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Photosynthetic light requirements, metabolic carbon balance and zonation of sublittoral macroalgae from King George Island (Antarctica)

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ABSTRACT: Photosynthesis, dark respiration, chlorophyll *a* contents and daily metabolic C balance were determined in 5 species of brown and red algae from Potter Cove (King George Island) during the Antarctic spring. *In situ* irradiance data were used to determine the light requirements of plants collected at 10, 20 and 30 m depth. Average daily maximum quantum irradiances measured in spring-summer reached up to 23 µmol photons m^{-2} s^{-1} at 30 m depth indicating that macroalgae can effectively be exposed to non-limiting quantum irradiances for photosynthesis. Net photosynthetic rates (P_{max}) were high in the brown alga *Desmarestia anceps* and the red algae *Palmaria decipiens* with values close to 33 and 36 µmol O_2 g^{-1} FW h^{-1}, respectively, at 20 m depth. With the exception of the brown alga *Himantothallus grandifolius*, all the species showed lower P_{max} in plants collected at 30 m than at 10 and 20 m depth. The photosynthetic efficiency (α) varied strongly among species, but no clear depth-dependent relations were found. Saturation (I_k) and compensation (I_c) points for photosynthesis were, in general, lower in plants growing at deep locations. In plants from 10 and 20 m, photosynthesis was saturated at significantly lower irradiances than *in situ* quantum irradiances. Values of I_k varied between 58 µmol photons m^{-2} s^{-1} in *D. anceps* and 15 µmol photons m^{-2} s^{-1} in the red alga *Gigartina skottsbergii*, while I_c ranged between 1 and 10 µmol photons m^{-2} s^{-1} in most of the species. *D. anceps* exceptionally had I_c values close to 26 µmol photons m^{-2} s^{-1} in plants from 10 m depth. Overall, photosynthetic performance in these species was comparable to rates measured in macroalgae from upper littoral zones and did not provide evidence for metabolic acclimation with depth. Apparently, the daily periods for which plants are exposed to saturation and compensation irradiances (H_{sat} and H_{comp}) and, consequently, the metabolic C balance account for the acclimation of macroalgae to deep sublittoral zones. At 10 m, H_{sat} for many species was between 12 and 14 h, while at 30 m these periods decreased to 7 h in *D. anceps* or 9 h in the red alga *Kallymenia antarctica*. The H_{comp} periods were longer, in the case of the red algae up to 16 h. The daily carbon balance decreased with depth. At 30 m, algae exhibited C gains lower than 1 mg C g^{-1} FW d^{-1} and in *D. anceps*, due to its high respiration rates, carbon balance was negative at saturation and compensation irradiances. In general, greater C gains relative to losses were found in plants growing at 20 m depth. Although data on P_{max}, α, I_c and I_k indicate that Antarctic macroalgae are metabolically able to inhabit greater depths during spring-summer, the shortening of the daylengths for which algae are exposed to saturating or compensating irradiances impose a maximum depth limit at depths around 30 m.

KEY WORDS: Antarctic · Depth · Macroalgal zonation · Photosynthesis · Daily quantum irradiance · Carbon balance

INTRODUCTION

Light availability for photosynthesis is a major factor determining the distribution limits of sublittoral macroalgae (Lüning & Dring 1979, Lüning 1981). Species with broad vertical distributions are able to acclimate to the various light climates at different depths which differ in spectral composition (Jerlov 1976, Kirk 1983) and quantum irradiance (Dring 1981, Ramus 1981). Some physiological adjustments often described in algae occurring in deep waters are increased contents of light-harvesting

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pigment (Ramus et al. 1977), high photosynthesis:respiration ratios and low light-saturation (I_k) or compensation (I_c) points (Markager & Sand-Jensen 1992).

In the Antarctic region, benthic marine macroalgae are restricted almost exclusively to subtidal habitats (Lamb & Zimmermann 1977). Prolonged ice-cover in winter (Zielinski 1990, Drew & Hastings 1992) and local attenuation of light penetration due to phytoplankton blooms or melt-water during summer (Klöser et al. 1993) constitute additional constraints limiting light for photosynthesis. Despite these adverse factors, the occurrence of macroalgae in deep waters of the Antarctic region (>40 m) has frequently been reported (Arnoud 1974, DeLaca & Lipps 1976, Zielinski 1981, 1990). *In situ* irradiance measurements indicate that optical characteristics during spring of some Antarctic waters allow light to penetrate to greater depths (Priddle et al. 1986, Drew & Hastings 1992). According to Klöser et al. (1993), growth of macroalgae at Potter Cove, King George Island (South Shetlands Islands), may be possible down to a depth limit of 40 m, where ca 0.2% of the surface irradiance is available during optimum light conditions. This suggests that the exceptionally high transmittance of shallow waters in the Antarctic during spring-summer accounts for the present vertical distribution patterns of macroalgae.

In the area of King George Island, the incident solar radiation during spring-summer is highly variable and depends strongly on the weather conditions: on sunny days algae are exposed to favourable light conditions, but during prolonged periods of cloud cover some subtidal species may be exposed to quantum irradiances below the photosynthetic saturation points (Klöser et al. 1993). This raises the question: Which factors determine the minimal light requirements for photosynthesis in macroalgae living at the boundaries of light penetration? This question has been previously addressed in seagrasses (Dennison & Alberte 1982, 1985) and in some macroalgae (Ramus & Rosenberg 1980, Matta & Chapman 1991), and duration of the exposure to photosynthetic irradiances (e.g. daylength) rather than the intensity of irradiance has been shown to determine plant productivity in sublittoral populations. For polar macroalgae, such considerations are particularly pertinent: for example, it has been demonstrated that linear growth and C content of *Laminaria solidungula* during the summer open-water in the Alaskan High Arctic were highly correlated to the daily periods for which plants were light saturated (H_{sat}; Dunton 1990).

Up to now, studies on light requirements for growth and photosynthesis in sublittoral Antarctic macroalgae have not given conclusive evidence on the acclimation potential of these algae to the light climate at different water depths. Some physiological studies using cultured material have revealed that Antarctic macroalgae have very low light requirements for growth and photosynthesis, which are a prerequisite for survival in deep waters (Wiencke 1990a, b, Thomas & Wiencke 1991, Wiencke et al. 1993, Gómez et al. 1995a, b). Only recently has it been demonstrated that certain deep water macroalgae have higher photosynthetic efficiencies (α) at low irradiances and lower light-saturation points (I_k) than algae restricted to the upper sublittoral (Weykam et al. 1996). However, studies focusing on inter and intraspecific comparisons of photosynthetic characteristics in algae with broad vertical distributions are lacking. Therefore, the present study constitutes an initial effort to explain the algal zonation from a physiological point of view. Effects of depth on several photosynthetic parameters were determined in 5 species of brown and red algae growing over a wide range of vertical distribution at Potter Cove (Fig. 1) during spring-summer. This period coincides with the highest seasonal growth rates and abundance of macroalgae in this area (Wiencke 1990a, Klöser et al. 1994, 1996). Light requirements for photosynthesis and estimates of daily metabolic carbon balance are analysed in relation to the incident irradiances and the daily photon exposure.

