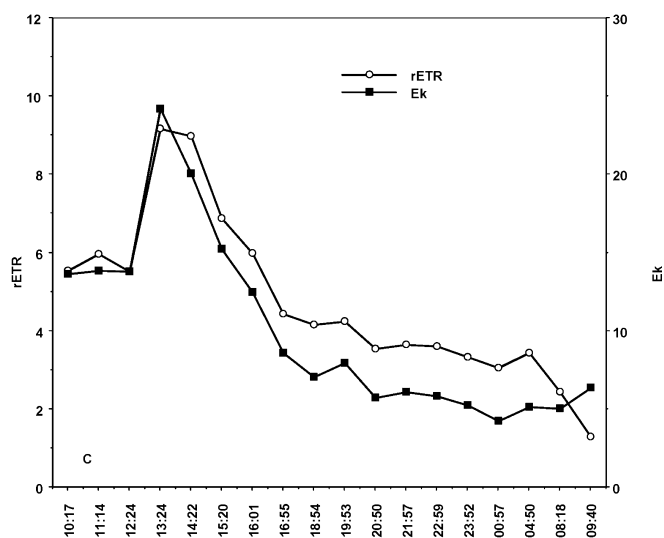
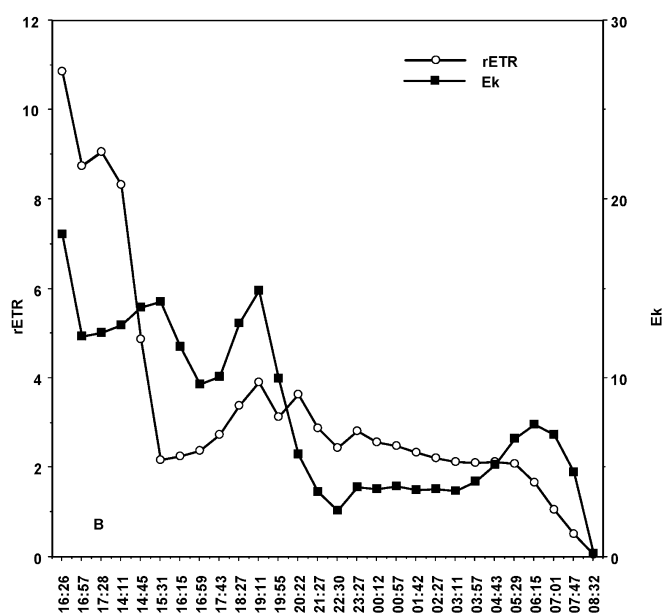
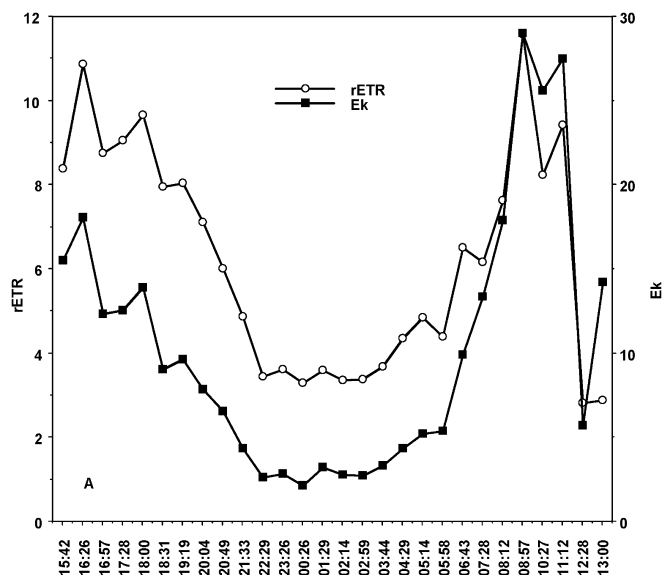


Fig. 3A–C Relationship between F_v/F_m (ϕ_p), irradiance and time of day. **A** 26 October 2001, **B** 29 October, **C** 30 October. Irradiance units, pfd (photon flux density), are equivalent to $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. *X* axis shows sampling times and is not a time axis



from later in the evening, the yield at the highest ambient light level (at 1730 hours) showed an increase in yield from 0.35 to 0.44 with increasing actinic light up to $20 \mu\text{mol photons m}^{-2} \text{s}^{-1}$.

