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# Adaptation and acclimation of growth and photosynthesis of five Antarctic red algae to low temperatures

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**Abstract** Temperature requirements for growth, photosynthesis and dark respiration were determined for five Antarctic red algal species. After acclimation, the stenothermal species *Gigartina skottsbergii* and *Ballia callitricha* grew at 0 or up to 5 °C, respectively; the eurythermal species *Kallymenia antarctica*, *Gymnogongrus antarcticus* and *Phyllophora ahnfeltioides* grew up to 10 °C. The temperature optima of photosynthesis were between 10 and 15 °C in the stenothermal species and between 15 and 25 °C in the eurythermal species, irrespective of the growth temperature. This shows that the temperature optima for photosynthesis are located well below the optima from species of other biogeographical regions, even from the Arctic. Respiratory rates rose with increasing temperatures. In contrast to photosynthesis, no temperature optimum was evident between 0 and 25 °C. Partial acclimation of photosynthetic capacity to growth temperature was found in two species. *B. callitricha* and *Gymnogongrus antarcticus* acclimate to 0 °C, and 5 and 0 °C, respectively. But acclimation did in no case lead to an overall shift in the temperature optimum of photosynthesis. *B. callitricha* and *Gymnogongrus antarcticus* showed acclimation of respiration to 5 °C, and *P. ahnfeltioides* to 5 and 10 °C, resulting in a temperature independence of respiration when measured at growth temperature. With respect to the acclimation potential of the species, no distinction can be made between the stenothermal versus the eurythermal group. (Net)photosynthetic capacity:respiration (*P*:*R*) ratios showed in all species highest values at 0 °C and decreased continuously to values lower than 1.0 at 25 °C. In turn, the low *P*:*R* ratios at higher temperatures are assumed to determine the upper temperature growth limit of the studied species. Estimated daily carbon balance reached values between 4.1 and 30.7 mg C $g^{-1}$ FW $day^{-1}$ at 0 °C, 16:8 h light/dark cycle, 12–40 μmol $m^{-2}$ $s^{-1}$.

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## Introduction

Marine macroalgae of the Antarctic region are exposed to very low temperatures throughout the year. At the coasts of the Antarctic continent, the water temperature is about −1.8 °C in winter and reaches a maximum in summer of about 5 °C at the northern border of the Antarctic region (Wiencke and tom Dieck 1989).

Endemic Antarctic species show the world-wide lowest temperature requirements for growth and survival. They only grow up to 5 °C (or 10 °C) and exhibit very low upper survival temperatures (USTs) of 9–15 °C (Wiencke and tom Dieck 1989, 1990; Bischoff-Bäsmann and Wiencke 1996). This high degree of cold adaptation is obviously the result of the long cold-water history of the Antarctic Ocean, which has lasted for at least 14 million years (Crame 1993; Wiencke et al. 1994). In comparison, glaciation occurred in the Arctic no earlier than 3.5 million years ago (Flohn 1984) and resulted in a less strong adaptation to low temperatures of macroalgae from this region (Wiencke et al. 1994).

The temperature demands for growth and survival of 15 red macroalgal species from the Antarctic have been described by Bischoff-Bäsmann and Wiencke (1996). These authors distinguished two groups, according to their temperature requirements for growth and survival: one group with a more stenothermal temperature characteristic and one group with a more eurythermal one. Among these are four of the five species investigated here. The stenothermal species *Gigartina skottsbergii* and

*Ballia callitricha* grow in a narrow temperature range, between 0 and 5 °C. The USTs determined for this group are 9–12 °C. The eurythermal species *Gymnogongrus antarcticus* and *Phyllophora ahnfeltioides* grow between 0 and 10 °C and exhibit USTs of 18–21 °C.

The purpose of the present study was to determine how the low temperature requirements for growth are reflected in the temperature demands of photosynthesis and dark respiration. There are only a few previous reports on the temperature requirements of photosynthesis in Antarctic macroalgae. Drew (1977) and Wiencke et al. (1993) demonstrated high light-saturated photosynthetic rates even at low temperatures. Temperature optima for photosynthesis were lower than in cold-temperate species but still far above the maximum temperatures in Antarctic waters.