MATERIAL AND METHODS

Study site and algal sampling. The subtidal locations of Potter Cove are characterized by hard substrate (pebbles, solid rocks, stones, etc), pronounced slope, moderate wave exposure and deep light penetration (Klöser et al. 1993). Macroalgal assemblages are dominated by the large Desmarestiales (e.g. *Desmarestia* and *Himantothallus*) which exhibit broad ranges of vertical distribution (10 to >30 m). Likewise, red algae such as *Gigartina skottsbergii* and *Palmaria decipiens* are abundant in the upper sublittoral, but are often found also in deeper locations (Klöser et al. 1994, 1996).

The brown algae *Desmarestia anceps* Montagne and *Himantothallus grandifolius* (A. et E. S. Gepp) Zinova and the red algae *Kallymenia antarctica* Hariot, *Palmaria decipiens* (Reinsch) Ricker and *Gigartina skottsbergii* (Bory) Setchell et Gardner were collected by SCUBA diving at 10, 20 and 30 m from a site located at the northern margin of Potter Cove (Fig. 1) during November and December 1993. After collection, discs of 15 mm diameter were cut by a cork borer from the middle part of the lamina for the leathery species. In the case of the terete *D. anceps*, the apical branches of the thallus were selected. In all species, pieces were weighed and kept overnight in natural seawater at 0°C to avoid wound effects [see Hatcher (1977), Drew (1983) and Arnold & Manley (1985) for methodological considerations about the use of thallus pieces in photosynthetic measurements].

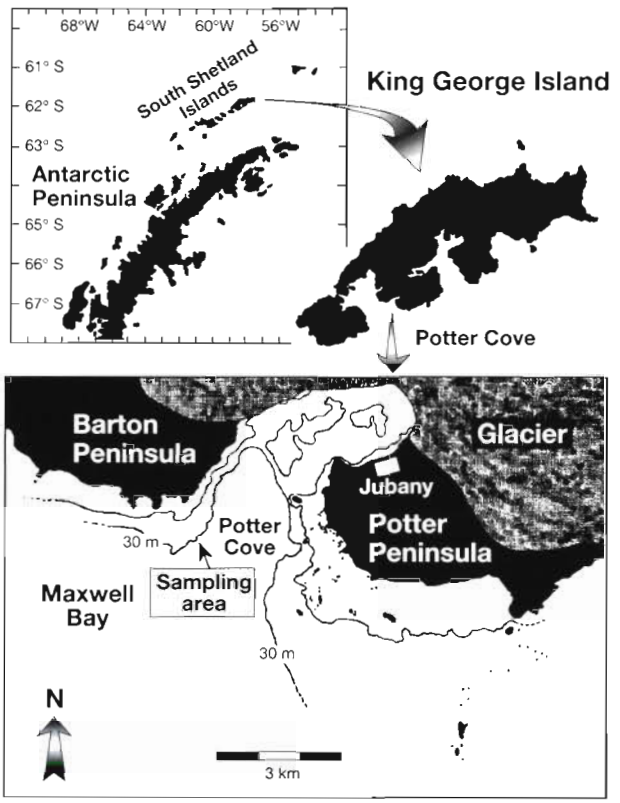

Fig. 1. Location of the study area in Potter Cove, King George Island

Oxygen flux measurement and photosynthetic parameters. Photosynthesis and dark respiration were measured in a glass chamber (21 ml volume) fitted with a polarographic oxygen electrode and a magnetic stirrer (Wissenschaftlich-Technische-Werkstätten, WTW, model OXI 92). The medium consisted of filtered natural sea water buffered with 8 mM Tris/NaOH (pH 8.0). To avoid depletion of the inorganic carbon in the chamber during the measuring period (ca 3 h), 5 mM $NaHCO_3$ were added. The whole system was submerged in a glycerin-water bath kept at a temperature of 0 ± 0.01°C. A slide projector (Leica, Pradovit) equipped with neutral density glass filters (Schott) was used as a light source. Incident irradiance in the measuring chamber was determined by use of a Licor Li-1000 quantum-meter equipped with a UWQ cosine quantum sensor. The dark respiration rate was measured for 20 min, followed by determinations of net oxygen production under 15 different irradiances from 1 to 800 µmol photon m^{-2} s^{-1}. Four replications were carried out using discs taken from 4 single plants of each species.

Photosynthesis vs irradiance curves (*P-I*) were used to calculate photosynthetic parameters. A non-linear (exponential) function was fitted to the data for each sample disc [see Nelson & Siegrist (1987) and Henley (1993) for details]. This equation is expressed as:

$$P = P_{max} (1 - \exp^{\alpha I / P_{max}}) + R$$

where P is the photosynthetic rate, P_{max} is the maximum photosynthetic rate at saturating irradiances, α is the initial slope of the curve at low irradiance; I is incident irradiance, and R is the dark respiration rate. Accuracy of the curve fit was assessed by non-linear least square regression at 95% probability. The light saturation point (I_k) of photosynthesis was calculated from the quotient between α and P_{max} and the light compensation point (I_c) as the intersection of α and the irradiance axis.

Quantum-irradiance measurements and calculations of daily irradiance regimes (H_{sat} and H_{comp}). Photosynthetically active radiation (PAR) was measured using a Li-193Sb spherical (4π) quantum sensor and a LI-185B datalogger (Li-Cor Inc) as described previously by Klöser et al. (1993). The instantaneous PAR data (µmol m^{-2} s^{-1}) obtained for 10, 20 and 30 m depth were then plotted against time of day (h) and the total daily photon exposure (mol m^{-2} d^{-1}) was determined by integrating the area under the light-time curves. The daily light-saturation (H_{sat}) and light-compensation (H_{comp}) periods for each species and depth were calculated according to Matta & Chapman (1991). These parameters are defined as the number of hours per day above light saturation and compensation respectively and were calculated from the intersection of I_k or I_c points and the time in the daily light curves (see Fig. 4). Values of I_k and I_c used in these calculations were obtained from the *P-I* curves.

Estimated daily metabolic carbon balance. Calculations of daily net carbon balance (mg C g^{-1} FW d^{-1}) were made as described by Dennison & Alberte (1982) by multiplying the gross photosynthetic rates (P_{max} + dark respiration), obtained from the photosynthetic data, by the average daily period of light-saturation (H_{sat}) and then subtracting the daily (24 h) dark respiration. Oxygen data were converted to equivalent carbon units using the ratio $gC:gO_2 = 0.3$ (Matta & Chapman 1991). For these calculations it was assumed that dark respiration was constant throughout the day and that the photosynthetic quotients (*PQ*) of the plants were close to 1.0 (Hatcher et al. 1977). It must be emphazised that these estimates of productivity refer only to a photosynthetic carbon balance as other sources of C losses such as exudation, grazing or release of reproductive cells as well as the C gains derived from light-independent carbon fixation were not considered.

