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Macroalgal photosynthesis near the southern global limit for growth; Cape Evans, Ross Sea, Antarctica

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Abstract Photosynthetic characteristics of the red macroalgae *Phyllophora antarctica* and *Phymatolithon foecundum* collected from under sea ice at Cape Evans, McMurdo Sound (Ross Sea) were determined using in situ fluorometric and lab-based oxygen exchange techniques. Only 0.16% of incident irradiance penetrated the 2.5 m thick ice cover and photosynthetic parameters for both taxa were characteristic of highly shade-adapted plants. Saturation onset parameter (E_k) did not exceed $13 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ in either taxon. For *Phyllophora antarctica* the light saturated photosynthetic rate at -1°C was $10 \mu\text{mol O}_2 \text{g}^{-1} \text{FW h}^{-1}$ and respiration averaged $3.3 \mu\text{mol O}_2 \text{g}^{-1} \text{FW h}^{-1}$ between sampled depths of 10 and 25 m. A light meter deployed at 15 m depth for a year recorded a marked increase in underwater irradiance on the last day of January 2002 coinciding with ice-breakout, and a maximum value for irradiance of $120 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ on 9 February 2002. The 2-month ice-free period was the only time when irradiance consistently exceeded compensation (photosynthesis = respiration) and enabled *Phyllophora antarctica* to accumulate sufficient carbon to result in a measurable increase in thallus area equivalent to a biomass increment of 1.87 mg (DW) per frond. Near the southern global limit for marine macroalgae, conditions that dictate the availability of underwater irradiance are extremely variable from year to year. Low respiration rates enhance longevity of the *Phyllophora antarctica* thallus, enabling it to not only survive the winter

darkness, but also to retain photosynthetic capacity and thus take advantage of windows of higher irradiance.

Introduction

McMurdo Sound in Antarctica's Ross Sea, bound in the east by Ross Island and the west by the Antarctic mainland, is the world's most southerly marine ecosystem that is not permanently covered by thick glacial ice. It is here that the southernmost benthic macroalgae occur (Zaneveld 1966; Dayton 1990; Miller and Pearse 1991; Cormaci et al. 1998). Coralline algal crusts have been observed to grow on most rocky outcrops as far south as Hut Point Peninsula on Ross Island (Dayton 1990), where a few fronds of the branched red algae *Phyllophora antarctica* A. and E.S. Gepp (Phyllophoraceae) have also been found. In addition to *P. antarctica*, a second red algal species, the foliose *Iridaea cordata* (Turner) Bory (Gigartinaceae), has been recorded 25 km north of Hut Point at Cape Evans (Zaneveld 1966; Miller and Pearse 1991). The gradient of diversity seen along this short section of the Ross Island coast reflects the greater phytogeographical gradient that has been described in the Ross Sea from Cape Adare in the north to McMurdo Sound in the south (Zaneveld 1966; Wiencke and Clayton 2002). This has been attributed to the coupling of increased duration of winter darkness and persistence of sea-ice cover (Cormaci et al. 1998).

Recent polar macroalgal studies have advanced understanding of the photosynthetic tolerances of Antarctic macroalgae to the special conditions of low light intensity (Wiencke 1990; Kirst and Wiencke 1995; Lüder et al. 2002) and low temperatures (Thomas and Wiencke 1991; Bischoff- Bäsman and Wiencke 1996). The primary effect of low temperature is to reduce respiration relative to photosynthesis, thereby lowering the compensation irradiance for photosynthesis (Wiencke et al. 1993). There is strong evidence that light is the primary driving factor for the growth and production of high latitude Antarctic macroalgae (Miller and Pearse 1991;

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Wiencke and Clayton 2002). However, studies of the role of physiological processes in determining the limits to Antarctic macroalgal distribution and biomass have largely been restricted to higher latitudes (e.g. the Antarctic Peninsula or East Antarctica ($<70^{\circ}\text{S}$) (Kirst and Wiencke 1995) with some work in Terra Nova Bay ($74^{\circ}70'\text{S}$) (Gambi et al. 2000)), where environmental conditions such as the availability of irradiance are somewhat more benign than in McMurdo Sound ($77\text{--}78^{\circ}\text{S}$). On the Antarctic Peninsula, sufficient accretion of carbon by macroalgae can occur during the ice-free period to fuel growth during the subsequent winter or spring, even before ice break-out (Drew and Hastings 1992; Kirst and Wiencke 1995).

The more extreme characteristics of the light environment in McMurdo Sound mean that macroalgae are likely to be growing closer to their limits of physiological tolerance than at lower latitudes. This area experiences complete darkness for 4 months each year, and ice cover may persist all year, or break out for a few months during late summer. The ability to colonise the southern part of McMurdo Sound must include the ability to tolerate prolonged darkness, exploit extremely low irradiance for much of the year, make the most of short periods of relatively high irradiance, and to persist through years when there is a short or no open-water window for photosynthesis and growth.

During spring 2001 (November–December) we investigated the photosynthetic responses of two macroalgal taxa at Cape Evans on Ross Island in relation to ambient irradiance. The focus was on *P. antarctica* that occurred attached to rocks, as drift and carried on the spines of urchins. This branched growth form lent itself to both our fluorescence and oxygen exchange techniques, but some measurements were also made on the common crustose coralline, which we refer to as *Phymatolithon foecundum* (Kjellman) Düwel & Wegeberg comb. nov. according to Alongi et al.'s (2002) taxonomic revision of the Corallinaceae from the Ross Sea. *Phyllophora antarctica* is distributed through Antarctic and sub-Antarctic regions (Cormaci et al. 1992) making it an ideal species for investigations of adaptations to different light conditions over vertical and latitudinal gradients.

The aims of this study were to investigate whether these perennial macroalgae exhibited photosynthetic characteristics that supported an ability to utilise the extremely low light levels available in spring while still ice-covered, and to relate photosynthesis and growth characteristics to the light climate over the course of a year. The characteristics of the under-ice light climate were described during the period of the study and underwater light loggers were deployed to capture changes over the course of the following year. We used photosynthetic relationships with light, measurements of annual growth and the measured light environment to postulate the response of these macroalgae near the southern limit of their distribution to variable ice cover over time.

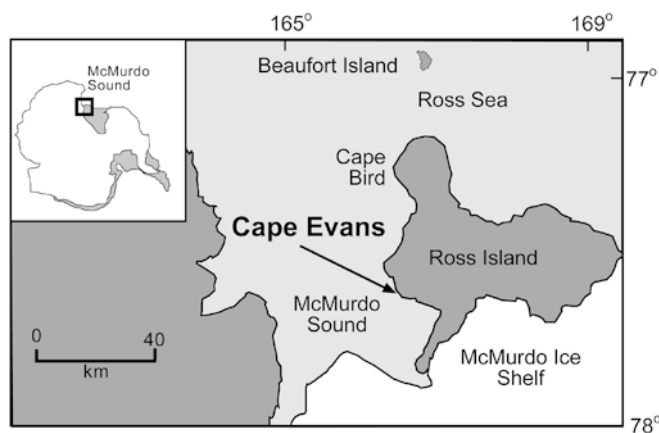


Fig. 1 Map of McMurdo Sound, Ross Sea, Antarctica showing the location of Cape Evans

Materials and methods

Study site

The study was carried out at Cape Evans, McMurdo Sound (Fig. 1) between 9 November and 2 December 2001. At the time of the study the site was completely covered with a 2.5 m thick layer of annual ice.