In this study, the short-term effects of temperature on photosynthetic and respiratory metabolism were determined. Subsequently, phenotypic changes that occur in response to growth at different temperatures (i.e. acclimation) of photosynthesis and respiration were studied. Stenothermal and eurythermal species were chosen in order to investigate genetic differences in the degree of cold adaptation and the potential for temperature acclimation.

## Materials and methods

The investigated species were *B. callitricha* (Agardh) Kützing (AWI culture no. 2102), *Gigartina skottsbergii* (Bory) Setchell et Gardner (no. 2007), *Gymnogongrus antarcticus* Skottsberg (no. 2104), *Kallymenia antarctica* Hariot (no. 2106) and *P. ahnfeltioides* Skottsberg (no. 2099). The species were collected by H. Klöser and C. Wiencke on King George Island (Antarctica) in 1992/1993 and 1993/1994 and since then they have been maintained as unialgal cultures at 0 °C. Cultivation methods were the same as described by Wiencke and tom Dieck (1989).

The temperature-growth experiments were performed in constant-temperature rooms under a light/dark cycle of 16:8 h. Different photon fluence rates (fluorescent tubes, L58/12 W day light, Osram) were used in the various species in order to offer favourable growth conditions: 40 μmol $m^{-2}$ $s^{-1}$ in *Gigartina skottsbergii*, 30 μmol $m^{-2}$ $s^{-1}$ in *P. ahnfeltioides*, 20 μmol $m^{-2}$ $s^{-1}$ in *K. antarctica* and *Gymnogongrus antarcticus* and 12 μmol $m^{-2}$ $s^{-1}$ in *B. callitricha*.

For determination of growth, fresh weight was measured weekly over a period of at least 6 weeks at 0 °C, 5 °C, 10 °C, and 15 °C, using the method described by Bischoff-Bäsmann and Wiencke (1996). For each interval, the specific growth rate, expressed in % increase $day^{-1}$, was calculated using the following equation:

$$\mathrm{RGR} = \ln(W_t/W_i)\Delta t^{-1}$$

where RGR = relative growth rate, $W_i$ = initial fresh weight, $W_t$ = fresh weight on day $t$, and $\Delta t$ = time interval in days.

For describing temperature-growth relationships, growth rates of non-acclimated (1st week) and acclimated (6th week) plants were taken.

Photosynthetic performance was studied by measuring oxygen evolution in the light and respiration as oxygen consumption in the dark. In order to minimise the effect of wounding on photosynthetic and respiratory rates, thallus pieces were cut 24 h before experimentation and kept under the culture conditions described above. Oxygen fluxes were determined using a Clark oxygen electrode (OXI 92, WTW, Germany) in a closed measuring system. The measurements were made in culture medium adjusted with Tris/NaOH to a pH of 8.0. $NaHCO_3$ (4 mM) was added to ensure saturation of inorganic carbon. The experimental measuring chamber (Huppertz et al. 1990) was submerged in a water bath to maintain a constant temperature (±0.01 °C). A halogen lamp (24 V, 250 W, Philips) was used as light source and photon fluence rates were adjusted using neutral grey glass filters (Schott, Germany).

In order to determine photosynthesis versus irradiance (*P-I*) curve parameters, *P-I* curves were measured at optimal growth temperature. Dark respiration was measured for 20 min, followed by determinations of net oxygen production for 10 min under 15 different irradiances up to 800 μmol $m^{-2}$ $s^{-1}$. The *P-I* curves were fitted to the following function:

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

where $P$ is the photosynthetic rate, $P_{\max}$ is the net maximum photosynthetic rate at saturating irradiances, $\alpha$ is the initial slope of the curve at low irradiances, $I$ is the incident irradiance, and $R$ is the dark respiration rate. The light saturation point ($I_k$) of photosynthesis was calculated from the quotient between $P_{\max}$ and $\alpha$, and the light compensation point ($I_c$) as the intersection of $\alpha$ and the irradiance axis.