Chlorophyll *a*, nitrogen, and carbon determinations. These determinations were made using material taken simultaneously with that used for photosynthetic measurements. Extraction of chl *a* was carried out using

N,N-dimethylformamide (DMF) as described by Inskeep & Bloom (1985) Extinction (Ext) was measured in a spectrophotometer (Milton Roy, Spectronic 401) at wavelength of 664.5 nm and the chl *a* content was calculated using the equation:

$$\text{chl } a = 12.7\ \text{Ext}_{664.5}$$

The samples used for carbon (C) and nitrogen (N) were freeze-dried in a lyophylizer (Lyovac GT 2, Finn-Aqua) for 48 h at 0.02 mbar and then stored at room temperature until later analysis. Total C and N were determined in duplicate sub-samples (ca 0.5 to 1 mg in tin cups) with a Carlo-Erba 1500 elemental analyser calibrated with acetanilide (Iken 1996). Dry weight relative to fresh weight in the samples was calculated as the weight difference after lyophylization.

Statistical treatment. For statistical treatments data were previously logarithm transformed. In the case of ratios and percentages, the arcsin transformation was used. Differences among species and depths were tested for each photosynthetic parameter using a 2-way analysis of variance (ANOVA, Model II). Multiple comparisons of means were carried out using the Fisher test (least significant difference, LSD) at $p < 0.05$ (Sokal & Rohlf 1981).

RESULTS

Underwater quantum irradiance

The seasonal changes in light penetration through the water column at Potter Cove are shown in Fig 2A. No significant variations in the profiles of light penetration occurred during November and a great part of December but in late December light penetration was reduced strongly. The surface irradiance was also influenced by cloud cover (Fig. 2B). The seasonal variations in daily sunshine exposure indicated that many days in the Antarctic spring-summer are characterized by permanent or partial cloud cover (0 to 5 h sunshine d^{-1}), whereas days with more than 10 h sunshine were exceptional.

Fig. 3 shows the depth profiles of *in situ* irradiance measured at midday in days with different cloud cover (Days 1, 2 and 3 from Fig. 2B). Incident irradiances at the surface varied between 700 µmol photons m^{-2} s^{-1} on a cloudy day (1 Nov) up to 1700 µmol photons m^{-2} s^{-1} on sunny days (8 Nov; Fig. 3A). At 10 m depth, the incident irradiance varied between 400 and 146 µmol photons m^{-2} s^{-1}. In contrast to the surface, irradiance measured at 20 and 30 m was not affected by cloud cover: on a sunny day (8 Nov), maximal values of 170 and 50 µmol photons m^{-2} s^{-1}, respectively; however on 19 Oct (also a sunny day), the irradiance available at 20 and 30 m depth did not exceed 16 µmol photons m^{-2} s^{-1} These patterns of light attenuation determined the depth of the 1% surface irradiance (I_0) between 20 and 40 m (Fig. 3B).

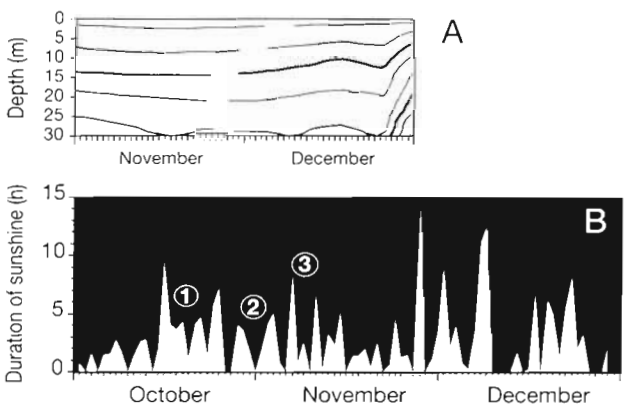

Fig. 2. (A) Temporal changes in light penetration in the water column (re-drawn after Klöser et al. 1993). (B) Duration of sunshine at Potter Cover. Heliographic data were provided by the Estación Meteorológica, Base Jubany (Argentina). Numbers indicate days when depth profiles of irradiance were measured

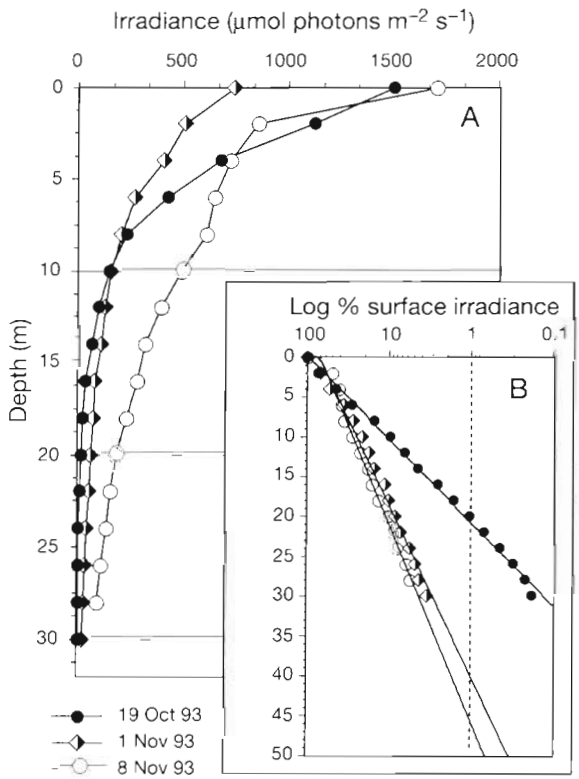

Fig. 3. (A) Depth profiles of quantum irradiance (Photosynthetic Active Radiation, PAR) measured on 3 different days at Potter Cove. (B) Vertical light expressed as % of the surface irradiance (% I_0). The dotted line indicates the lower limit of the photic zone (1% I_0). Measurements were made at midday

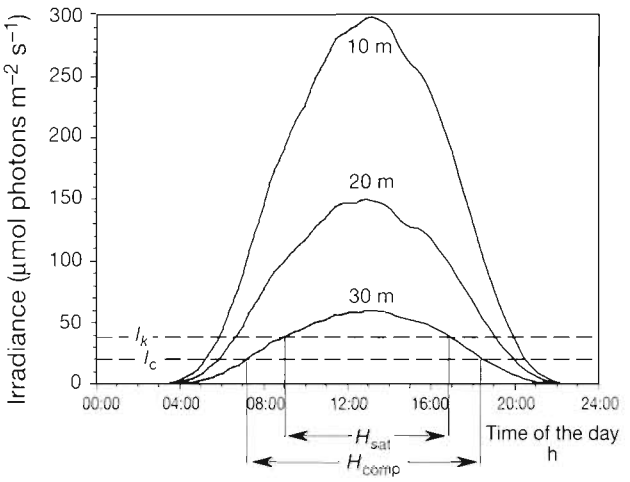

Fig. 4. Daily course of irradiance at 3 different depths in Potter Cove. Data are averages of 15 d (October-November 1993). These curves were used to estimate saturation (H_{sat}) and compensation (H_{comp}) periods according to the saturation (I_k) and compensation (I_c) points for photosynthesis

The daily course of irradiance measured at different depths during spring (Fig 4) revealed that subtidal habitats in this area were illuminated over a period of 17 to 18 h per day. Although no obvious decrease in the light period with depth was observed, significant changes in the integrals of daily irradiance were evident. Whereas at 10 m depth daily irradiance reached 6.7 mol m^{-2}, plants growing at 20 and 30 m received only 50% (3.4 mol m^{-2}) and 20% (1.3 mol m^{-2}) of this value, respectively.