Quenching response

The relationship between non-photochemical quenching (NPQ) and rETR is shown for 1500 hours and 2330 hours on 26 October (Fig. 7). There is an apparent relationship between high rETR and high NPQ and low rETR and low NPQ.

Effects of UV

Dark-adapted ice core samples

Ice core samples were taken from beneath the three plastic-covered experimental blocks after being covered for 12 days (Table 1).

An ANOVA of the F_v/F_m values from these ice cores showed that the differences between the groups were not significant (at $P=0.05$). These results show that the algal response to UV radiation is heterogeneous, and if there was a response it was too small to be detected by our experimental procedure.

In situ UV treatments

Two in situ experiments were run, the first using a mylar screen and the second using a polycarbonate screen. The results are shown in Table 2. There was no consistent response when either the mylar or the polycarbonate screen was added or removed. In the mylar treatment ϕ_{PSII} rose, but E_k and $rETR_{max}$ fell when the mylar screen was added. When it was removed, ϕ_{PSII} , E_k and $rETR_{max}$ all rose. In the polycarbonate treatment, ϕ_{PSII} , $rETR_{max}$ and E_k all rose when the screen was added. When it was removed, ϕ_{PSII} , $rETR_{max}$ and E_k all fell. However, there was no significant difference (at $P=0.05$) between the treatments. As these experiments were done in situ, there was no control over the natural irradiances. The screens themselves reduced under ice irradiance levels by approximately 9% (Ryan et al. 2002), and there was also a gradual decline in light levels during the afternoon of the mylar experiment, from 16.5 to $13.0 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. Cloud cover interrupted the polycarbonate treatment, causing the under ice irradiances to drop sharply from 17 to $7.5 \mu\text{mol photons m}^{-2} \text{s}^{-1}$.

Fig. 4A–C Relationship between E_k (squares), Relative ETR (open circles) and time of day. A 26 October 2001, B 29 October, C 30 October. X axis shows sampling times and is not a time axis

Fig. 5 Rapid light curves (RLC) from 26 October 2001. The *outer curves* were taken in mid afternoon, the *inner curves* were taken close to midnight. Irradiance units, pfd (photon flux density), are equivalent to $\mu\text{mol photons m}^{-2} \text{s}^{-1}$

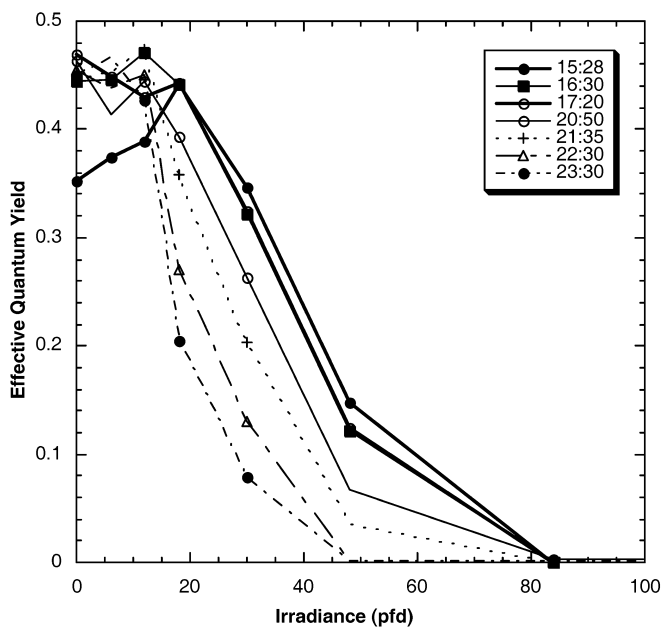
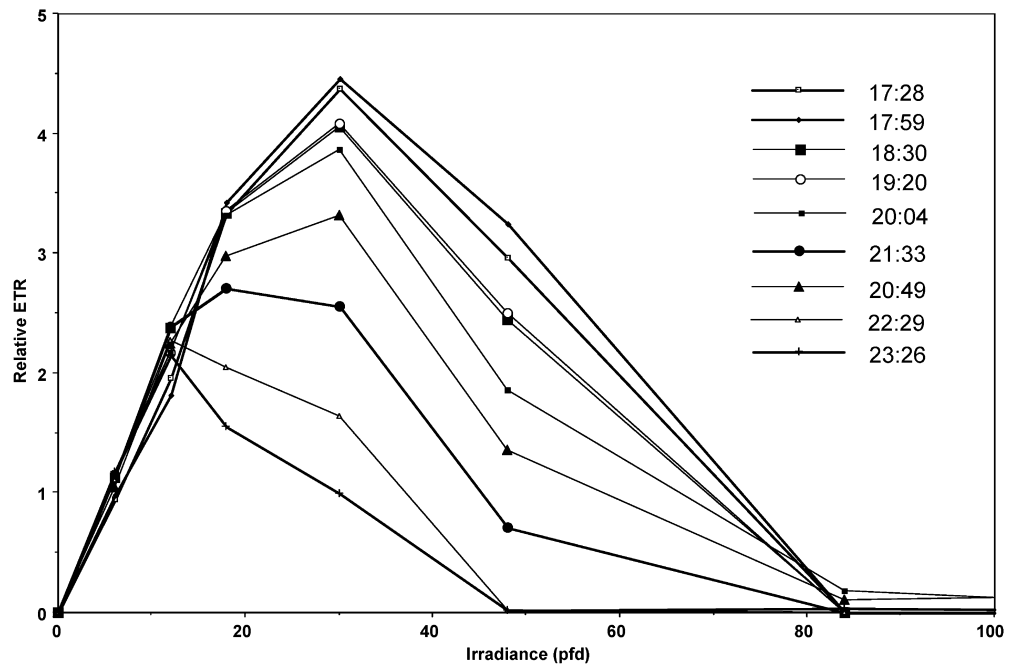