Dive holes drilled through the ice were used to provide access for SCUBA divers to sample macroalgae. The main dive hole for macroalgal work ($77^{\circ}38.072'\text{S}$, $166^{\circ}24.883'\text{E}$) was situated over a water depth of 21 m enabling access to four sampling depths (10, 15, 20, 25 m) selected on the basis of the depth zonation related to the abundance of attached and drift *Phyllophora antarctica*. In situ measurements and collections of material were made on a depth profile located to one side of the dive access hole. All depths refer to depth in metres below the piezometric water level in the access hole.

Environmental data

The physical structure of the water column was measured using an AML conductivity / temperature / depth (CTD) probe, lowered through a hole drilled through the ice. Each variable was measured continuously while lowering to, and retrieving from, a depth of 40 m.

Surface and underwater photosynthetically available radiation (PAR) were measured using LiCor quantum sensors (Li190SA for surface and Li192SB for underwater irradiance). Incident irradiance was logged at 5-min intervals using a LiCor Li-1000 data logger for 14 days and under-ice irradiance was logged concurrently for five of those days. The under-ice sensor was deployed using SCUBA diving and attached to the underside of the ice using an ice screw at a distance of 20 m from the dive hole to avoid the effect of light focusing through the hole. The percent transmission of light through the ice cover was calculated for the period that simultaneous records were available. On an additional six occasions on different days, SCUBA divers made spot measurements of PAR at water depths from below the ice to 25 m using a Li192SB underwater sensor attached to a LiCor Li145 meter in a waterproof housing. These measurements, made on cloud-free days at a distance of more than 20 m from the hole, enabled the calculation of an attenuation coefficient for downward irradiance (K_d) in the water column. K_d was estimated from the slope of the regression of log transformed PAR values with depth (Kirk 1994).

The spectral distribution of irradiance just below the ice was measured using a TRIOS, RAMSES spectroradiometer. The sensor was attached to the TRIOS frame and suspended under the ice

from the ice screw 20 m from the dive hole and controlled from a computer on the surface. Scans were recorded on clear sky days and incident PAR was also recorded as described above. Each 8 s scan recorded a spectrum between 270 and 700 nm, at 2 nm intervals. As simultaneous surface and under-ice spectra were not possible for calculation of wavelength-specific % transmission, a surface spectrum taken at a similar time, but on a different day, was adjusted so that the sum of the 400–700 nm waveband equalled the measured surface PAR at the time the under-ice spectrum was obtained.

To provide an indication of the seasonal pattern of light at the site, and particularly during the late summer ice-out phase when we could not be present, we deployed logging light meters. Hobo light intensity data loggers (Onset Computer Corporation) were placed into specially constructed waterproof housings with a modified light diffuser that approximated a spherical acceptance angle. In this modification, light collected by a 3 mm diameter diffuser made of clear epoxy resin impregnated with titanium oxide, was channelled via an optical fibre to the original photodiode sensor of the Hobo. Diffusers were checked for spherical acceptance by rotating them in a unidirectional light field; only those giving an equal response ($\pm 5\%$) from all directions were accepted. The sensors were calibrated under a range of light intensities against a LiCor Li190SA quantum sensor. At the end of December 2001, two of these modified loggers were deployed at depths of 15 and 16 m. The loggers remained in situ for a year and were recovered in mid November 2002. The instantaneous value for underwater irradiance was logged at five equal time intervals every day over this period.

Photosynthesis and respiration

We used a combination of oxygen exchange and pulse amplitude modulated (PAM) fluorometry to estimate photosynthetic activity, and oxygen consumption to estimate respiration. PAM measurements were made both in situ and on material returned to the on-site surface laboratory to investigate the relationships between irradiance and photosynthetic activity in natural and controlled variations in irradiance. Oxygen exchange was only measured in the laboratory and was used to determine oxygen exchange in the dark and at saturating irradiance.

Sample collection

Samples of *Phyllophora antarctica* and *Phymatolithon foecundum* were collected from depths of 10, 15, 20 and 25 m by SCUBA divers. For *Phyllophora antarctica* at 10 and 15 m small rocks with attached plants were collected for return to laboratory, while at 20 and 25 m only unattached drift plants were available. Small rocks with a crust of *Phymatolithon foecundum* were collected from each depth. At the water surface samples were immediately transferred into plastic containers ensuring they were maintained in low light and constant temperature conditions. Each depth was sampled on a different day and laboratory measurements of photosynthesis and respiration were carried out on site within the following 6 h.

PAM measurements

Measurements of fluorescence yield were made using a diver-operated submersible PAM fluorometer (Diving-PAM, Walz). Underwater this was used autonomously, in the laboratory it was operated through a laptop computer that allowed access to enhanced recording options. The locations on the *Phyllophora antarctica* thallus or on a coralline crust for all Diving-PAM measurements were visually selected to be as free from epiphytes as possible and for *P. antarctica* care was taken to standardise all measurements to within 5 cm of the apical tip.

The principle measurement made using the Diving-PAM was the effective quantum yield (Y) of photosystem II (PS II) (Schreiber

et al. 1986). A relative value of electron transport rate (RETR) can be calculated from Y , using the equation:

$$\text{RETR} = Y * \text{PAR}_i \quad (1)$$

where PAR_i is the incident irradiance.

For comparison with oxygen exchange measurements, Eq. 1 was modified to include measurements of the fraction of irradiance absorbed by photosystems I and II to give an estimate of absolute electron transport rate (ETR - $\mu\text{mol electrons m}^{-2} \text{ s}^{-1}$).

$$\text{ETR} = Y * \text{PAR}_i * 0.5 * Af \quad (2)$$

where Af is the proportion of incident irradiance absorbed by the thallus (measurement described below) and 0.5 assumes an even split of absorbed photons between PSI and PSII.

Laboratory measurements

In the laboratory two series of Y versus irradiance measurements were made on each species from each depth. The first utilised the rapid light curve (RLC) function and nine, 15-s periods of actinic light provided by the Diving PAM in ever-increasing intensities from darkness. The aim was to provide a snapshot of the current status of light adaptation to the ambient light conditions enabling us to rapidly assess the range of irradiance required to obtain a saturation curve in the following experiments.