Variations in chl *a*, C and N contents and fresh weight:dry weight ratios

Chl *a*, C, N and dry weight contents varied with species and depth (2-way Anova, $p < 0.001$; Table 1). Chl *a* was high in *Desmarestia anceps* with values between 680 and 703 µg g^{-1} FW, while in *Palmaria decipiens* the chl *a* content did not exceed 312 µg g^{-1} FW. In *Himantothallus grandifolius*, a clear vertical pattern in chl *a* content with depth was observed, with values varying from 303 µg g^{-1} FW in plants collected at 10 m to 452 µg g^{-1} FW in plants from 30 m. In contrast, the chl *a* contents of *Gigartina skottsbergii* and *Kallymenia antarctica* decreased with depth with significantly higher ($p < 0.05$) values in plants from 10 m (413 and 387 µg g^{-1} FW, respectively) than in plants from 30 m (292 and 265 µg g^{-1} FW, respectively).

In general, C contents did not show obvious differences with depth. The highest C contents were determined in *Desmarestia anceps* (between 312 and 355 mg g^{-1} DW), whereas *Gigartina skottsbergii* exhibited the lowest values (243 and 280 mg g^{-1} DW). N contents were generally high (>2% DW) and no changes with depth were found. *Palmaria decipiens* was the species with the highest N content (47 and and 55 mg g^{-1} DW), while in the other algae N contents did not exceed 36 mg N g^{-1} DW. This species also showed a low dry weight content relative to fresh weight (between 7 and 9%), whereas, in *D. anceps*, dry matter accounted for ca 18% of the total weight.

Table 1. Summary of the variation in chl *a*, C and N contents, as well as dry weight (DW) contents expressed as % of fresh weight (FW) in Antarctic macroalgae collected at 3 different depths in Potter Cove during October-November 1993. Data are means (± SD) (n = 3 or 4); nd: not determined. Statistical significances are described in the text

Species	Depth (m)	Chl *a* (µg g^{-1} FW)	C (mg g^{-1} DW)	N (mg g^{-1} DW)	Dry weight (% FW)
Brown algae					
Desmarestia anceps	10	682.0 (39.2)	355.7 (2.4)	35.2 (0.3)	18.7 (2.3)
	20	683.8 (34.9)	312.3 (4.3)	31.8 (1.7)	16.5 (1.1)
	30	703.6 (34.9)	330.9 (9.2)	31.3 (0.7)	18.9 (2.7)
Himantothallus grandifolius	10	303.9 (37.4)	313.9 (3.0)	20.7 (0.8)	12.7 (0.4)
	20	365.4 (14.7)	319.5 (8.0)	23.0 (0.4)	12.6 (0.3)
	30	451.8 (22.2)	284.8 (24.6)	22.9 (1.8)	11.5 (0.4)
Red algae					
Kallymenia antarctica	10	386.9 (30.6)	nd	nd	nd
	20	325.0 (102.2)	nd	nd	nd
	30	287.6 (96.8)	nd	nd	nd
Palmaria decipiens	10	290.2 (30.8)	326.0 (5.7)	55.0 (2.4)	7.0 (0.9)
	20	312.6 (16.6)	291.3 (1.3)	58.1 (0.3)	8.7 (0.5)
	30	264.9 (10.4)	275.0 (16.0)	47.5 (3.1)	9.4 (1.0)
Gigartina skottsbergii	10	413.1 (31.1)	254.6[a]	17.3	nd
	20	301.0 (13.5)	280.3	43.0	nd
	30	292.7 (18.9)	243.1	19.6	nd

[a]Only one measurement was made of N and C contents in *G. skottsbergii*

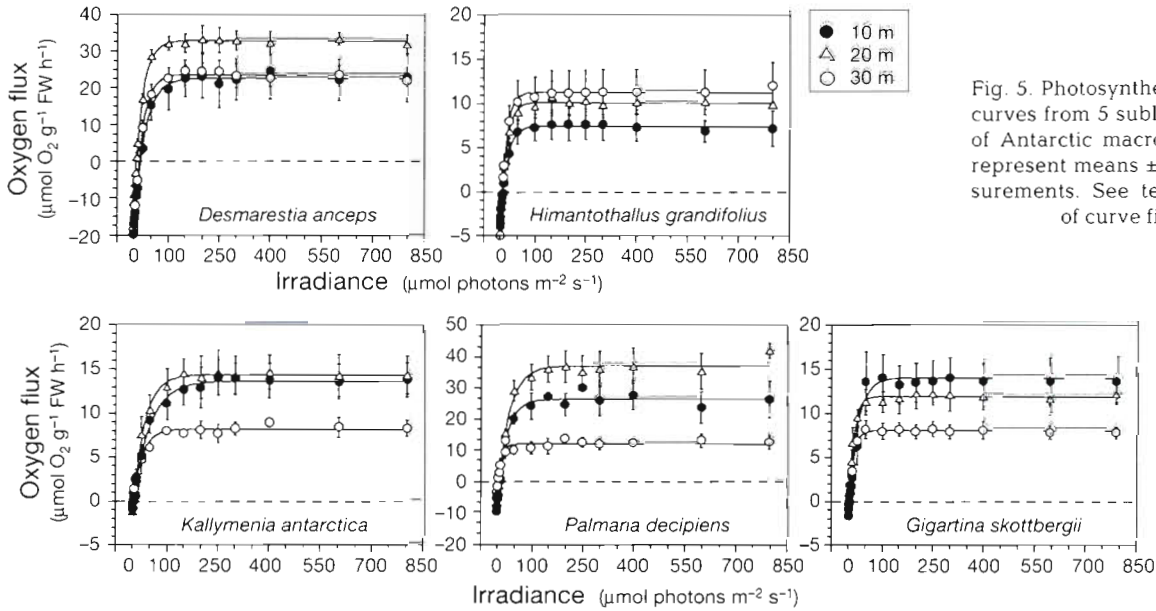

Fig. 5. Photosynthesis-light (*P-I*) curves from 5 sublittoral species of Antarctic macroalgae. Points represent means ± SD of 4 measurements. See text for details of curve fitting

Photosynthetic performance

The photosynthesis-irradiance (*P-I*) curves determined for the different species and depths are shown in Fig. 5. In general, the red algae exhibited lower P_{max} values at 30 m compared to 10 and 20 m. In the brown algae, no clear pattern was observed. Although plants were exposed to high saturating irradiances (400 to 800 µmol O_2 g^{-1} FW h^{-1}), no signs of photoinhibition were observed during the experiments. Apparently the short period of exposure to these irradiances (30 min in total) did not affect photosynthetic performance.