Fig. 6 Yield measurements of the sea ice algae on 26 October 2001. Each data set is the output of a rapid light curve: the lowest actinic light levels are represented on the left, the highest on the right. Irradiance units, pfd (photon flux density), are equivalent to $\mu\text{mol photons m}^{-2} \text{s}^{-1}$

Discussion

The values of ϕ_{PSII} found at Cape Evans were relatively low (0.2–0.51) compared to either maximal values from other aquatic plants (Schreiber et al. 1995) or the only other values for sea ice algae, determined from the Arctic, which were in the range 0.2–0.65

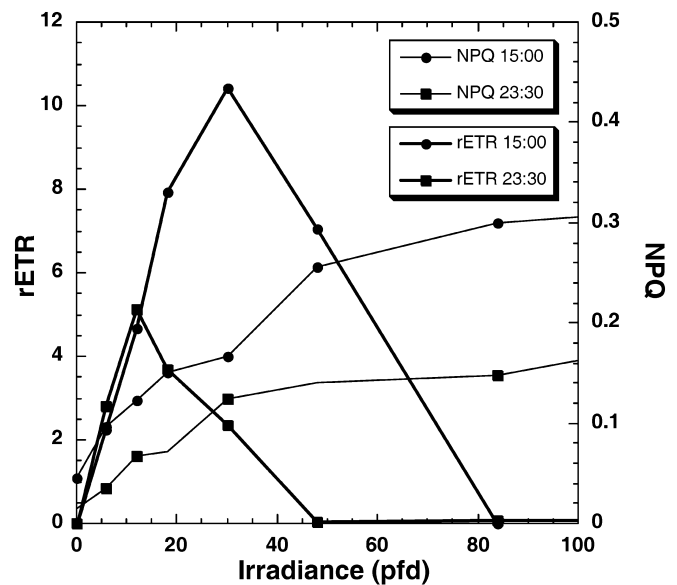


Fig. 7 Relationship between rETR and NPQ at 1500 hours and 2330 hours on 26 October 2001

(Kühl et al. 2001). Robinson et al. (1998) noted a drop in F_v/F_m values (using a FRRF) of platelet ice algae from approximately 0.5 to 0.3 during their 2-week field study. They suggested that either decreased light due to surface algal growth or increasing nutrient limitation were the most likely causes. Neither of these explanations, however, adequately explains our observations because under ice light levels were gradually increasing with higher late spring sun angles, and reduced snow cover and nutrient levels beneath the ice at this time of year are known to be high (McMinn et al.