The second series of Y versus irradiance measurements differed from the RLCs in that we used an independent light source. The beam of light derived from a quartz-halogen bulb was passed through a transmission filter, maximum transmittance 400–500 nm (Hawes and Schwarz 2001), which altered the spectrum to more closely mimic that measured under-ice. The beam was then channelled to the experimental thallus through a fibre optic cable. A light curve was then constructed by manually increasing the intensity of the light incident on the algal thallus (calibrated using a LiCor sensor). After each increase in irradiance the fluorescence of the plant was monitored until it stabilised (usually 20 s) before a yield measurement was made. The resultant values of RETR versus PAR_i for all replicates from a given depth, were fitted to a modification of the hyperbolic tangent relationship of Jassby and Platt (1976), using a curve fitting procedure in Sigmaplot (SPSS Inc, Chicago, Ill., USA); thus

$$\text{RETR} = \text{RETR}_{\text{max}} \tanh(\text{PAR}_i / E_k) \quad (3)$$

The equation yielded estimates with standard errors for light saturated RETR (RETR_{max}) and the irradiance at the onset of saturation (E_k , in $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$).

In situ measurements

In addition to laboratory measurements, at each sampling depth, in situ assessments of yield under ambient under-ice irradiance were made on both *Phyllophora antarctica* and *Phymatolithon foecundum*. At least ten spot measurements were made on separate days for each sampling depth, at a standard distance of 5 mm from the plant surface. At depths of 10 and 15 m measurements were made between 1500 and 1600 hours. At 20 and 25 m measurements were made at 1100 and 1120 hours. To compare their physiological status, at a depth of 15 m measurements were made on both attached and drift plants held on the spines of urchins. Irradiance adjacent to the measurement location was recorded using the LiCor Li192SB sensor at the same time (we found the Diving PAM irradiance sensor insufficiently sensitive at the ambient PAR of $< 1 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$).

On two occasions the Diving-PAM was positioned on the bottom and programmed to take a yield measurement on the same piece of material every 30 min. At a depth of 20 m (18 November) and 10 m (25 November) a piece of *Phyllophora antarctica* thallus was positioned in a leaf clip attached to the measuring fibre, ensuring that the tip of the fibre was held firmly at a distance of

5 mm from the thallus. The Diving-PAM was left recording overnight; at ambient temperatures of -1.9°C the battery lasted long enough to collect data for up to 19 h.

Oxygen exchange measurements

In the laboratory, respiration and irradiance-saturated rates of photosynthesis (for *P. antarctica* only) were measured using oxygen exchange techniques. Rates for three to six replicates from each depth were determined in the dark and at saturating light intensities (determined from RLC's) using a Hansatech (Chlorolab 3) oxygen electrode and associated software (Hansatech Instruments Ltd., Norfolk, U.K.). Thallus tips 2 cm long were placed into the chamber in 10 ml of filtered seawater in the holder designed for that purpose. Seawater pumped through a water jacket maintained the incubation vessel at less than -1°C at all times. The thallus was oriented to the light source (fibre optic white light passed through a blue filter), the intensity of which was measured at the back of the Hansatech chamber when filled with water but without plants in it. Oxygen consumption (in the dark) and release (at saturating irradiance) were calculated from the slope of the continuous trace recorded using the Hansatech OXYREC software. The pieces of thallus were then frozen for determination of fresh weight (FW) and chlorophyll-*a* content for normalisation of oxygen exchange rates.

Additional samples from each depth were frozen for later analysis of fresh weight (FW), freeze-dry weight (DW), and DW to surface area (estimated from scanned images of the samples) ratio. Samples for analysis of carbon (C) and nitrogen (N) content were prepared according to the methods described in Gómez and Wiencke (1998) and analysed in a Perkin-Elmer CHN analyzer. Chlorophyll-*a* analysis was performed on a 0.28 cm^2 core taken from each replicate and freeze-dried prior to extraction in 50:50 dimethyl sulphoxide:90% acetone using a modification of the method of Seely et al. (1972). Extraction was performed in the dark at 4°C for 24 h and extracts were read on a JASCO 7850 UV/VIS spectrophotometer.

Absorption of incident irradiance and estimating A_f

An estimate of the amount of incident irradiance absorbed by the *P. antarctica* thallus, and therefore potentially available for absorption by photosynthetic pigments, was estimated by difference from the relative proportion of blue filtered light source transmitted through a piece of thallus (e.g. Beer et al. 1998). This was repeated for three to six replicates from each depth and the average calculated.

Spectral absorption from 270–700 nm by the thallus of *P. antarctica* from a depth of 10 m was measured by placing a wet piece of plant material over the sensor of the TRIOS spectroradiometer. On a uniformly overcast day three replicate scans were performed with and without the thallus and the transmission spectrum of the thallus calculated.

Growth

Annual growth measurements were made in situ by repeat area measurements of tagged fronds. In December 2001, nine rocks with attached *P. antarctica* were collected from a depth of 15 m. Under subdued lighting in a hut situated directly over the dive hole, two plants on each rock were tagged by tying a coloured string around an individual stipe at the holdfast. Each tagged plant was spread out on a white background next to a ruler and photographed using a digital camera before being returned to a depth of 15 m. In November 2002, almost 12 months later, the rocks were recovered. The tagged plants were carefully removed from the rocks and placed into plastic bags with silica gel for storage. In the lab in New Zealand, plants were re-hydrated in seawater, as many fronds as

possible were identified on the original photographs and then re-photographed. Digital images were used to estimate the length of individual fronds in both years enabling new terminal growth to be identified. The area of the region of new growth was estimated in cm^2 and areal increments were converted to DW using an average ratio to area for plants from a depth of 15 m.

Results

Environmental data

The depth zone between the ice and a depth of 10 m was largely bare of macroalgae. *Iridaea cordata* was encountered only rarely and then as drift plants in shallow water; insufficient material was obtained to use for photosynthetic experiments. Attached *Phyllophora antarctica* was most abundant between 10 and 18 m with the relative proportion of drift to attached plants increasing with depth. Occasional attached plants were seen at a depth of 20 m. Drift *P. antarctica* was most abundant from 15 to 30 m (the limit for SCUBA diving) and *Phymatolithon foecundum* was abundant throughout the depth gradient (10 to 30 m). Drift *Phyllophora antarctica* occurred either as a patchy cover on the bottom, accumulated in hollows or attached to the spines of sea urchins (*Sterechinus neumayeri*).

Over the duration of the field programme no temperature gradients in the water column could be identified. Temperature was -1.9°C and salinity was 34.1 ppt from immediately below the 2.5 m thick ice cover to at least 40 m depth.

Irradiance incident on the ice surface ranged between approximately 200 and $1,500\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$ in a diel pattern over the study period. Between 13 and 17 November average incident irradiance was $688\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$ (Fig. 2) and on average 0.16% penetrated the 2.5 m thick, snow-free ice cover. There was a tendency for transmission through the ice to peak just after midday (Fig. 2). The light that the ice transmitted was dominated by blue-green wavelengths with a strong peak at 570 nm (Fig. 3). The water column was very clear with an attenuation coefficient for downward irradiance (K_d) of $0.09\ \text{m}^{-1}$.