The P_{max} and dark respiration rates were significantly different among species and depths ($p < 0.001$, 2-way ANOVA; Fig. 6). In the 3 red algae studied here, P_{max} significantly decreased in plants collected at 30 m depth ($p < 0.05$) relative to individuals from 10 and 20 m. Photosynthetic performance in *Kallymenia antarctica* and *Gigartina skottsbergii* was similar, and no obvious differences were found among plants from 10 and 20 m depth ($p > 0.05$). *Palmaria decipiens* had significantly higher P_{max} in plants from 20 m depth (38 µmol O_2 g^{-1} FW h^{-1}, $p < 0.01$; Anova-Fisher LSD) than in plants growing at 10 m (25 µmol O_2 g^{-1} FW h^{-1}) and 30 m (12 µmol O_2 g^{-1} FW h^{-1}). In the case of *Desmarestia anceps*, the highest P_{max} values were recorded in plants from 20 m depth (33 µmol O_2 g^{-1} FW h^{-1}). The highest rates of dark respiration were measured in *D. anceps* plants from 10 and 30 m depth (ca 20 µmol O_2 g^{-1} FW h^{-1}). In *Palmaria decipiens*, plants from 10 m depth showed the highest dark respiration rates (9 µmol O_2 g^{-1} FW h^{-1}, $p < 0.05$). In contrast, *Himantothallus grandifolius*, *K. antarctica* and *G. skottsbergii* were characterised by low to very low respiratory activities (<2 µmol O_2 g^{-1} FW h^{-1}, $p < 0.05$).

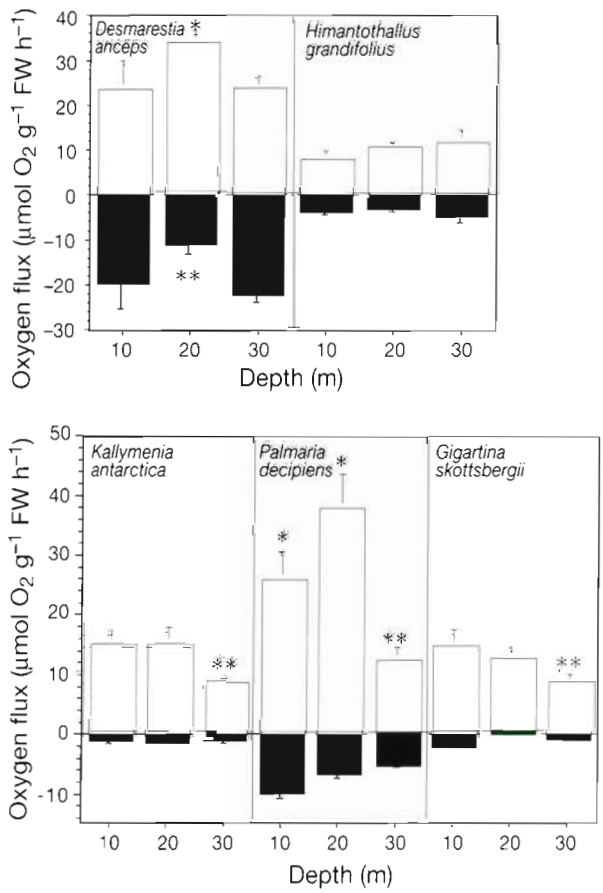

Fig. 6. Saturated net photosynthesis (P_{max}) and dark respiration of 5 Antarctic macroalgae collected at 3 different depths at Potter Cove. Error bars show +SD. Data were obtained from *P-I* curves as illustrated in Fig. 5. Asterisks indicate significant differences: *$p < 0.05$; **$p < 0.01$. Parameter calculations and details of statistical treatments are described in text

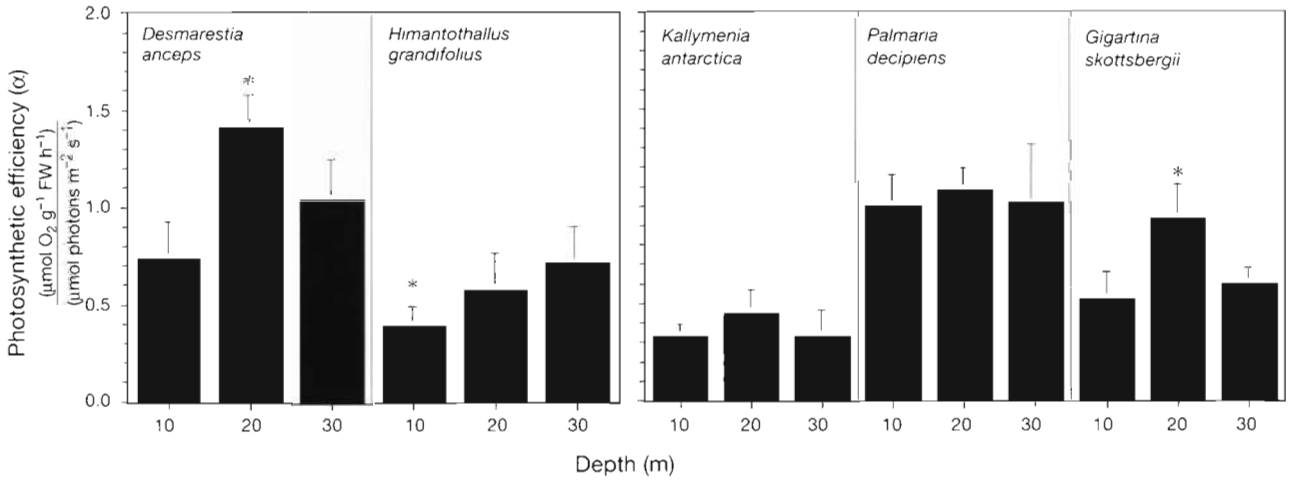

Fig. 7. Photosynthetic efficiency (α) determined in 5 species of Antarctic macroalgae collected at 3 different depths in Potter Cove. Data are means (+ SD) of 4 measurements. Asterisk indicates significant difference: *$p < 0.05$. See text for details of statistical treatment

Photosynthetic efficiency (α) in the studied algae was high (Fig. 7), especially in *Desmarestia anceps* and *Palmaria decipiens*, which showed the highest α values among the studied species [>1 μmol O_2 g^{-1} FW h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$; $p < 0.05$, Fisher test]. There were no significant effects of depth on α in the red algae, but α increased significantly ($p < 0.05$) with depth in the brown algae, with values close to 1.4 μmol O_2 g^{-1} FW h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$ at 20 m for *D. anceps* and 0.7 μmol O_2 g^{-1} FW h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$ at 30 m for *Himantothallus grandifolius*.