The temperature experiments were started with the determination of dark respiration, followed by measurement of net photosynthetic oxygen production at light-saturating photon fluence rates. In order to determine short-term temperature response curves, the species were cultivated at optimum growth temperature for 6 weeks. Dark respiration and photosynthetic capacity were recorded in one series at 0, 5, 10, 15, 20, and 25 °C. (Net)photosynthetic capacity:respiration ratio (*P*:*R*) was calculated. The temperature dependence of respiration and photosynthetic rates was calculated as the ratio of reaction rates at 10 °C and 0 °C ($Q_{10}$). In order to investigate the acclimation potential, species were cultivated at 0, 5 or 10 °C for 4 weeks, and short-term temperature response curves were determined for algae acclimated to these temperatures in the same way as described above.

Estimations of the daily carbon balance were made by multiplying gross photosynthetic rates with an assumed daily period of light-saturated photosynthesis ($H_{sat}$) of 16 h and then subtracting the daily (24 h) dark respiration. Oxygen data were converted to equivalent carbon units using the ratio g C:g $O_2$ = 0.3 (Matta and Chapman 1991). This calculation presumes a constant dark respiration throughout the day and a photosynthetic quotient (*PQ*) of 1.25. This estimate of productivity refers only to a photosynthetic carbon balance and excludes other carbon losses or gains (Gómez et al. 1997).

After the photosynthetic measurements, the samples were stored in liquid nitrogen. Chlorophyll *a* was analysed in a spectrophotometer (Milton Roy, Spectronic 401, USA) using *N*,*N*-dimethylformamide as extraction medium, according to Inskeep and Bloom (1985), and calculated using the following equation:

$$\mathrm{Chl}\ a = 12.70 \times A_{664.5}$$

where $A_{664.5}$ is the absorption at wavelength 664.5 nm.

Multiple comparisons of means were performed using one-way ANOVA and Scheffé test at $P < 0.05$.

## Results

### Growth

During the 1st week, non-acclimated plants of the three eurythermal species grew over a broad range of temperatures up to at least 15 °C (Fig. 1). In contrast, the stenothermal species *Gigartina skottsbergii* and *B. callitricha* grew up to 5 °C (Fig. 2).

After 6 weeks, temperature-acclimated plants of *K. antarctica* and *Gymnogongrus antarcticus* grew up to 10 °C with an optimum at 0–5 °C (Fig. 1A, B); *P. ahnfeltioides* (Fig. 1C) grew up to 15 °C with an optimum at 5–10 °C. The species are therefore more eurythermal than the stenothermal species *Gigartina skottsbergii* (Fig. 2A) and *B. callitricha* (Fig. 2B), which grew optimally at 0 °C with no growth (*Gigartina skottsbergii*) or reduced growth (*B. callitricha*) at 5 °C. In all species except *B. callitricha*, growth rates at 0 °C were low at the beginning compared to the end of the experiment, in spite of the fact that they had been previously kept at 0 °C.

## Photosynthetic light demands

The photosynthetic parameters of the *P-I* curves measured at optimal growth temperatures are listed in Table 1. With the exception of *B. callitricha*, $I_c$ values were lower than 10 μmol $m^{-2}$ $s^{-1}$. In *B. callitricha*, values up to 28 μmol $m^{-2}$ $s^{-1}$ were measured. Photosynthesis was light-saturated between 23 and 51 μmol $m^{-2}$ $s^{-1}$ in *Gigartina skottsbergii*, *K. antarctica*, and *P. ahnfeltioides*. Higher values were obtained in