The two light loggers at 15 and 16 m showed the same pattern in irradiance over the course of the year with only marginal differences in intensity. At the start of the record Cape Evans was ice covered. A 100-fold increase in underwater irradiance occurred in both loggers on the last day of January, most likely indicating the timing of ice breakout (Fig. 4a). A few days after this date observations confirm that the region was ice-free (S. Mercer, personal communication). The maximum irradiance recorded was $120\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$ at 15 m depth on 9 February 2002. A marked drop in irradiance in late March may indicate the beginning of ice formation. Between 22 April and 27 August 2002 no measurable irradiance penetrated to 15 m depth. From 27 August until early October 2002 there was a steady increase in underwater irradiance as the sun angle

Fig. 2 Irradiance incident on the ice surface and measured under the ice over a 4-day period between 13 and 17 November 2001. The percent of irradiance transmitted through the ice is also shown

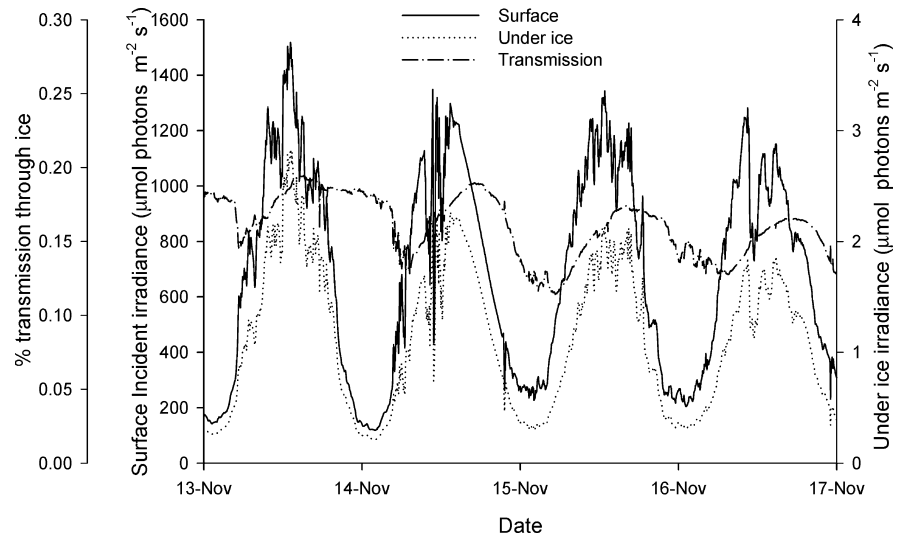
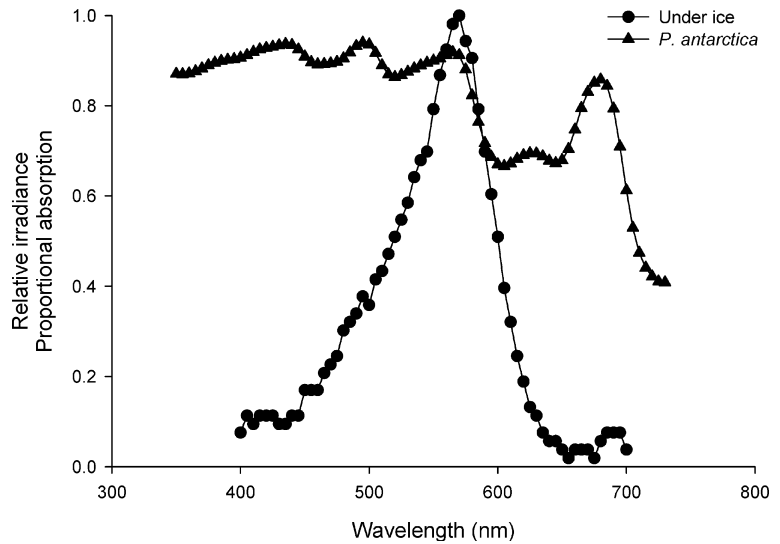


Fig. 3 The spectrum of irradiance immediately below the ice, normalised to the maximum transmission wavelength and the absorption spectrum of *Phyllophora antarctica*



increased. After October 2002, underwater irradiance decreased again from around $2 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ to values of $0.1\text{--}0.3 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, similar to those recorded in December, one year prior.

Pigments in *P. antarctica* and absorption of incident irradiance

Chlorophyll-*a* in *P. antarctica* collected from 10, 15, 20 and 25 m ranged from 48.0 to $71.1 \mu\text{g g}^{-1}$ (FW) (Table 1) and there were no significant differences (ANOVA, $P=0.37$) between depths; however, *Af*, which ranged from 0.88 to 0.76 between 10 and 25 m (Table 1) was significantly less at 25 m than any of the shallower depths (ANOVA, post-hoc Tukey's test for unequal N, $P<0.05$). The relatively flat absorption spectra of the thallus in the blue-green region of the spectrum, with peaks close to maximum transmission of ice (Fig. 3) means that absorption efficiency was high under ice

cover. We calculated that *P. antarctica* from a depth of 10 m would absorb 85% of under-ice irradiance in a single thallus layer.

Photosynthetic measurements

Phyllophora antarctica

Initial RLCs using the actinic light source of the PAM and conducted over a 2-min period, showed light saturation of RETR to occur at irradiance intensities of approximately $15 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ for *P. antarctica* from all depths. In some runs a degree of inhibition was evident at irradiances greater than $20 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. We used these to guide the irradiance applied in the blue light experiments. For the blue light RETR curves the irradiance at which saturation began to be evident (E_k) varied little between depths, at