Variations of I_c, I_k, H_{comp} and H_{sat} with depth

The saturation (I_k) and compensation (I_c) points of photosynthesis for the different species and depths are shown in Fig. 8. In general, plants collected at 10 m had the highest I_k values, especially in *Desmarestia anceps* and *Kallymenia antarctica* (58 and 47 μmol photons m^{-2} s^{-1}). However, there was not a uniform pattern in the I_k variations in plants from 20 and 30 m. For example, in *D. anceps*, the mean I_k of 31 μmol photons m^{-2} s^{-1} in plants collected at 20 m was significantly lower ($p < 0.05$) than in plants growing at 30 m (44 μmol photons m^{-2} s^{-1}). In contrast, *Palmaria decipiens* showed higher I_k values in plants from 20 m (41 μmol photons m^{-2} s^{-1}, $p < 0.05$) than in samples from 30 m (18 μmol photons m^{-2} s^{-1}). In *Gigartina skottbergii* and *Himantothallus grandifolius*, no differences between 20 and 30 m were observed. Interestingly, the I_k values determined in plants from 10 and 20 m were markedly lower than the average quantum irradiances at these depths (ca 250 and 85 μmol photons m^{-2} s^{-1}, respectively). However, at 30 m depth, I_k values generally exceeded the average *in situ* quantum irradiances (23 μmol photons m^{-2} s^{-1}).

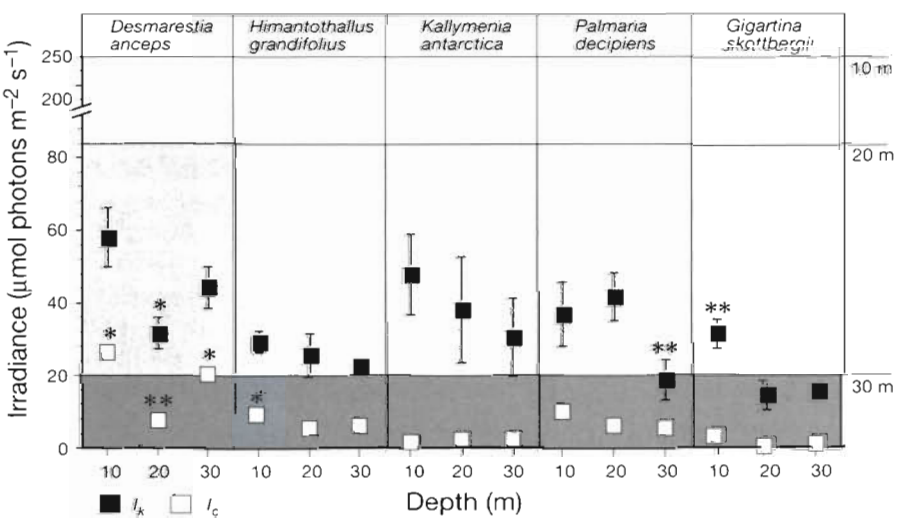

Fig. 8. Saturation (I_k) and compensation (I_c) points of photosynthesis estimated for 5 species of Antarctic macroalgae collected at 3 different depths in Potter Cove. Data are means ± SD of 4 measurements. The quantum irradiance (means of midday measurements) at the collection depths are also indicated. Asterisks indicate significant differences: *$p < 0.05$; **$p < 0.01$. See text for details of statistical treatment

The studied algae showed very low light compensation (I_c) points for photosynthesis. With the exception of *Desmarestia anceps*, all the species had I_c <14 µmol photons m^{-2} s^{-1}, and thus, significantly lower than *in situ* quantum irradiances measured at 30 m depth. With the exception of *Kallymenia antarctica*, I_c from plants collected at 10 m were found to be higher than in individuals of the same species growing at deeper habitats. The high I_c in *D. anceps* results from the high dark respiration rates of this species, particularly at 30 m, where photosynthesis compensates respiration at irradiances only slightly lower than the mean *in situ* irradiance.

On a daily basis, the duration of the exposure at irradiances above saturation (H_{sat}) and compensation (H_{comp}) of photosynthesis varied from 7 and 14 and 11 to 17 h, respectively (Table 2). At 10 and 20 m depth and under the light conditions measured in this study, all the species were exposed to irradiances above saturation longer than 12 h, i.e. ≥70% of the actual daylength at these depths. However, at 30 m depth, the H_{sat} periods significantly decreased, especially in *Himantothallus grandifolius* and *Kallymenia antarctica*, which were exposed to only 7.1 and 9.5 h of saturating irradiances. The H_{comp} periods varied less with depth. The brown algae *Desmarestia anceps* and *H. grandifolius* were the species with shortest compensation irradiance periods, particularly at 30 m (11.2 and 14.3 h, respectively). In the red algae, the daily exposure periods at irradiances above the compensation point for photosynthesis were longer than 15 h, i.e. ≥90% of the daylength (Table 2).

Table 2. Light availability for photosynthesis of Antarctic macroalgae at different depths in Potter Cove during October-November 1993. H_{sat} and H_{comp} are the hours per day for which plants are exposed to irradiance levels above the saturating (I_k) and compensation (I_c) points of photosynthesis, respectively. Calculations were made using the daily photon flux curves from each depth as shown in Fig. 4

Species	Depth (m)	H_{sat} (h)	H_{comp}
Brown algae			
Desmarestia anceps	10	12.8	14.4
	20	12.7	15.3
	30	7.1	11.2
Himantothallus grandifolius	10	14.4	15.5
	20	13.4	15.5
	30	11.1	14.3
Red algae			
Kallymenia antarctica	10	13.4	16.4
	20	12.3	16.2
	30	9.5	15.8
Palmaria decipiens	10	13.9	15.5
	20	12.0	15.4
	30	11.4	15.2
Gigartina skottsbergii	10	14.2	15.8
	20	14.4	16.8
	30	12.2	16.2

Estimated metabolic carbon balance

The daily metabolic C balance (metabolic carbon gained vs loss), estimated from the *P-I* data and multiplied by the H_{sat} periods, varied significantly among species and depths (2-way ANOVA, $p < 0.05$; Table 3). Algae inhabiting deep subtidal locations (30 m) had a lower primary productivity. Between the red algae collected at 30 m, metabolic C balance did not show significant differences (between 0.6 and 0.86 mg C g^{-1} FW d^{-1}; $p > 0.05$). In contrast, the estimates from 10 and 20 m varied significantly between species ($p < 0.05$, 2-way ANOVA): at 20 m *Desmarestia anceps*, *Himantothallus grandifolius* and *Palmaria decipiens* had the highest ($p < 0.05$) net C gains above the saturating irradiance, with values close to 2.8, 1.0 and 3.5 mg C g^{-1} FW d^{-1}, respectively. Only in *Kallymenia antarctica* and *Gigartina skottsbergii* was daily carbon balance higher or similar in plants collected from 10 m depth. The largest variations in metabolic C balance between depths were observed in *D. anceps* with C balances above saturation varying between 2.8 mg C g^{-1} FW d^{-1} at 20 m and −1.9 mg C g^{-1} FW d^{-1} at 30 m.