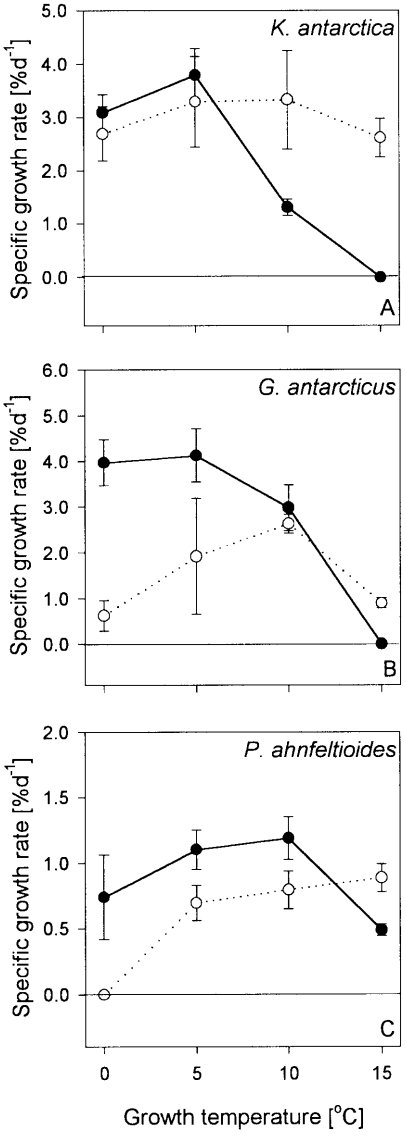


**Fig. 1A–C** Temperature requirements for growth in eurythermal group. Results are shown of acclimated (*solid line*, *filled circles*) and non-acclimated plants (*dashed line*, *unfilled circles*). Data represent means ± SD of five measurements

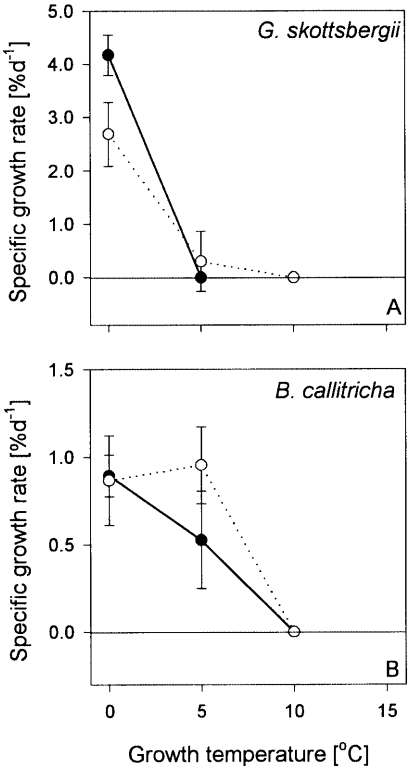


**Fig. 2A, B** Temperature requirements for growth in stenothermal group. Results are shown of acclimated (*solid line*, *filled circles*) and non-acclimated plants (*dashed line*, *unfilled circles*). Data represent means ± SD of five measurements

**Table 1** Photosynthetic light compensation $I_c$ (μmol $m^{-2}$ $s^{-1}$), initial light saturation $I_k$ (μmol $m^{-2}$ $s^{-1}$) and photosynthetic efficiency α [μmol $O_2$ $g^{-1}$ FW $h^{-1}$/(μmol $m^{-2}$ $s^{-1}$)] of algae measured at optimal growth temperature. Data represent means ± SD of three measurements

| Algal species | Growth temperature (0 °C) | $I_c$ | $I_k$ | α |
|---|---|---|---|---|
| *Ballia callitricha* | 0 | 27.8 ± 16.4 | 111.0 ± 74.6 | 0.276 ± 0.215 |
| *Gigartina skottsbergii* | 0 | 2.2 ± 0.8 | 23.1 ± 2.9 | 0.936 ± 0.233 |
| *Gymnogongrus antarcticus* | 5 | 5.8 ± 3.8 | 118.1 ± 47.2 | 0.454 ± 0.144 |
| *Kallymenia antarctica* | 5 | 0.7 ± 0.1 | 36.3 ± 3.9 | 0.237 ± 0.060 |
| *Phyllophora ahnfeltioides* | 10 | 8.1 ± 1.9 | 51.2 ± 9.3 | 0.364 ± 0.156 |

*B. callitricha* and *Gymnogongrus antarcticus* (110–120 μmol $m^{-2}$ $s^{-1}$). Photosynthetic efficiency at non-saturating irradiances (α) was highest in *Gigartina skottsbergii* [0.9 μmol $O_2$ $g^{-1}$ FW $h^{-1}$/(μmol $m^{-2}$ $s^{-1}$)]; α ranged between 0.2 and 0.5 μmol $O_2$ $g^{-1}$ FW $h^{-1}$/(μmol $m^{-2}$ $s^{-1}$) in the other species.

## Short-term temperature response of photosynthesis and respiration

The short-term temperature response curves of photosynthetic capacity and respiration of algae grown at optimum growth temperatures are shown in Figs. 3 and 4.

