

***In situ* photosynthesis and estimated annual production of the red macroalga *Myriogramme mangini* in relation to underwater irradiance at Signy Island (Antarctica)**

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Abstract: For the first time, photosynthesis of *Myriogramme mangini* (Gain) Skottsberg, one of the dominant red macroalgae in the sublittoral of Signy Island (South Orkney Islands), was studied *in situ* under natural irradiance levels in specially developed incubation chambers. *M. mangini* is adapted to low irradiance levels. Water transparency varied over the year. A maximum attenuation coefficient (k_d) of 0.328 m^{-1} was reached in January, and the water was clearest in September with a k_d value of 0.079 m^{-1} . Classification of the water type on a Jerlov scale, gave water type 4 in January and II in May and June. The mean k_d value over the year was 0.158 m^{-1} and the water was classified as Jerlov's water type 1. The euphotic depths (Z_{eu}) for 1%, 0.1% and 0.01% surface irradiance levels were 29.1 m, 43.7 m and 58.3 m, respectively. Photosynthetic characteristics were determined, with the oxygen production rates and irradiance levels measured *in situ*, using P-I curves. The initial saturation irradiance (I_k) varied significantly from $18.0 \pm 1.5\ \mu\text{mol m}^{-2}\text{ s}^{-1}$ in autumn to $10.5 \pm 1.8\ \mu\text{mol m}^{-2}\text{ s}^{-1}$ in early spring. Mean photosynthetic capacity ($P_{g\text{max}}$) ranged from $57.2 \pm 1.3\ \mu\text{mol O}_2\text{ g}^{-1}\text{DW h}^{-1}$ to $63.1 \pm 1.6\ \mu\text{mol O}_2\text{ g}^{-1}\text{DW h}^{-1}$. The photosynthetic efficiency (α) was $3.2 \pm 0.2\ \mu\text{mol O}_2\text{ g}^{-1}\text{DW h}^{-1} (\mu\text{mol m}^{-2}\text{ s}^{-1})^{-1}$ in autumn and $6.0 \pm 1.0\ \mu\text{mol O}_2\text{ g}^{-1}\text{DW h}^{-1} (\mu\text{mol m}^{-2}\text{ s}^{-1})^{-1}$ in early spring. Compensation irradiance (I_c) was low and ranged from 2.5 to $2.8\ \mu\text{mol m}^{-2}\text{ s}^{-1}$. Estimates of annual net production rates were 128.1 and $0.6\text{ mmol O}_2\text{ g}^{-1}\text{DW y}^{-1}$ at 5 m depth and 20 m depth, respectively. A maximum depth of occurrence of *M. mangini* was predicted at 22.9 m (2.7% of the surface irradiance).

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Introduction

Vertical and horizontal distribution patterns of macroalgal communities have recently been described from several sites in Antarctica (Amsler *et al.* 1995, Brouwer *et al.* 1995, Chung *et al.* 1994, Cormaci *et al.* 1992, Klöser *et al.* 1994, 1996). On the rocky coast of the South Orkney Islands and the Antarctic Peninsula, the main contributors to the biomass of sublittoral vegetation are usually the large overstorey Phaeophyta. The Rhodophyta are more abundant in species number and form the understory, or grow at sites where large Phaeophyta are not present.

Primary production studies of Antarctic macroalgae *in situ* have been few, probably because of the inaccessibility of the area and the demands of working under water. Studies of the growth of Antarctic macroalgae have utilized laboratory cultures (Wiencke 1990a, 1990b). The Rhodophyta in these studies showed a seasonal optimum in growth rate between October and December. Wiencke *et al.* (1993) studied photosynthetic characteristics of several macroalgae from Antarctica cultivated under different light and temperature regimes, while the photosynthesis and respiration of some Antarctic macroalgae collected at Signy Island were studied by Drew (1977). Weykam *et al.* (1996) gave an overview of the photosynthetic characteristics of numerous macroalgae

collected on King George Island. The only seasonal photosynthesis measurements carried out *in situ* to date are on the large kelp-like brown macroalga *Himantothallus grandifolius* (Drew & Hastings 1992) and in a parallel study on *Desmarestia anceps* (Brouwer 1996). Data on seasonal photosynthetic performance of algae carried out in laboratory experiments on samples collected in the field are available from the Phaeophyta *Adenocystis utricularis* (Gutkowski & Maleszewski 1989) and *Ascoseira mirabilis* (Gómez *et al.* 1995). Data on seasonal photosynthetic performance of Rhodophyta collected in the field are not available in the literature, although Weykam & Wiencke (1996) examined the seasonal photosynthetic performance of the endemic Antarctic alga *Palmaria decipiens* in laboratory cultures under simulated Antarctic light conditions. They found that a growth optimum under spring conditions coincided with a higher photosynthetic activity.