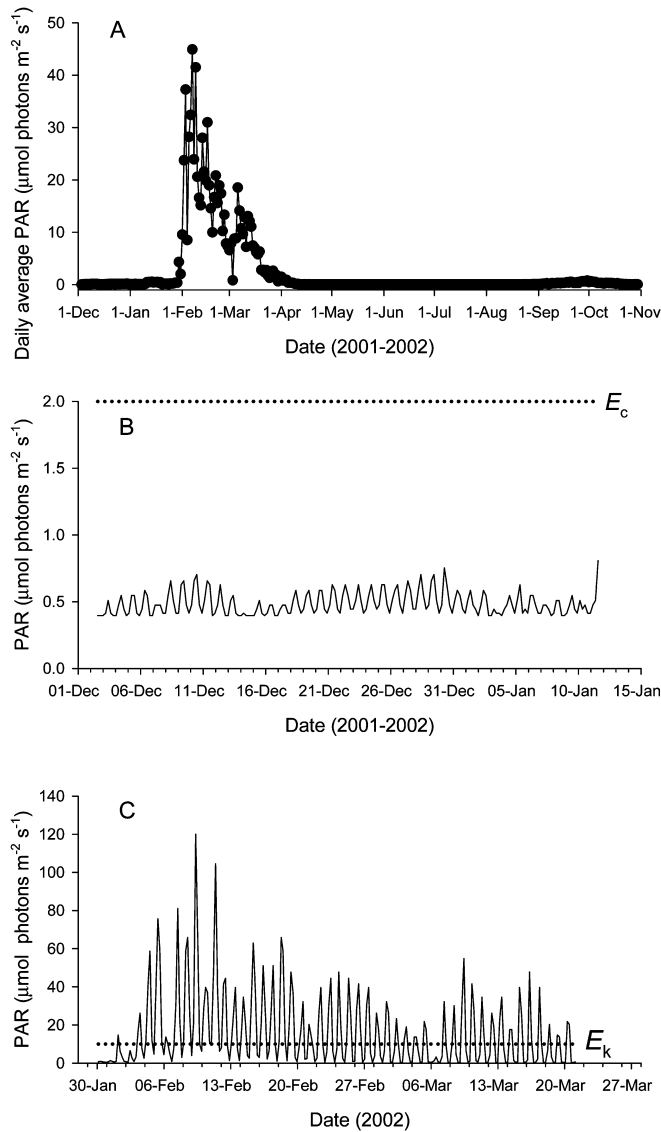


Fig. 4 Patterns of irradiance at 15 m depth at Cape Evans shown as **A** daily average of 5 readings/day over a full annual cycle; **B** each logged value (5 readings/day) during spring, dotted line indicates compensation irradiance for photosynthesis (E_c) of *P. antarctica*; and **C** each logged value (5 readings/day) during late summer; dotted line indicates saturating irradiance for photosynthesis (E_k) of *P. antarctica* measured during spring

8–10 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Fig. 5a, Table 2). No inhibition of RETR was evident up to 30 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Fig. 5a)

To ensure that maximum rates of photosynthesis were achieved in measuring oxygen exchange, we used a

Table 1 Mean \pm standard error of A_f ($n=5$) and chlorophyll- a , ($n=3$)

Depth (m)	A_f	Chl- a $\mu\text{g g}^{-1}$ (FW)
10	0.88 ± 0.01	48.0 ± 6.0
15	0.84 ± 0.01	71.1 ± 3.9
20	0.81 ± 0.01	60.5 ± 11.3
25	0.76 ± 0.02	55.9 ± 11.3

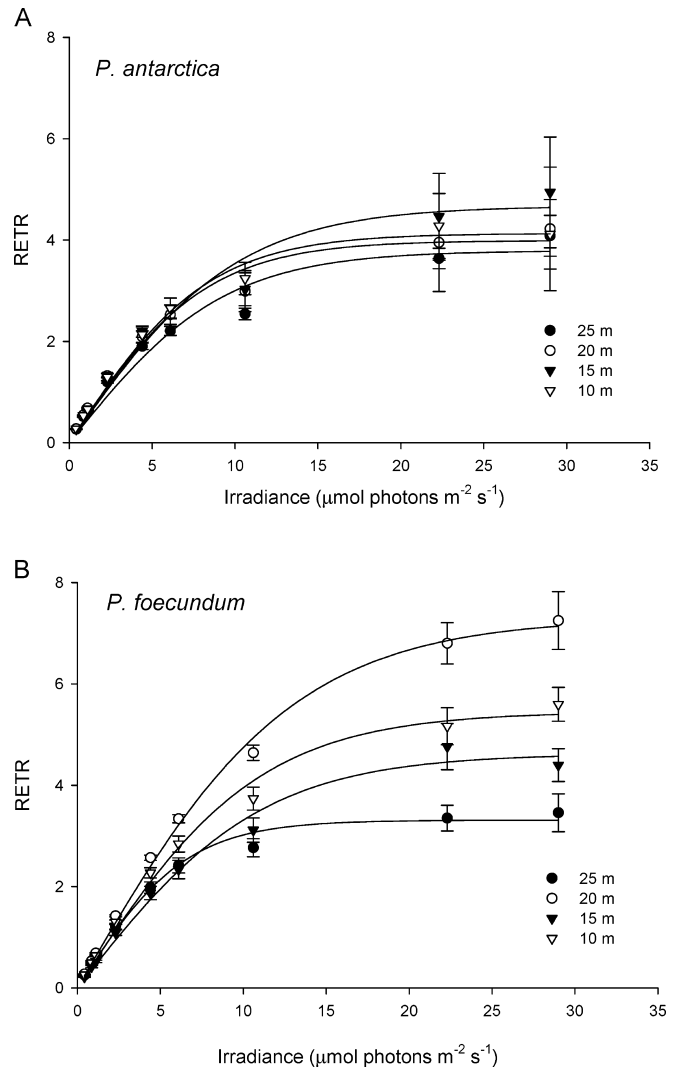


Fig. 5 Relative electron transport rate from four depths, measured in the lab using the PAM fluorometer and a light source corrected to mimic the under-ice spectrum. Each point is the mean and standard error of $n=5$ from 25 m and $n=6$ for 20, 15, and 10 m for **A** *Phyllophora antarctica*, and $n=5$ for each depth for **B** *Phymatolithon foecundum*

blue irradiance of 20 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. The average light-saturated rates of net photosynthesis measured as oxygen evolution, ranged from 10 $\mu\text{mol O}_2 \text{g}^{-1} \text{FW h}^{-1}$ for plants collected from 10 m to 6.3 $\mu\text{mol O}_2 \text{g}^{-1} \text{FW h}^{-1}$ for drift plants at 25 m (Table 2). There was no significant difference (ANOVA, $P=0.48$) between depths in oxygen exchange rates, consistent with patterns of RETR_{max} measured using the Diving-PAM and the blue light source (Fig. 5a). Respiration rates for *P. antarctica* averaged 3.3 $\mu\text{mol O}_2 \text{g}^{-1} \text{FW h}^{-1}$ over all depths (Table 2).

ETR has a theoretical relationship to oxygen evolution (4 mol electrons from PSII mol^{-1} oxygen evolved in photosynthesis) (Schreiber et al. 1986) and good correlations between the two have previously been found for some macroalgae (Henley 1993; Hanelt et al. 1995). We did not conduct oxygen production measurements at all

Table 2 RETR, E_k ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$) and ETR ($\mu\text{mol electrons m}^{-2} \text{s}^{-1}$) measured using blue-filtered irradiance in the on-site laboratory. Values are mean \pm standard error of the parameter estimate, based on five curves each with nine irradiances. $P_{\text{max}}(\text{net})$ (measured at a saturating irradiance of $20 \mu\text{mol photons m}^{-2} \text{s}^{-1}$; see Fig. 5) and respiration of *Phyllophora antarctica*

($\mu\text{mol O}_2 \text{ g}^{-1} \text{ FW h}^{-1}$) are shown as mean \pm standard error. P_{max} was not determined for plants from 20 m; nd no data. E_c ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$) and α ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ FW h}^{-1}$ ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$) $^{-1}$) are estimated values calculated for comparison with published data using E_k values derived from RETR curves