Table 1 Dark adapted PAM response to different UV treatments. Errors are standard deviations, and ten measurements were taken for each treatment

Treatment	Cover	F_v/F_m
PAR + UVA + UVB	Uncovered	0.217 ± 0.078
PAR + UVA + UVB	PVC control	0.229 ± 0.149
PAR	Polycarbonate	0.321 ± 0.048
PAR + UVA	Mylar	0.223 ± 0.090

Table 2 In situ PAM response to changing UV radiation. A set of PAM measurements was taken at the beginning of each experiment. A UV absorbing covering (i.e. mylar or polycarbonate) was then added and measurements taken again. The covering was later removed and the measurements retaken. Errors are standard deviations, and three measurements were taken for each treatment

	F_v/F_m	rETR _{max}	E_k	PAR
Treatment 1				
Control	0.086 ± 0.015	3.11 ± 0.79	31	16.7 ± 0.1
Mylar	0.145 ± 0.038	2.90 ± 0.43	10.5	15.4 ± 0.5
Control	0.200 ± 0.011	3.47 ± 0.15	12.5	12.5 ± 1.2
Treatment 2				
Control	0.255 ± 0.056	6.34 ± 1.55	13.8	16.3 ± 0.8
Polycarbonate	0.304 ± 0.016	7.48 ± 1.19	19.7	12.3 ± 6.7
Control	0.270 ± 0.051	6.09 ± 0.75	12.5	7.1 ± 1.2

2000). It is possible that the ϕ_{PSII} values were reduced as a result of high UVB levels, but this suggestion runs counter to the outcomes of the experiments conducted specifically to investigate the effects of UV radiation. Another possibility is the influence of high dissolved oxygen levels (Thomas and Dieckmann 2002; McMinn et al. 2000). High dissolved oxygen levels are potentially toxic to marine algae (Mallick and Mohn 2000). McMinn et al. (2000) found extensive oxygen bubble formation and oxygen-saturated boundary layers beneath fast ice algal mats in McMurdo Sound, and similar conditions were also present in the current field season. The actual toxicity of these conditions awaits further investigation.

The actual rETR values are not quantitative, because the absorptional cross sectional area (essential for estimating ETR) cannot be calculated, however the values measured here (rETR) are approximately proportional to the true ETR. In each of the RLCs taken at Cape Evans in 2001 the rETR_{max} occurred at actinic light levels greater than the maximum ambient irradiances. For instance, at 1730 hours on 26 October the ambient under ice irradiance was $14.5 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, while the irradiance at which the rETR_{max} was attained was $30 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. The same situation occurred at low light levels. At 2330 hours on 26 October the ambient under ice irradiance was $0.5 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, while the irradiance of the rETR_{max} was $12 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. These results imply that the sea ice algae at Cape Evans never reach light saturation at ambient irradiances, and that they are continually light-limited. These results are supported by data from the same area