Since water temperature and salinity are relatively constant, and nutrient levels are generally high in Antarctic waters, light is the most important seasonal factor affecting the growth of macroalgae. Antarctic macroalgae are classified as shade-adapted because they have high photosynthetic efficiency values (α), a low compensation point (I_c) and low saturation irradiances (I_k) (Wiencke *et al.* 1993). Antarctic

macroalgae not only have to deal with strong seasonal changes in daylength, but also with ice cover in winter and phytoplankton blooms in summer. To date, no underwater irradiance levels have been available for the periods of winter ice cover and summer phytoplankton blooms, both of which influence irradiance levels at greater depths.

The irradiance penetrating the water column in Antarctica undergoes large spatial and temporal variations, caused by a variety of factors. They include not only latitude, wave action at the surface, phytoplankton blooms or turbidity of the water column, but also changes in ice thickness and the structure of the ice. The last in particular is determined by whether the ice is sea ice or pack ice, and whether it is frozen solid or still soft and full of holes. Also important is the state of the ice surface, and especially the presence of snow, melt ponds, or drainage of melt water, for determining the amount of light penetrating the water column. Snow in particular attenuates light: Palmisano *et al.* (1986) found a transmittance of 0.01–3% of incident light for a 50 cm layer snow, while the

transmittance of a layer of 1 m sea ice will be about 20% of incident light (Maykut & Grenfell 1975). An overview of the influence of ice cover on the irradiance penetrating into the water column is given by Knox (1994), while Eicken (1992) discusses the role of sea ice in structuring Antarctic ecosystems.

Myriogramme mangini (Gain) Skottsberg is one of the dominant Rhodophyta of the macroalgal vegetation of Signy Island (Brouwer *et al.* 1995). Aims of this study were (1) to determine the photosynthetic characteristics of *M. mangini* thalli *in situ*, (2) to study seasonality in irradiance levels under water and discuss transparency of the water column, and (3) to predict annual production rates.

Material and methods

Study area and macroalgal material

The present study was carried out from January to November 1993 at three different sites of Signy Island (60°42'S, 45°36'W): Factory Cove, Billie Rocks and the seawater sampling site (SW) in Borge Bay (Fig. 1). Factory Cove and Billie Rocks were used for shallow measurements (0.5 and 5 m depth) and bad weather conditions (windspeed > 23 knots), and the seawater sampling site for deep measurements at 25 m depth and good weather conditions (windspeed ≤ 23 knots). Daylength in summer reaches a maximum of 19 h and in winter a minimum of 6 h. During winter, light penetration to greater depths is limited by sea ice, which is present for on average 140 days per year, with a large year-to-year variation (Murphy *et al.* 1995). Seawater temperature shows little seasonal variation, from -1.8°C in winter to about +0.3°C in summer, while salinity is constant at 33.9‰ (± 0.5) (Clarke *et al.* 1988). Nutrient levels in the water vary seasonally, but none routinely reach levels where they would be regarded as limiting. Minimum levels for nitrate, nitrite and phosphate are reached in summer during phytoplankton blooms, and minimum levels for ammonia in late winter (Clarke *et al.* 1988).

Macroalgae are abundant in the sublittoral of the rocky coast of Signy Island and *M. mangini*, one of the dominant Rhodophyta at Signy Island, was found abundantly at depths of 2–14 m below mean low water (MLW) (Brouwer *et al.* 1995). *M. mangini* is an endemic pseudoperennial species which is known from the Antarctic Peninsula, the South Shetland Islands and the South Orkney Islands (Lamb & Zimmermann 1977, Price & Redfearn 1966, Richardson 1979, Ricker 1987). This species overwinters by shedding parts of the blades and retaining the midribs. In early spring, plant material therefore consists mainly of the midribs with thin new leaves developed. Thalli (varying between 1.7–20.5 g wet weight) were sampled by SCUBA diving at Billie Rocks and either directly used in the incubation experiment or kept, for up to two days, in the laboratory with a continuous flow of seawater pumped directly from Factory Cove. Table I shows the incubation sites and depths, and ranges of dry