The relationship between (net)photosynthetic capacity and temperature is represented by an optimum curve (Fig. 3). The stenothermal species *Gigartina skottsbergii* had a narrow optimum at 15 °C. For the other member of this group, *B. callitricha*, a broader optimum region was evident at 10–15 °C. In comparison, the eurythermal species *K. antarctica*, *Gymnogongrus antarcticus* and *P. ahnfeltioides* had higher temperature optima over a broad range of temperatures between 10 and 20 °C or up to 25 °C. In the 0–10 °C interval, photosynthetic $Q_{10}$ values between 1.7 and 3.5 were obtained (Table 2).

In general, dark respiration rates increased linearly with incubation temperatures (Fig. 4). In the 0–10 °C interval, $Q_{10}$ values varied between 3.4 and 5.1 (Table 2).

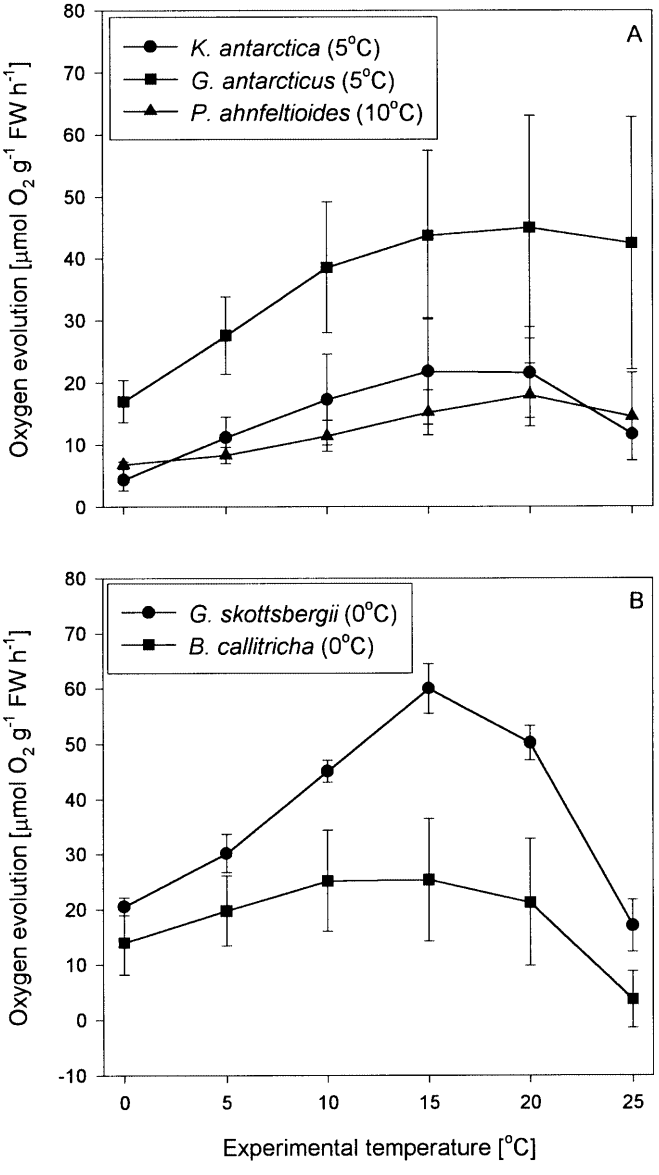


**Fig. 3A, B** Short-term temperature response curves of (net)photosynthetic capacity of plants grown at optimal growth temperatures (shown *in parentheses*). **A** Eurythermal group; **B** stenothermal group. Data represent means ± SD of three measurements