	Depth (m)	RETR _(max)	E_k	ETR _{max}	P_{max} (net)	n	Respiration	n	E_c	α
<i>Phyllophora antarctica</i>	10	4.13 \pm 0.22	8.3 \pm 1.0	1.82	10.0 \pm 2.1	6	3.8 \pm 1.7	6	2.2	1.67
	15	4.67 \pm 0.36	10.1 \pm 1.8	1.96	9.4 \pm 1.9	2	2.3 \pm 0.6	5	2.0	1.16
	20	3.99 \pm 0.36	8.2 \pm 1.8	1.61	nd	–	3.1 \pm 0.7	6	nd	nd
	25	3.79 \pm 0.14	9.3 \pm 0.8	1.44	6.3 \pm 1.1	3	3.9 \pm 2.1	4	3.5	1.09
<i>Phymatolithon foecundum</i>	10	5.45 \pm 0.15	10.9 \pm 0.7	–	–	–	–	–	–	–
	15	4.62 \pm 0.17	11.1 \pm 1.0	–	–	–	–	–	–	–
	20	7.30 \pm 0.21	12.9 \pm 0.9	–	–	–	–	–	–	–
	25	3.31 \pm 0.11	6.5 \pm 0.6	–	–	–	–	–	–	–

the same irradiance intensities at which we measured fluorescence parameters, but we tested the relationship for *P. antarctica* at saturating intensities. When P_{max} (gross) was calculated [$P_{\text{max}}(\text{gross}) = P_{\text{max}}(\text{net}) + \text{respiration}$] and normalised to plant area to obtain units of $\mu\text{mol O}_2 \text{ m}^{-2} \text{s}^{-1}$, the ratio of $P_{\text{max}}(\text{gross})$ to ETR_{max} (calculated using equation 2) was 0.29 mol O₂ mol⁻¹ electrons for *P. antarctica* from 10 m, 0.20 for 15 m and 0.26 for 25 m, yielding values very close to the expected theoretical ratio of 0.25.

For the purpose of comparing with other published data we assumed that the average ETR to oxygen production ratio of 4:1 was consistent across irradiance and depth, enabling us to calculate a compensation irradiance for photosynthesis (E_c - the light intensity at which photosynthesis and respiration are equal). We first converted the light curve obtained using the Diving-PAM (blue light source) to ETR, then to P_{max} (gross) ($\mu\text{mol O}_2 \text{ cm}^{-2} \text{ h}^{-1}$) using the 4:1 ratio. This approximation of a gross photosynthesis versus irradiance curve

was normalised to FW per unit area to give units of $\mu\text{mol O}_2 \text{ g}^{-1} \text{ FW h}^{-1}$. By re-incorporating the respiration term it was possible to convert this to a net photosynthesis curve and to estimate compensation irradiances for photosynthesis of between 2 and 4 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ for *P. antarctica* from 10, 15 and 25 m (Table 2). The initial slope of the light limited relationship α was calculated as $P_{\text{max}}(\text{gross})/E_k$ and ranged between 1.67 and 1.09 $\mu\text{mol O}_2 \text{ g}^{-1} \text{ FW h}^{-1}$ ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$) $^{-1}$ (Table 2).

In situ yield measurements of *P. antarctica* from 10 m showed a diel pattern that followed the available irradiance (Fig. 6) with the highest values of 0.63 measured when incident PAR was lowest, between midnight and 0600 hours. Midday yield was reduced, and for this plant reflected a 14% reduction in F_m' relative to the maximum overnight value. At 20 m depth, almost no reduction in Y was observed over the course of the day, which is consistent with the slightly lower light intensities than at 10 m. Light levels were however very low at

Fig. 6 In situ yield measurements on two *P. antarctica* thalli from 10 and 20 m over a diel period. Irradiance incident on the ice surface during the deployment at 20 m on 18 November is also shown. Incident irradiance on 25 November during the deployment at 10 m followed a similar pattern with the same intensities

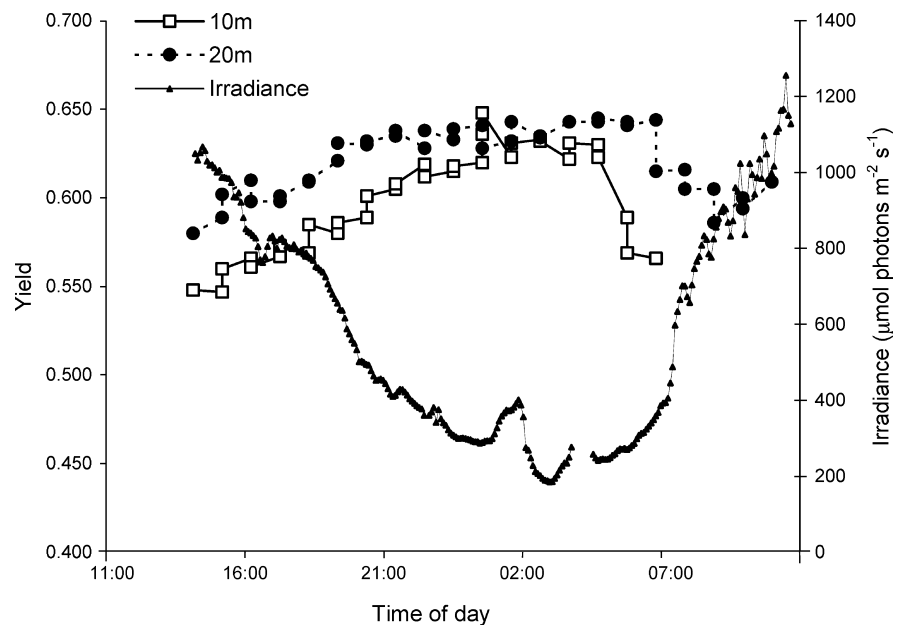


Table 3 In situ yield measurements for *P. antarctica* (attached to rocks and drift algae on urchins) and *P. foecundum*. Values are mean and standard error (SE) of a minimum of 8 and a maximum

Depth (m)	<i>P. foecundum</i>		<i>P. antarctica</i> (attached)		<i>P. antarctica</i> (drift on urchins)	
	Mean	SE	Mean	SE	Mean	SE
10	0.630	0.033	0.690	0.022	nd	–
15	0.661	0.024	0.739	0.016	0.703	0.013
20	0.631	0.013	0.661	0.023	nd	–
25	0.564	0.017	nd	–	0.519	0.021

both depths over these periods, not exceeding $0.7 \mu\text{mol photons m}^{-2} \text{s}^{-1}$.