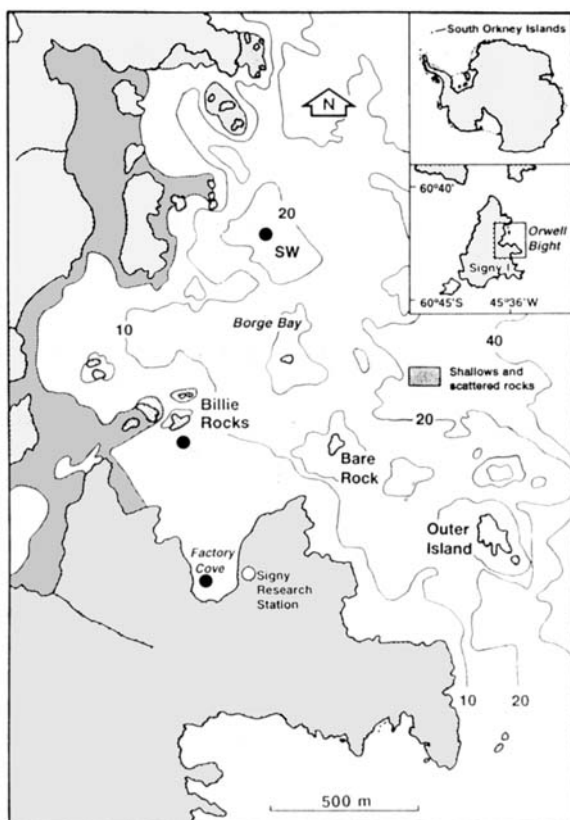


Fig. 1. Location of the incubation experiments (●) at Billie Rocks and Factory Cove, and the seawater sampling site (SW) in Borge Bay; the light dotted areas are supralittoral and terrestrial areas; the dark dotted areas are shallows and scattered rocks; depth in metres (m).

Table I. Incubation sites and depths (m), dry weights (DW in g, as % of wet weight) of the *Myriogramme mangini* thalli sampled at Billie Rocks at a depth of 5 or 6m. SW = seawater sampling site, FC = Factory Cove, BR = Billie Rocks; *n* = number of plants used.

Season	Incubation site	Incubation depth	<i>n</i>	DW range
Autumn ¹	SW	5	4	16.2-20.4
	SW	25	4	6.9-20.9
	FC	0.5	10	20.5-25.0
Spring ²	FC	0.5	2	20.3-23.2
	BR	5	3	13.6-19.2

¹ incubation dates: 4, 7, 9 and 12 March and 27, 28, 29 and 30 April and 7 May 1993

² incubation dates: 15, 21 and 23 September 1993

weights of the *M. mangini* thalli used in the experiment.

Oxygen evolution measurements in situ

Incubations *in situ* were conducted using two 13 l cylindrical self-registering closed plexiglass incubation chambers as described in more detail by Brouwer (1996). Each incubation chamber contained a 2π PAR (photosynthetic active radiation) light sensor (BPW 21, Skiltronics BV, Leeuwarden), two YSI 5739 oxygen electrodes with temperature sensors (Yellow Springs Instruments Inc., Ohio) and a custom-built stirring mechanism. Oxygen concentration, water temperature and irradiance were recorded every 90 seconds by a data logger (Seawise, Den Helder) on a scale from 0–998 units.

The relationship between the gross oxygen production and the irradiance was determined by non-linear curve fitting, using the model of Platt & Jassby (1976):

$$P(I) = P_{\max} \tanh(\alpha I / P_{\max})$$

where $P(I)$ is the gross oxygen production in $\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$ and I is the irradiance under water in $\mu\text{mol m}^{-2} \text{ s}^{-1}$. The programme used was PrimProd, version 2.1 (de Hoop 1994), giving mean values with SD of the light-saturated rate of gross oxygen production (P_{gmax}), the photosynthetic efficiency (α) as the initial slope of the P-I curve in $\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1} (\mu\text{mol m}^{-2} \text{ s}^{-1})^{-1}$ and the initial saturating irradiance level ($I_k = P_{\text{gmax}} / \alpha$). Gross production was estimated by adding the mean measured respiration (R) during the night to the measured net oxygen production (P_n). An indication of the irradiance compensation point (I_c) was obtained by plotting the modelled net oxygen production.

Winkler titrations (Grasshoff *et al.* 1983) were carried out in the laboratory in order to calibrate the oxygen electrodes with seawater from Factory Cove under the same temperatures as in the field. The light sensor of each incubation chamber was cross-correlated in the laboratory with a Li-cor quantum

meter and sensor (LI-185B and LI-192SB, Li-cor Inc., Lincoln, USA) and results were integrated hourly in $\mu\text{mol m}^{-2} \text{ s}^{-1}$. Photosynthetic rates were expressed in units of $\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$.