Table 3. Daily metabolic carbon balance in Antarctic macroalgae collected at different depths at Potter Cove during October-November 1993. Values correspond to the net gain or loss of C above the saturation irradiances for photosynthesis (I_k). SD shown in parentheses. Productivity was standardized to C units by multiplying the O_2 production or consumption by a factor of 0.3. Calculations and results of statistical analyses are described in the text

Species	Depth (m)	Daily carbon balance (mg C g^{-1} FW d^{-1})
Brown algae		
Desmarestia anceps	10	0.65 (0.62)
	20	2.82 (0.34)
	30	−1.98 (1.96)
Himantothallus grandifolius	10	0.66 (0.21)
	20	0.99 (0.15)
	30	0.58 (0.11)
Red algae		
Kallymenia antarctica	10	1.96 (0.22)
	20	1.56 (0.29)
	30	0.60 (0.14)
Palmaria decipiens	10	2.45 (0.56)
	20	3.54 (0.69)
	30	0.66 (0.28)
Gigartina skottsbergii	10	1.74 (0.31)
	20	1.63 (0.22)
	30	0.86 (0.14)

DISCUSSION

Photosynthetic performance

Photosynthetic rates determined in this study are consistent with previous data from laboratory and field studies and confirm that Antarctic macroalgae are able to use low irradiances efficiently (Wiencke 1990a, b, Thomas & Wiencke 1991, Wiencke et al. 1993, Weykam & Wiencke 1996). However, in terms of physiological adaptation, no clear inter-specific variations in photosynthetic characteristics with depth could be demonstrated. For example, P_{max} rates obtained in red algae from plants collected at 30 m were generally lower than values measured in plants collected at 10 and 20 m and the variations found in plants from the latter depths were erratic. In contrast, the 2 studied brown algae growing at 30 m had similar or higher P_{max} than those from shallower depths. Previous data reported in macroalgae from Potter Cove (Weykam et al. 1996) support this idea: P_{max} values of 22.7 (*Desmarestia anceps*), 11.6 (*Kallymenia antarctica*) or 30 µmol O_2 g^{-1} FW h^{-1} (*Palmaria decipiens*), which were measured in plants from shallower habitats (2 to 6 m depth), are comparable to rates measured in this study. The results on light-limited photosynthesis (α), defined as the photosynthetic efficiency (revised in Henley 1993), also provide no conclusive evidence for depth-dependent effects. In general, maximal α values determined in brown and red algae varied between 1.4 µmol O_2 g^{-1} FW h^{-1} (µmol photons m^{-2} s^{-1})$^{-1}$ in *D. anceps* and 0.3 µmol O_2 g^{-1} FW h^{-1} (µmol photons m^{-2} s^{-1})$^{-1}$ in *K. antarctica*, agreeing with data reported in field (Weykam et al. 1996) and cultured material (Wiencke et al. 1993). The lack of depth-dependent variations in P_{max} and α found in this study may suggest that the photoacclimatation to different quantum irradiances in the various water depths is not or is only partially possible in these species. Similarly, Drew & Hastings 1992) found no differences in net photosynthesis (^{14}C method) between *Himantothallus grandifolius* growing at 6 and 11 m depth at Signy Island (South Orkney Islands). Based on these data it may be argued that these macroalgae maintain optimal photosynthetic performances over a broad range of irradiances, which do not necessarily correspond to irradiances required for growth (Ramus et al. 1976a, Markager & Sand-Jensen 1992).

The dark respiration rates measured in this study were, in general, lower than 10 µmol O_2 g^{-1} FW h^{-1}, with *Kallymenia antarctica* and *Gigartina skottbergii* having the lowest respiratory activities (<1.4 µmol O_2 g^{-1} FW h^{-1}). In contrast, high respiration rates were measured in *Desmarestia anceps* and *Palmaria decipiens*, which reached up to 22 µmol O_2 g^{-1} FW h^{-1} in *D. anceps* from 30 m. The factors explaining these findings can be multiple. One reason for the increased respiration activity in these algae may be elevated growth rates. Biomass formation in endemic Antarctic macroalgae generally occurs in spring (Wiencke et al. 1990a, b, Weykam & Wiencke 1996) and is closely related to dark respiration in species such as *Ascoseira mirabilis* (Gómez et al. 1995b) and *Desmarestia menziesii* (Gómez & Wiencke 1997a). Another possible factor explaining high respiration in *D. anceps* and *P. decipiens* may be an unusually large wound effect. In general, dark respiration vs depth has not been intensively studied in macroalgae; however some evidence indicates that algae living at deep habitats exhibit very low respiratory activity, a strategy to avoid excessive carbon losses (Littler et al. 1986). In this sense, some interspecific patterns were reported by Weykam et al. (1996) indicating that deeper understory red algae and *Himantothallus grandifolius*, for example, have lower dark respiration rates than species growing mainly at upper sublittoral zones. In the particular case of *P. decipiens*, we found that dark respiration rates decreased with increasing water depth, but in general values were still high. Apparently, non-limiting light conditions for photosynthesis might favour high rates of dark respiration as has been discussed by Markager & Sand-Jensen (1992).

Changes in chl *a*, C and N contents

The question of whether the adaptation of algae to depth is primarily dependent on changes of pigment content has been broadly discussed in macroalgal ecology (Ramus et al. 1976a, b, Dring 1981, Ramus 1983). In our study, chl *a* significantly increased with depth only in *Himantothallus grandifolius*, which intuitively may indicate adjustments of the light-harvesting pigments with depth in this species. In the red algae, plants collected at upper sublittoral zones (10 or 20 m) generally show higher chl *a* than those measured at 30 m depth, while in *Desmarestia anceps* no changes were observed. These results suggest that the available light over the vertical profile studied here in spring did not cause changes in chl *a*. Accessory pigments rather than chl *a* might be more strongly involved in the capacity of the algae to absorb light in deeper waters. On the other hand, the accumulation of chl *a* in plants growing in upper sublittoral zones might be associated with its higher absorption efficiency at higher irradiances compared to phycobilins, whose activity may become more rapidly light-saturated (Larkum & Weyrauch 1977).

When the chl *a* contents were related to the photosynthetic effiency (α), in 4 of the studied species, no obvious enhancement of the oxygen production by an increase of chl *a* with depth could be demonstrated. Only in *Himantothallus grandifolius* was a correlation between α and the chl *a* content found. In any case, a factor that may account for the negligible correlation between chl *a* and depth is the complex anatomy of these plants. All of the species studied have a leathery or terete structure (low ratios of photosynthetic:non-photosynthetic cells), which results in a more accentuated light attenuation through the thallus, and consequently, photosynthesis often becomes uncoupled from the pigment content (Ramus 1978, 1983).

The variations in internal C and N contents were erratic and no depth-related patterns could be demonstrated. In general, data on elemental composition in Antarctic macroalgae are scarce, making comparisons difficult. Macroalgae (9 species of green, brown and red algae) from Vestfold Hills, East Antarctica, were reported to have C levels ranging between 15 and 34% DW and N levels between 2 and 4.7% DW (Dhargalkar et al. 1987). Similarly, Weykam et al. (1996) reported a mean C content of 32% DW for brown and red algae from Potter Cove. In contrast, N contents were significantly higher in red than in brown algae (4.8 and 3.2% DW, respectively). The C and N contents found in the present study, varying from 24 to 35.5% C (DW) and 1.7 to 5.5% N (DW), are consistent with these investigations and reveal high levels, particularly of N. The high and relatively constant ambient N concentrations in the Antarctic littoral systems (Lipski 1987, Clarke et al. 1988, Drew & Hastings 1992) appear to account for these increased macroalgal N contents. Seasonal studies carried out in the Antarctic kelp *Ascoseira mirabilis* (Gómez & Wiencke 1997b) indicate that, although monthly variations occur, N contents are always higher than 2% DW, which confirms that N is not limiting in these algae.