In situ spot measurements of *Y* provided a greater number of replicates than the diel measurements and showed that at all sampling depths both *Phyllophora antarctica* and *Phymatolithon foecundum* exhibited a *Y* greater than 0.5. The highest average *Y* was 0.739 for *Phyllophora antarctica* at a depth of 15 m and an irradiance of $0.21 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Table 3). ANOVA showed that there were no significant differences between *Y* of *P. antarctica* at depths between 10 and 20 m but at 25 m (where all material was drift) *Y* was significantly lower than at any other depth (post-hoc Tukey's test, $P < 0.05$) despite irradiance being $< 0.25 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. At a depth of 15 m where both attached and drift algae were compared at similar irradiance, there was no significant difference (*t*-test $P > 0.05$) between in situ *Y* for attached and drift plants. This suggests that the lower *Y* values at a depth of 25 m were likely to be depth-related rather than a consequence of the drift / attached status of the material.

Phymatolithon foecundum

Blue light irradiance versus RETR curves for *Phymatolithon foecundum* showed greater variability than for *Phyllophora antarctica* at high intensities (Fig. 5b) and RETR_{max} at 20 m was significantly greater than the other depths for this taxon (ANOVA $P < 0.05$). E_k was also more variable ranging from 6.5–12.9 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Table 2). The lowest values for both parameters were measured for *Phymatolithon foecundum* collected from 25 m. Under ambient irradiance in situ there were no significant differences (ANOVA $P > 0.05$) between values for *Y* at any depth for *P. foecundum* (Table 3).

Growth

Of the 18 *Phyllophora antarctica* plants that were tagged in December 2001, 10 fronds on six tagged plants collected in November 2002 were easily matched from photographs between years. In general, new growth, which appeared lighter in colour and was visible as an increase in length at the terminal end was not evident on every frond, and some had reduced in length, presumably lost to the drift. On fronds where new terminal

of 15 yield measurements depending on depth. Average PAR at the time of the measurements was 0.66, 0.21, 0.29, $0.24 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ for 10, 15, 20, and 25 m respectively

Table 4 Length increments and calculated increase in mass per frond for *P. antarctica* between December 2001 and November 2002

Initial frond length (mm)	Additional length increment over the year (mm)	New growth area in mm^2	Calculated mass increment (mg DW)
74	5	8	0.32
86	8	39	1.62
80	9	40	1.68
89	9	35	1.47
60	11	37	1.54
84	37	177	7.42
175	12	18	0.75
54	8	13	0.56
152	10	37	1.54
124	8	44	1.83

Table 5 Compositions of *P. antarctica* plants from the four sampling depths. Mean \pm standard error of carbon and nitrogen values ($n = 3$), DW/FW and FW/area ($n = 7$). ANOVA groupings are indicated for each column by subscript letters

Depth (m)	FW/area (mg cm^{-2})	DW/FW (%)	Carbon/DW (%)	Carbon/nitrogen (g/g)
10	$14.7 \pm 0.8_A$	$26.9 \pm 1.8_A$	$27.8 \pm 1.1_A$	$7.8 \pm 0.5_A$
15	$13.7 \pm 1.0_A$	$26.6 \pm 1.5_A$	$26.5 \pm 0.1_A$	$7.3 \pm 0.4_A$
20	$13.7 \pm 0.2_A$	$26.3 \pm 1.1_A$	$19.8 \pm 0.6_B$	$6.3 \pm 0.5_A$
25	$12.1 \pm 0.3_B$	$24.2 \pm 2.8_A$	$27.2 \pm 1.6_A$	$7.2 \pm 0.2_A$

growth was evident the area averaged $43 \pm 14 \text{ mm}^2$ and length increment averaged $10.6 \pm 2.7 \text{ mm}$ (Table 4). The relationships between area, fresh weight, freeze-dry weight, carbon and nitrogen contents are shown in Table 5. ANOVA showed the fresh weight per unit area to be slightly lower ($P = 0.006$) for 25 m than for 10, 15 or 20 m and % carbon to be significantly lower at 20 m than the other depths ($P = 0.004$) but there were no significant differences in % dry weight or C:N ratios between depths. These relationships suggest that the average areal increase in the tagged plants of 43 mm^2 per frond at 15 m equates to a biomass increment of 5.9 mg FW, 1.57 mg DW, 0.44 mg C or 0.06 mg N. There was no relationship between individual frond lengths and the amount of new growth meaning that over the period of the year calculated percent biomass increments were also variable, but were less than 7% of the biomass of the tagged plant.

Discussion

Values for RETR and E_k measured during this study for *Phymatolithon foecundum* showed the same values as those measured by Kühl et al. (2001) who presented data to show that Arctic coralline red algae had a lower E_c and E_k than corallines from lower latitudes. There was a suggestion in light curves from Cape Evans that *P. foecundum* growing at 25 m showed greater acclimation to low light than plants at depths through lower E_k and RETR_{max}. However further investigation of the oxygen exchange characteristics of *P. foecundum* is required to elucidate these depth-related patterns more clearly.

Phyllophora antarctica is clearly able to accumulate biomass and persist attached to rocks for a number of years at Cape Evans, nevertheless, the understanding of its light requirements gained in this study and the continuous record of irradiance at depth produce a picture of a plant growing at its physiological limits. Growth, as evidenced by accumulation of thallus length, was extremely slow, with the annual growth increment for 2001–2002 of 11 mm suggesting that the plants (on average 10 times longer than this) were many years old. Slow growth is consistent with the low availability of light energy through much of the year. For all except the two months after ice-out, irradiance was below the estimated compensation irradiance of 2–4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 4b). The strategy of *P. antarctica* is therefore likely to be one of surviving long periods of unfavourable conditions and exploiting brief periods when growth is possible. Such a strategy has been described for *I. cordata*, the other red algal species that persists at Cape Evans. This alga maintained photosynthetic capability during simulated winter darkness (Weykam et al. 1997) and as such was shown to be a “season responder” whereby photosynthetic activity and growth increased under favorable light conditions. Attributes that would favour success in this strategy are likely to be: shade adaptation while retaining the ability to use short periods of high light; efficient absorption and utilisation of light energy; and minimisation of respiration and grazing losses.

Parameters describing the irradiance-photosynthesis properties of *P. antarctica* are derived from a combination of oxygen exchange and fluorescence yield measurements. While these methods measure different properties of the photosynthetic system, there is a growing body of evidence to suggest that, except at high and damaging irradiance, they are quantitatively comparable (Hanelt et al. 1995; Beer et al. 1998; Beer and Björk 2000). Our test of comparability here was a single point calibration and made the assumption that our estimates of A_f accurately reflected the proportion of photons absorbed by photosynthetic pigments, while in reality this proportion may have been over-estimated due to absorption by non-photosynthetic components of the thallus. Nevertheless, the comparison showed that at saturating irradiance, photosynthetic estimates based on

fluorescence yield estimates closely matched those based on oxygen exchange, with approximately 4 mol of electrons passing PSII equivalent to 1 mol O_2 liberated.