Irradiance measurements

Irradiance at the surface was monitored by the British Antarctic Survey (BAS, unpublished data) using a CM 11-Pyranometer (spectral range 305–2800 nm, Kipp & Zonen, Delft). These readings were cross-correlated with those of the Li-cor quantum sensor by linear regression ($y = 1.59x + 1.63$, $r^2 = 0.98$, $n = 31$). Incidental irradiance measurements were carried out at the seawater sampling site, with the Li-cor quantum meter, to determine the percentage of surface irradiance available just underneath the water or ice surface and at 5–25 m depth, with 5 m depth intervals. The sensor was mounted on a 1.5 m long arm and lowered to the depth desired, avoiding shading effects of the boat or people standing on the ice surface. Thickness of sea ice and the layer of snow covering the ice were also measured by the British Antarctic Survey. The daily surface irradiance in combination with the incidental irradiance measurements and the variation in ice present on the water surface were used to calculate irradiance levels at the different water depths. Irradiance (I) at any depth (z) is a function of the intensity just below the water surface (or in this study also just below the ice surface) (I_0) and depth (z):

$$I_z = I_0 e^{-k_d z}$$

where k_d is the attenuation coefficient.

Daily and annual production

The daily net production was calculated from the estimated average irradiance levels at a specific water depth per day using the fitted net production. Predictions of annual net oxygen production were made by multiplying the average daily net production with the number of days per month and adding these monthly data. Production measurements carried out from March to early May and in September were used for the autumn and early spring P-I equations, respectively. As summer and winter measurements of the photosynthetic characteristics were missing, it was assumed that for estimates of annual production the autumn and early spring P-I equations covered May to October and November to April, respectively, using the changing irradiance levels through the year and interpolating for depth.

Data analysis

Significance of differences between photosynthetic characteristics of autumn and spring were tested using a t-test and a significance level set at $p = 0.05$.