Light availability vs light requirements for photosynthesis

In general, this study reveals clearly that the macroalgae do not suffer severe light limitation up to 20 m depth (the 1% I_0 was between 20 and 46 m depth). However, some species might be light limited at 30 m, where irradiance can reach values lower than saturation points for photosynthesis. If I_c values are considered, *in situ* irradiances measured here may be sufficient to support photosynthesis at sublittoral zones, at the least during spring, when active biomass formation takes place. Reported light requirements for growth, estimated from culture experiments, agree well with these values: for example, some Antarctic Desmarestiales exhibit annual light demands for growth as low as 31.4 mol photons m^{-2}, which correspond to a depth around 53 ± 23 m and ca 0.44% of the surface irradiance in clear Antarctic offshore waters (Wiencke 1990a). This value is significantly lower than the annual light demands required to support growth of the temperate kelp *Laminaria hyperborea* [70 mol m^{-2} yr^{-1} (0.7% I_0), Lüning & Dring 1979] or of the endemic Arctic *Laminaria solidungula* (49 mol m^{-2} yr^{-1}; Chapman & Lindley 1980). According to Klöser et al. (1993), light penetration and total daily quantum irradiance measured in Potter Cove match the compensation points for photosynthesis of some cultivated sublittoral macroalgae. These authors clearly demonstrated that light penetration during November was higher than in summer (from January onwards) with 2% I_0 being found at depths of ≥25 m. Similarly, values of annual irradiance close to 50 mol m^{-2} have been measured at a depth of 25 m in some coastal areas of Signy Island, which represents the 1% I_0 and is the lower limit at which growth of *Desmarestia anceps* may be possible (R. E. M. Brouwer unpubl. data).

The I_c values determined here were under the lower irradiance limit measured at 30 m (Fig. 8). In *Kallymenia antarctica* and *Gigartina skottsbergii*, values as low as 2 or 1 µmol photons m^{-2} s^{-1} were measured. As mentioned above, these species are potentially able to photosynthesise even at depths >30 m, which may imply a depth-independent ability. In this sense, light requirements for compensation of photosynthesis in *Palmaria decipiens*, with minimum I_c values close to 5.8 µmol photons m^{-2} s^{-1}, are not contrained at large depths. On the other hand, the high I_c values close to 20 µmol photons m^{-2} s^{-1} determined in *Desmarestia anceps* clearly do not agree with the occurrence of plants at 30 m. *In situ* measurements carried out in this species indicate very low I_c values of 1.04 to 1.13 µmol photons m^{-2} s^{-1} (Brouwer unpubl. data). Although no data on depth variation of I_c are available for comparison, the discrepances among both reports are probably explained by the high respiratory activity in the plants from Potter Cove, which has previously been reported in *D. anceps* plants from the same geographic area (Weykam et al. 1996).

Daily metabolic carbon balance

Lower C losses compared to gains is a major component of the growth strategy in macroalgae living at large depths (Dennison & Alberte 1985). In our study, the daily metabolic C balance above saturation points decreased in plants collected at 30 m, which is directly related to the decrease of H_{sat} at this depth. At

depths of 10 and 20 m, daily carbon balance was positive in all cases and the higher metabolic balances estimated in plants collected at 20 m is based on light-saturated photosynthesis for many hours per day. The studied species exhibit net metabolic C gains even at 30 m depth as photosynthesis is still possible under the light-limited conditions (Henley 1993). The negative daily balance close to -2 mg C g^{-1} FW d^{-1} in *Desmarestia anceps* was clearly exceptional and was the result of its low H_{sat} (7 h) and H_{comp} (11 h) periods. During these periods, the maximum photosynthetic activity (P_{max}) was always lower than respiration rates of these plants, which were assumed to be constant over 24 h indicating that a positive daily C balance cannot be expected at depths >20 m. In support of these data, Brouwer (unpubl. data) determined low $P:R$ ratios of 2 in *D. anceps* plants from 25 m depth in spring at Signy Island. The survival of these plants would then be supported by photosynthesis above the I_c point, i.e. plants need not necessarily be light saturated to exhibit positive net C gains as long as the cumulative net photosynthesis during the H_{comp} period exceeds the cumulative net respiration when $I > I_c$ (Henley pers. comm.).

Ecological considerations

Most of the eco-physiological studies conducted in Antarctic macroalgae assigned the seasonal light variation as the main factor determining phenological patterns (Wiencke 1990a, b, Drew & Hastings 1992, Gómez et al. 1995b, Weykam & Wiencke 1996). Shade adaptation characteristics, as have been widely demonstrated in several Antarctic species (summarized in Kirst & Wiencke 1995), have effectively developed to cope with the prevailing low light periods. Such a capacity to photosynthesise under very low light constitutes an advantage allowing algae to extend their vertical range of distribution towards deeper sublittoral locations when other factors such as substrate characteristics, competitive exclusion or herbivory (Richardson 1979, Iken 1996, Klöser et al. 1996) are not limiting. During the Antarctic spring, absence of ice cover, phytoplankton blooms or meltwater, together with a greater input of solar radiation and optimum daylengths, result in favourable conditions for macroalgal photosynthesis at high depths (Klöser et al. 1993). Taking into account all these environmental variables, it is reasonable to consider that algae under natural conditions must concentrate their growth and photosynthetic activity during the short spring period.

The results of this study agree well with previous data on these species. According to Wiencke (1990a, b), under optimum light conditions algae may inhabit water depths up to 49 m, a depth exceeding zonation limits of descriptive surveys (e.g. Klöser et al. 1996). Despite the known difficulties of predicting productivity from laboratory data, which may include discrepancies between *in situ* irradiances and those used during the measurements (Dring & Lüning 1994), our results on photosynthetic parameters and estimations of carbon balance of the studied red algae, especially *Palmaria decipiens* and *Gigartina skottbergii*, are consistent with the light availability over the depth gradient. Only *Desmarestia anceps*, due to their negative carbon balance at 30 m, might not be well suited to grow at depth exceeding 20 m, which has been also seen in populations from Signy Island (Brouwer unpubl. data). Probably, utilization of reserve carbohydrates to support metabolic activity may explain in part a negative photosynthetic C balance of these plants at depths close to 30 m. In any case, our results, especially of α, I_c, and H_{comp}, reveal that algae, due to their shade adaptation, are able to photosynthesize at 30 m depths in spring when increased solar radiation and high water light penetration are available (Klöser et al. 1993). However, when parameters such as H_{sat} and daily metabolic C balance are taken into account, optimum conditions for photosynthesis are found at 10 or 20 m. This may explain in part the less frequent occurrence of these algae, especially rhodophytes, at greater depths, and the increased species abundance at 10 and 15 m described recently in the literature (Klöser et al. 1994, 1996, Brouwer et al. 1995). Further studies focusing on annual C balance and seasonal organic composition at varying depths, as well as the effects of other ecological determinants such as herbivory competence or ice scouring, are indispensable to fully understanding the complex biological processes in polar macroalgae.

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