by McMinn et al. (2000) in 1997 and Trenerry et al. (2001) in 1999. These studies both produced dynamic photosynthesis versus irradiance curves using oxygen evolution across diffusive boundary layers. In both years, photosynthesis was never saturated, even though sustained sunny periods were experienced. Similar results were obtained by Palmisano et al. (1985) using carbon-14 incubations. The lack of saturating in situ irradiances would most likely have contributed to the lower ϕ_{PSII} values. The decline in rETR and ϕ_{PSII} values when measurements were sustained over a long period of time, i.e. greater than 15 h, is unlikely to have been caused by instrument error, as the battery voltage did not drop during measurement and the PAM remained attached to an external power supply. Furthermore, slight movement of the fibre tip to an adjacent area of algal mat resulted in a strong fluorescent (F) response. It is likely that the saturating pulse during the RLCs was set too high ($1,000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) and this caused a chronic inhibitory response. Antarctic stratospheric ozone depletion and hence UVB enhancement are at a maximum in late October to late November (Frederick and Lubin 1994). A severe ozone hole was experienced over the McMurdo Sound region in 2001 (http://jwocky.gsfc.nasa.gov/news/oz_hole_01_02.qt), so any deleterious effects should have been seen. However, the photosynthetic response of sea ice algae to UVB radiation is equivocal. Experimental studies using cultures or isolates of sea ice algae and artificial irradiance have documented DNA damage (Prezelin et al. 1998), increased mortality (McMinn et al. 1999), reduced photosynthesis (Schofield et al. 1995) or declines in productivity of approximately 5% (Ryan 1992; Ryan and Beaglehole 1994). Here we found low but biologically significant levels of UVA and UVB penetrating the sea ice. However, differences in F_v/F_m between the sea ice cores exposed to either ambient PAR + UVA + UVB or PAR + UVA or PAR were not significant. Similarly, with the in situ measurements there was no consistent response. The mylar treatment (PAR + UVA) showed a decline in rETR_{max} and E_k when the UVB-absorbing screen was added and a rise when it was removed. By contrast, when the polycarbonate screen (PAR only) was added, there was a decline in ϕ_{PSII} , ETR_{max} and E_k and a fall in all three parameters when the UVA and UVB absorbing screen was removed. The response of the sea ice algae to the polycarbonate treatment (PAR only) is what would have been predicted if UV radiation was affecting PSII. The response to the mylar treatment, where rETR_{max} and E_k rose when the screen was added, is difficult to explain. The lack of consistency in the in situ results highlights the difficulties of doing such experiments using very low ambient irradiances. Most of the experiments took at least an hour to execute. During this time the natural irradiances changed, sometimes by more than 50% (Table 2). Changes in photosynthetic parameters measured by the PAM are therefore a combined result of the response to the removal of the UVB (mylar) or UVB and UVA (polycarbonate) and also to the

natural changes caused by the acclimation of the sea ice algae to the lower irradiances. As the magnitude of the changes in photosynthesis caused by ambient UV on Antarctic microalgae are reported to be in the range of 5–15% (Smith et al. 1992; Ryan and Beaglehole 1994; McMinn et al. 1999), changes in ambient irradiance greater than this will mask the effects of UV. Our results also show that the micro algal response to UV radiation is heterogeneous, and if there was a response it was too small to be detected by our experimental procedure. In future, a great many more experiments would need to be run and only those with minimal changes in irradiance selected for further interpretation. The sea ice microalgae were clearly rapidly adapting to either increasing or decreasing ambient irradiances. These adaptations are reflected in the rapid response of the ETR and E_k . It is not surprising that both parameters respond similarly, as they are related, dependant variables. Changes in the photoadaptive index, E_k , track the changing irradiance throughout the day, with maximum values at midday and minimum values at midnight. Changes in ϕ_{PSII} were minimal. There is no evidence, for instance, of decreasing efficiency (ϕ_{PSII}) with decreasing light that would suggest photoadaptation (and an increase in Chl *a* content) (Kirk 1994). The unvarying ϕ_{PSII} values, regardless of irradiance, are interesting and imply that the photosystems of these micro algal communities are either not significantly adapting to changing light or require longer time periods of several days to adapt. NPQ is the dominant form of quenching at high actinic light levels (Fig. 6) and there is an apparent relationship between high rETR and high NPQ and low rETR and low NPQ. The quenching curves are in general consistent with those recorded in sea grasses (Ralph et al. 1998) and higher plants (Schreiber and Bilger 1993). Antarctic sea ice algal communities are clearly well adapted to their low light environment. They are extremely shade adapted, with very low E_k values, and yet are able to adjust their photosynthetic rates to suit changing diurnal irradiance levels. E_k values are often used as a measure of shade adaptation (Kirst and Wiencke 1995), but because our results show that they vary throughout the day, care must be taken to select a standard time for measurements before direct comparisons can be made. Our results demonstrate the value and potential of deploying submersible PAMs to examine photosynthesis in Antarctic microbial ecosystems. By not handling the communities at all, we ensure a minimal level of disruption. We have demonstrated both the adaptability of sea ice algal communities to changing diurnal light levels and also the need to refer to the time of day samples were collected when discussing parameters such as E_k . Unfortunately, we were not able to quantify the extent of inhibition caused by UV radiation, and this is likely to continue to be a problem for in situ studies.

Acknowledgements We would like to thank Louise Trenerry, David Clement, and Glenn Roberts for help in the field. Financial support came from ASAC and ARC. Mark Hovenden and Peter Ralph are thanked for reviewing a draft of the manuscript.

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