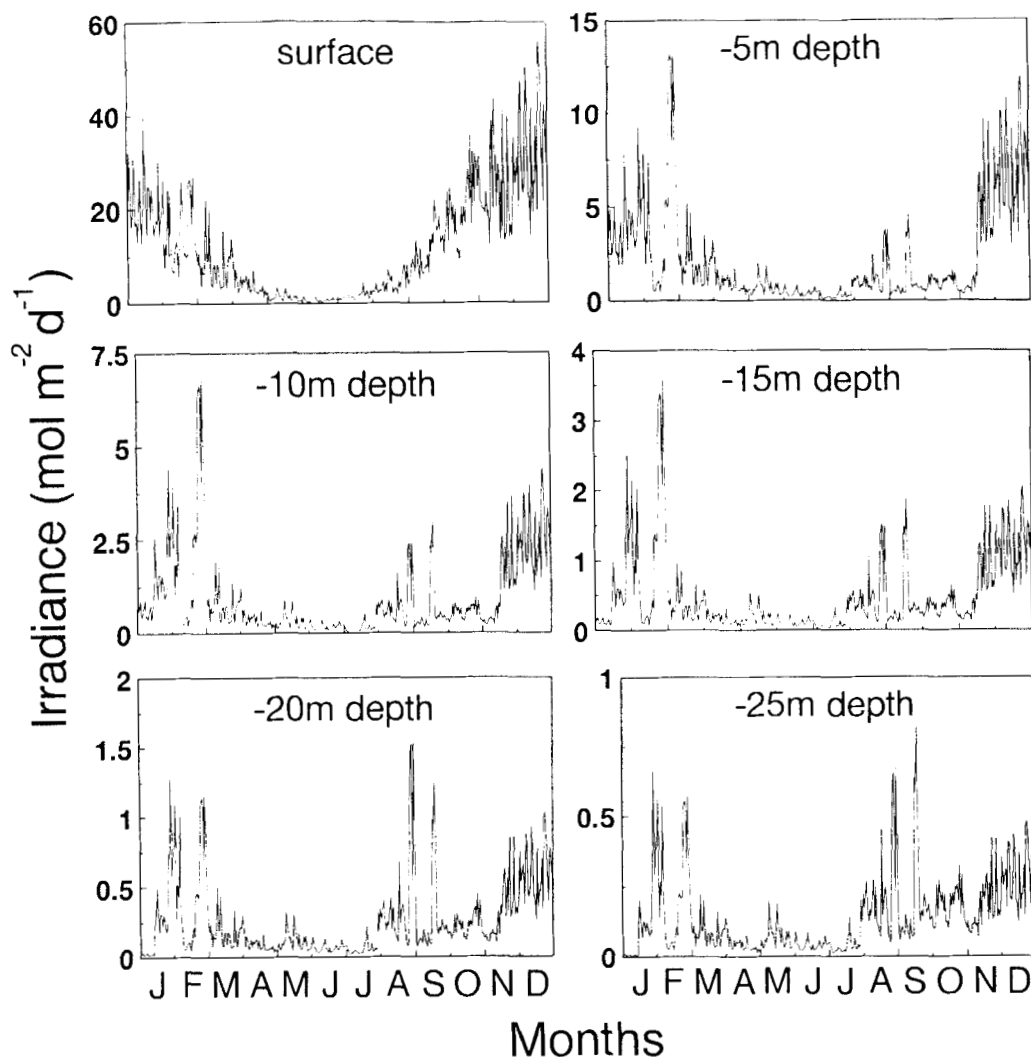


Fig. 2. Average daily irradiance levels (PAR, $\text{mol m}^{-2} \text{d}^{-1}$) measured on the surface and recalculated from incidental depth profiles at 5 m depth intervals from 5–25 m.

Table II. Predictions of annual net oxygen production (P_n in $\text{mmol O}_2 \text{g}^{-1} \text{DW y}^{-1}$) for *Myriogramme mangini*, based on the model equations for autumn and early spring of which the photosynthetic characteristics are given in Table III. Also shown are total annual irradiances and % of surface irradiance at different depths.

Depth (m)	P_n ($\text{mmol O}_2 \text{g}^{-1} \text{DW y}^{-1}$)	Irradiance ($\text{kmol m}^{-2} \text{y}^{-1}$)	% of surface irradiance
surface		4.42	
below water/ice surface		2.91	65.8
-5	128.1	0.80	18.1
-10	90.6	0.34	7.6
-15	43.8	0.17	3.9
-20	0.6	0.09	2.2
-25	-34.4	0.05	1.1

Results

The estimated irradiance levels at different depths in 1993 are given in Fig. 2. The seasonal surface pattern becomes less obvious with depth. The total annual irradiance received on the surface ($4.42 \text{ kmol m}^{-2} \text{y}^{-1}$) decreased to 0.80 at 5 m depth and $0.05 \text{ kmol m}^{-2} \text{y}^{-1}$ at 25 m depth (Table II), corresponding to 18.1 and 1.1% of the surface irradiance, respectively. The seasonal variation in light penetration, as percentage of the surface irradiance, and the extinction coefficient (k_d) in the water column are shown in Fig. 3. In January, less than 0.1% of the surface irradiance reached 25 m depth (Jerlov's water type 4; see Lüning 1990), while in May–June, when no ice was present, between 5 and 10% reached 25 m depth (Jerlov's water type II). From July until mid-September light penetration changed continuously due to the changing movements of the

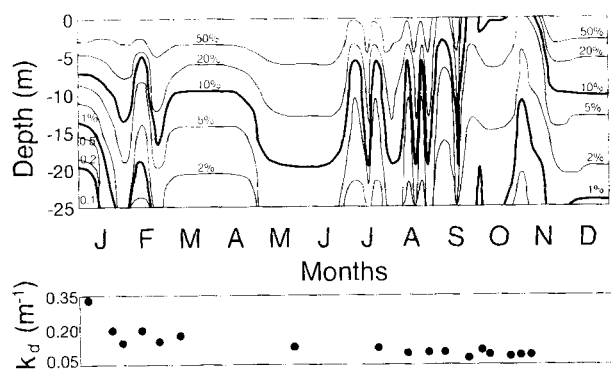


Fig. 3. Year-round series of light penetration and k_d values in Borge Bay, Signy Island, 1993.

ice. The k_d values show the clarity of the water column. The highest k_d value (0.328 m^{-1}) occurred in January, and the lowest (0.079 m^{-1}) at the end of September. The mean k_d value calculated over the whole year based on the annual irradiance levels was 0.158 m^{-1} . The euphotic depths (Z_{eu}), for 1%, 0.1% and 0.01% of the surface irradiance, were therefore 29.1, 43.7 and 58.3 m, respectively.