Our estimates of P_{max} , α , E_c and E_k are therefore likely to be reliable, and they compare closely to those obtained for a suite of macroalgae from Livingstone Island, on the Antarctic Peninsula (Weykam et al. 1996), and in particular to those measured at the end of winter dark conditions for *I. cordata* (Weykam et al. 1997). Weykam et al. (1996) found α values close to our values of 1–1.7 $\mu\text{mol O}_2 \text{g}^{-1} \text{FW h}^{-1}$ ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$)⁻¹ for several deep-growing or understory rhodophytes, though most of the 22 taxa they measured were less efficient than this. Rates of respiration and light-saturated photosynthesis recorded in this study were slightly lower than all those measured for rhodophytes by Weykam et al. (1996) while E_c and E_k values were similar to their lowest values, suggesting the plants at Cape Evans were highly shade-adapted at all sampled depths. Plants from 10 to 25 m would all have experienced limiting irradiance, and the near absence of significant differences in adaptation parameters is likely to reflect this. The lower rates that we measured may reflect the marginally lower temperature used (-1 cf. 0°C), but again confirm that *P. antarctica* at Cape Evans was strongly shade-adapted and metabolic activity was regulated to a low level at the time of sampling.

The lowest annual light requirements demonstrated so far for completion of life cycles in polar macroalgae are for the brown seaweeds *Himantothallus grandifolius* and *Desmarestia anceps* which require 31 mol photons $\text{m}^{-2} \text{year}^{-1}$ (Wiencke 1990). At Cape Evans during 2001–2002 this light level occurred between 20 and 25 m (Table 6) coinciding with the maximum depth limit for attached plants, which suggests that *P. antarctica* may require similarly low annual irradiance to complete its lifecycle.

Average E_k was between 6.5 and 12.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Maintenance of E_k well above ambient irradiance means that the plants at Cape Evans will be operating at maximum efficiency under ice cover. The diel and spot measurements of fluorescent yield, which showed little or no departure from maximum Y at depths shallower than 20 m, confirm that this was the case. Maintaining an E_k well above ambient also means that when irradiance increased suddenly in late January, the plants were pre-adapted to exploit this and is further evidence for a “season responder” strategy similar to *I. cordata*

Table 6 Estimated annual light dose based on irradiance measured at 15 m and a vertical extinction coefficient in the water column of 0.09 m^{-1}

Depth (m)	Mol photons $\text{m}^{-2} \text{year}^{-1}$
10	111.56
15	70.63
20	44.68
25	28.07
30	17.71

(Weykam et al. 1997). At present we are unable to determine whether *P. antarctica* would have acclimated to the brief period of high light experienced when ice cover is lost, but it seems likely, as shown for shallow water Antarctic algae (Hanelt et al. 1994) and for macroalgae from 10 m depth in Greenland (Kühl et al. 2001). Antarctic macro-algae are able to efficiently utilise low light intensities (Kirst and Wiencke 1995), but they are also capable of withstanding excessive light conditions. A number of studies have shown that Antarctic brown macroalgae take advantage of periods of high light which result from a combination of high incident irradiance and high water clarity during ice-free, phytoplankton bloom-free periods. Some species exhibit optimum photosynthesis under such conditions (Drew and Hastings 1992; Gutkowski and Maleszewski 1989). In support of an expected photoacclimation under ice-free irradiance conditions, an E_k of $100 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$, more characteristic of a higher irradiance environment, was shown for *P. antarctica* at Terra Nova Bay in summer (L. Mazzella, unpublished data in Gambi et al. 2000). For *P. antarctica* at Terra Nova Bay, E_k showed evidence of being the mechanism of acclimation rather than P_{max} which at $9 \mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$ was similar to values we measured in spring at Cape Evans. Even if there was no further acclimation of E_k , Fig. 4c suggests that during much of the ice-free period, photosynthesis at 15 m would have been light-saturated for part of each day.

While still ice-covered, photosynthesis under ice was likely to only make a very small if any contribution to net annual growth. Only plants at our shallowest sampling depth of 10 m could have been maintaining their carbon balance, but with little if any scope for growth. During the ice free period, plants at a depth of 15 m experienced PAR intensities above E_c for at least part of the day over a 10-week period, but there were only 16 days during February out of the whole year's record when irradiance at a depth of 15 m was above E_c for the entire day. At the end of winter, irradiance approached compensation levels at a depth of 15 m for a brief period in October 2002. The subsequent decrease in underwater irradiance at this depth between October and November 2001 is probably due to a combination of snow cover, a change in ice transparency as temperatures rise and accumulation of ice-algae biomass begins (Trodahl et al. 1989; Trodahl and Buckley 1990). While the slow growth of *P. antarctica* is consistent with the low light dose it receives, multi-year persistence at low growth rates is likely to depend not only on the low respiration loss, but also on low grazing rates. There is experimental evidence to suggest that *P. antarctica* is not grazed on by the dominant echinoderms (*Sterechinus neumayeri*) because of the toxic compounds that it contains (Amsler et al. 1999), and this is likely to be an important factor allowing the slow accumulation. Although apparently not grazed directly by *S. neumayeri* Amsler et al. (1999) suggested that fertile drift plants of *P. antarctica* are kept in the photic zone and have their vertical and horizontal distribution ranges extended by being

attached to the backs of urchins. The finding that drift thalli on urchins at a depth of 15 m in 2001 were photosynthetically active with a significantly higher yield than similar plants at 25 m is consistent with this hypothesis.

During the ice-free period there were days when light intensities would have been above E_c and occasionally above E_k at a depth of 25 m meaning that the photosynthetically viable drift algae would have been able to achieve net carbon gain over this time. However, lower in situ yields and a reduced value for A_f for the deepest drift plants that we measured (25 m) suggested evidence of reduced photosynthetic potential compared to drift plants at 15 m, and they may not have been as capable of photosynthesising effectively even during the ice-free period. Nevertheless, low respiration rates will be conducive to slowing the rate of decomposition and are likely to assist in longevity of the drift plants regardless of the irradiance they receive. Accumulations of slowly decomposing drift algae may therefore be an important source of carbon for higher trophic levels through the detrital food web, as shown for other macroalgae on the Antarctic Peninsula (Duntun 2001; Reichardt and Dieckmann 1985).

The overall picture is one of slow growth, persistent drift material and long-lived thalli. Survival depends on low loss rates, a combination of low respiration rates and grazer resistance. Efficient under-ice photosynthesis may supplement stored carbon reserves at some depths, and may even allow a small carbon gain at the upper limit of the plants; however, the extent of this will also be influenced from year to year by variable snow cover. This study was clearly carried out before the time that we would expect most net production and therefore the major accumulation of carbon to occur, as the ice cover did not break out until nearly 2 months later. In some years, however, we know that the sea ice does not break out of this location and yet the alga persist. While annual irradiance environment is often crucial to maintaining a net carbon balance and setting distribution limits, in years of prolonged ice cover at Cape Evans this may not be possible. It may be that in such a consistently low temperature environment, achieving an overall compensation irradiance dose over a period of longer than a year needs to be considered as the distribution-limiting factor.

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