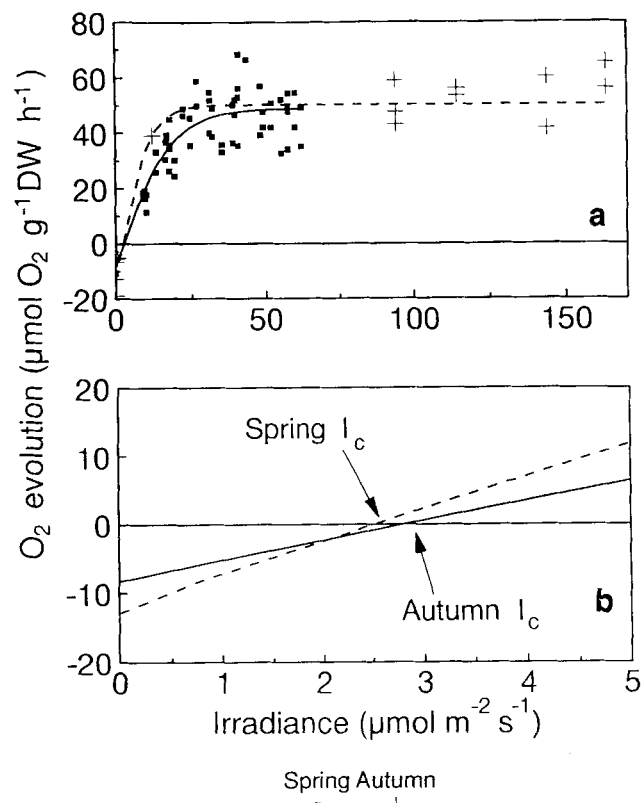


Fig. 4. a. Relationship between net oxygen production rate, respiration rate and the irradiance, with fitted P-I curves for autumn and early spring measurements. Individual points show the original data pooled per season. b. Enlargement of the low irradiance levels shows the modelled irradiance compensation points (I_c) for autumn and early spring.

Table III. Photosynthetic characteristics of *Myriogramme mangini* thalli based on field incubations with maximum irradiance level of $163 \mu\text{mol m}^{-2} \text{ s}^{-1}$. Units: $P_{g\text{max}}$, $P_{n\text{max}}$ and R ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$); α ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1} (\mu\text{mol m}^{-2} \text{ s}^{-1})^{-1}$); I_c and I_k ($\mu\text{mol m}^{-2} \text{ s}^{-1}$); mean values with SD in brackets. For comparison, photosynthetic characteristics determined in a previous laboratory study are included.

Parameter	This study autumn ¹	This study early spring ²		Weykam <i>et al.</i> (1996) spring-summer ³
$P_{g\text{max}}$	57.2 (1.3)	63.1 (1.6)	ns	143.6
α	3.2 (0.2)	6.0 (1.0)	ns	7.5 (0.8)
I_k	18.0 (1.5)	10.5 (1.8)	*	18.7 (3.7)
R	8.4 (3.4)	12.8 (6.6)	ns	35.5 (5.2)
I_c	2.8	2.5		4.5 (1.0)
$P_{n\text{max}}$	48.8	50.3		108.1 (44.8)

¹ Total number of plants used is 18, with P_g in duplicate at 31 irradiance levels; number of plants used for determining R is 2.

² Total number of plants used is 5, with P_g in duplicate at 10 irradiance levels; number of plants used for determining R is 3.

³ Fresh material sampled at King George Island from the end of October to start of December, and used in laboratory experiments, $n = 3-4$

*: significant different between autumn and early spring ($P \leq 0.05$)

ns: not significant different between autumn and early spring ($P > 0.05$)

The autumn and early-spring P-I curves of *M. mangini* are given in Fig. 4, while the photosynthetic characteristics are summarized in Table III. Field irradiance levels measured during these incubations ranged from 0–163 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. $P_{g\text{max}}$ was $57.2 \pm 1.3 \mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$ in autumn and $63.1 \pm 1.6 \mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$ in early spring, and the photosynthetic efficiency (α) was $3.2 \pm 0.2 \mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1} (\mu\text{mol m}^{-2} \text{ s}^{-1})^{-1}$ in autumn and $6.0 \pm 1.0 \mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1} (\mu\text{mol m}^{-2} \text{ s}^{-1})^{-1}$ in early spring but differences were not significant ($P > 0.05$). The initial saturating irradiance level (I_k) in autumn ($18.0 \pm 1.5 \mu\text{mol m}^{-2} \text{ s}^{-1}$) was significantly higher ($P < 0.05$) than in early spring ($10.5 \pm 1.8 \mu\text{mol m}^{-2} \text{ s}^{-1}$). Low irradiance compensation points (I_c) from 2.5 and 2.8 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ were found. Respiration rates were low and did not vary significantly between $8.4 \pm 3.4 \mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$ in autumn and $12.8 \pm 6.6 \mu\text{mol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$ in early spring. Table III also gives the photosynthetic characteristics of *M. mangini* tissue obtained from laboratory experiments with field material (Weykam *et al.* 1996). They found higher values for α , $P_{g\text{max}}$ and R , and comparable I_k values.

The estimated daily net oxygen production rates for different depths are shown in Fig. 5. These were calculated from the observed mean irradiance values and the experimental data relating oxygen production to irradiance. The pattern follows the average number of hours of daylight occurring at Signy Island, which increases from 6 h in June to 19 h in December. The winter of 1993 was characterized by continuous changing ice conditions and the late appearance of fast ice. Pack ice moved in and out of Borge Bay, but fast ice was only present from 16 September to 11 November (Fig. 5), which slowed down the increase in production rates. Only the *M. mangini* plants at 5 m depth showed a positive daily P_n during the

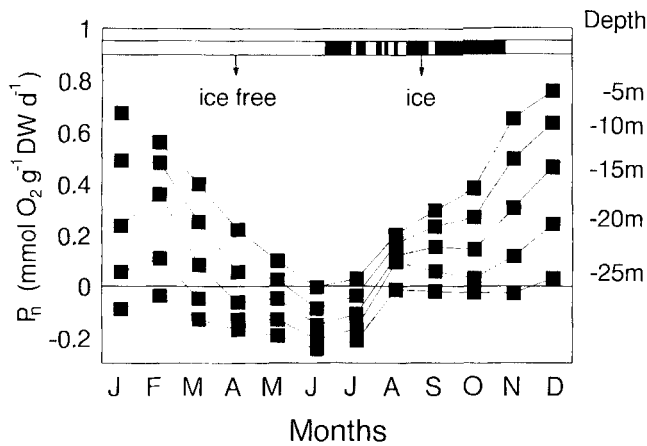


Fig. 5. Predicted annual course of daily net production for 5 m depth contours, based on the modelled equations and integrated irradiance levels per depth, taking the ice observations into account.

whole year. Estimated annual net oxygen production rates were still positive to 20 m depth (Table II), and decreased from 128.1 mmol O₂ g⁻¹DW y⁻¹ at 5 m depth to 0.6 mmol O₂ g⁻¹DW y⁻¹ at 20 m depth.

Discussion

This study attempts for the first time to determine *in situ* photosynthetic characteristics of an Antarctic red macroalga, *Myriogramme mangini*, in relation to changes in irradiance over the year at several depths. For *M. mangini* no significant differences were found in the photosynthetic characteristics α and $P_{g,max}$ between autumn and early spring, although I_k in early spring was significantly lower than in autumn. Irradiance levels at 5 m depth were comparable in these periods, and were 37 and 31 mol m⁻² month⁻¹, respectively. Compared to red macroalgae in other parts of the world (Dawes & Kovach 1992, Enríquez *et al.* 1995), I_c and I_k values were low and α high, indicating that *M. mangini* is well adapted to low irradiance levels. An earlier laboratory study using thallus parts of field grown *M. mangini* (Weykam *et al.* 1996) gave higher values of photosynthetic parameters, mostly referring to P_{max} and respiration, than field measurements (Table III). These are almost certainly explained by the naturally fluctuating irradiance levels occurring in the field and the use of whole thalli in the field incubations. Using fragments of plants can produce adverse effects on photosynthesis and respiration measurements (Arnold & Manley 1985, Drew 1983, Hatcher 1977). In another study of Weykam (1996), no significant differences were found in α and P_{max} between the end of winter and early summer. One explanation might be that *M. mangini* is so well adapted to low irradiance levels, that no differences in response occur between different times of the year. Another possibility is that pigments play an important role, and expressing photosynthetic characteristics

on a pigment basis might give a better indication of photosynthetic performance in the field.

A third option might be that the growth strategy of *M. mangini* is of a season responder (Weykam 1996). Season responders are algae starting growth in spring and summer when they experience high light conditions, while season anticipators start growth in the winter season in response to short days (Kain 1989). No information is available on the growth strategy of this endemic species, but photosynthetic measurements carried out in the present study and by Weykam (1996) showed no significant variation in P_{max} . Weykam (1996) concluded that the slight variation in P_{max} was comparable to the seasonal variation in photosynthesis of the more intensively studied red macroalgae *Iridaea cordata*, which was classified as season responder. During winter, the blades of *M. mangini* degraded and only the midribs remained. The first growth of fresh young material was observed in September. At this time of the year irradiance levels increased under water as a result of ice conditions. It is thus possible that *M. mangini* might act as a season responder, but more information of the growth strategy is required.

A maximum irradiance level of 163 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was measured during the incubations, indicating that photoinhibition is unlikely to occur at Signy Island. Photoinhibition occurs in macroalgae collected from deeper water at irradiance levels above 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, while macroalgae from shallower depths are inhibited above 300–500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (reviewed in Lüning 1990). In Antarctica photoinhibition has been demonstrated in the eulittoral and upper sublittoral species *Palmaria decipiens* and *Adenocystis utricularis* (Hanelt *et al.* 1994). Similarly, in other parts of the world many macrophytes of the eulittoral and upper sublittoral showed photoinhibition during tidal emersion in the field (Hanelt 1992, Henley *et al.* 1992, Huppertz *et al.* 1990). Irradiance levels at Signy Island might be low, as the sky is overcast most of the time and the average total number of hours of sunshine per month from January 1993 to November 1993 was only 79 h.

The percentage surface irradiance entering the water column is dependent critically on the nature of the surface layer, and particularly whether there is ice on the surface or not. Water transparency is expressed by the attenuation coefficient (k_d), which is determined from just underneath the water surface or ice surface to a depth of 25 m. The k_d value was high in January because of phytoplankton blooms, (Clarke *et al.* 1988), and storms causing turbidity. Water became clearer in May when turbidity decreased. At this time, water column phytoplankton blooms disappeared and storms had less influence on the upwelling of sediments because of the presence of surface ice around the island. When sea ice was formed and remained present in October and November k_d values decreased further. The classification of the water type according to Jerlov (1976) changed from 4 in January to II in May and June, with water types for open ocean waters

numbered from I–III and water types for coastal waters numbered from 1–9. With the average k_d of 0.158 m^{-1} over the whole year, the water type can be classified as 1 (clearest for coastal waters, see Mobley 1994).

Observations on Rhodophyta at Signy Island were limited to a depth of 38 m, but some macroalgae can probably occur deeper. It must be kept in mind, however, that the present conclusions are restricted to the sites studied and depend on water transparency and irradiance level. Differences were observed in water transparencies between Borge Bay and a site on the west coast. Also Klöser *et al.* (1993) found higher water transparencies at the outer edge of Potter Cove than inside, because of high sediment loads inside. Therefore, k_d values or classifications of the water type might give more information on the sites studied, and make comparison of production rates and photosynthetic characteristics of macroalgae easier.

The pattern of daily net production (Fig. 5) at all depths was principally the same as the pattern of irradiance levels measured at the surface (Fig. 2), except for the period when ice was present. Only at 5 m water depth was a positive balance between production and respiration found throughout the year. Annual production was just positive at 20 m depth (Table II). Extrapolation of the relationship between the annual net production and the logarithm of the % surface irradiance ($P_n = 1.60 \ln (\%I) - 0.943$, $r^2 = 0.96$), would give a zero annual net production rate for *M. mangini* at 22.9 m depth, which is at 2.7% of the surface irradiance. Wiencke (1990b) found in a culture experiment that the minimum level of irradiance needed for completing the life cycle for two other Antarctic Rhodophyta, *Iridaea cordata* and *Gigartina skottsbergii*, was at a similar level of 2% surface irradiance. In a previous study carried out at Signy Island, *M. mangini* was mainly found between 2–14 m depth but occasionally deeper (Brouwer *et al.* 1995). At Anvers Island (Antarctic Peninsula), Amsler *et al.* (1995) found a similar distribution pattern of *M. mangini* to that at Signy Island, with highest biomass for *M. mangini* at 10 m depth. The depth distribution of *M. mangini* is probably determined by the topography of the sites. Shaded sites, such as under other macroalgae or between rocks and crevices, will restrict *M. mangini* mainly to shallower depths, but where the overstorey macroalgae are less dense, *M. mangini* might occur deeper.

M. mangini at Signy Island was one of the 24 species of Rhodophyta found. Competition for light, space and/or nutrients with other species, such as *Plocamium cartilagineum* and *Pantoneura plocamioides*, whose probability of occurrence increased towards greater depths (Brouwer *et al.* 1995), might well be the reason why *M. mangini* was not abundant deeper than 14 m. But as studies of competition in marine benthic algae are few and consequences and complications are still not understood completely (Paine 1990), this is only conjecture. There is a lot of work still ahead of us in understanding the whole Antarctic macroalgal community and explaining why a

given species occurs at certain depths.

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