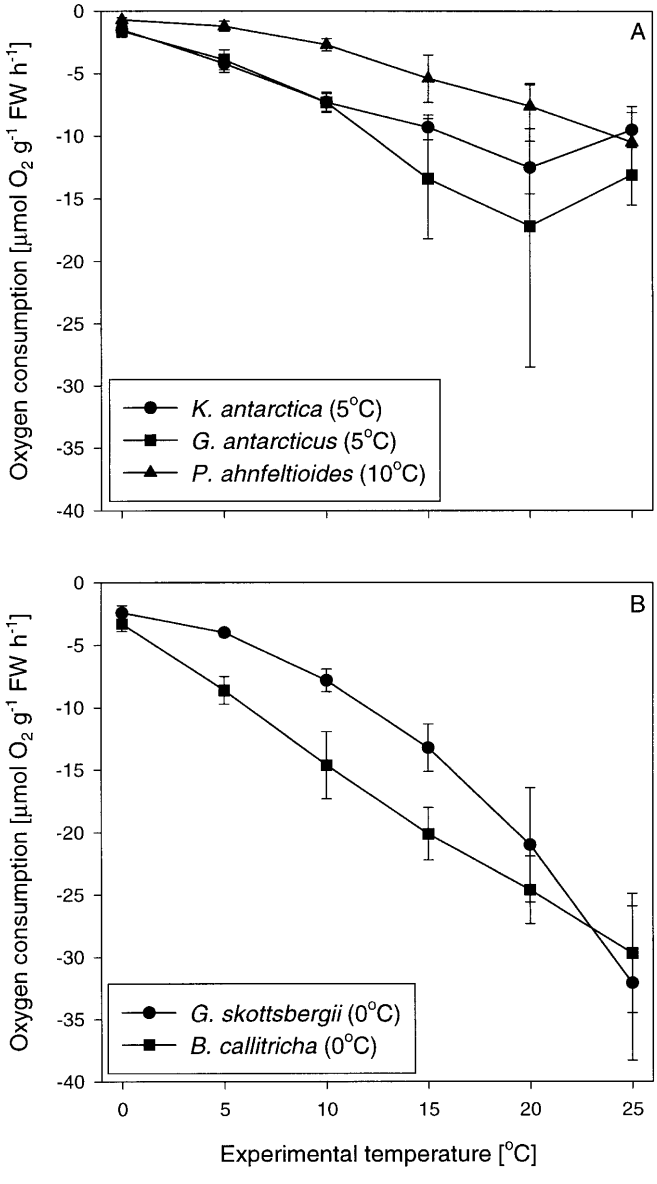


**Fig. 4A, B** Short-term temperature response curves of dark respiration rates of plants grown at optimal growth temperatures (shown *in parentheses*). **A** Eurythermal group; **B** stenothermal group. Data represent means ± SD of three measurements

**Table 2** $Q_{10}$ values (0–10 °C interval) of dark respiration and (net)photosynthetic capacity of the studied algae. Plants were cultivated at optimal growth temperatures. Data represent means ± SD of three measurements

| Algal species | Growth temperature [°C] | Respiration | Photosynthesis |
|---|---|---|---|
| *Ballia callitricha* | 0 | 4.4 ± 0.4 | 1.9 ± 0.3 |
| *Gigartina skottsbergii* | 0 | 3.4 ± 0.7 | 2.2 ± 0.2 |
| *Gymnogongrus antarcticus* | 5 | 5.0 ± 1.2 | 2.2 ± 0.2 |
| *Kallymenia antarctica* | 5 | 5.1 ± 0.5 | 3.5 ± 0.8 |
| *Phyllophora ahnfeltioides* | 10 | 4.4 ± 1.6 | 1.7 ± 0.2 |

The higher temperature sensitivity (i.e. higher $Q_{10}$) of the respiratory versus the photosynthetic metabolism resulted in all species in a decrease of the *P*:*R* ratios with increasing temperature from 0 to 25 °C (Table 3). The highest values of about 10.0 were found for *Gymnogongrus antarcticus*, *P. ahnfeltioides* and *Gigartina skottsbergii* at 0 °C. The overall lowest value of 0.1 was found for *B. callitricha* at 25 °C.

### Acclimation potential of photosynthesis and respiration

Acclimation of the photosynthetic metabolism did not lead to an overall shift in optimum temperature of photosynthesis in any of the species (Fig. 5). No temperature acclimation to the growth temperature was evident in *K. antarctica* (Fig. 5A). Cultivation at 0 °C did not lead to increased photosynthetic rates at this temperature. Similarly, *P. ahnfeltioides* did neither acclimate to 0 °C nor to 5 °C (Fig. 5D). However, in two cases acclimation to growth temperature was found, compensating for short-term temperature effects. The stenothermal species *B. callitricha* showed a temperature acclimation to 0 °C, since plants grown at 0 °C reached, overall, higher photosynthetic rates in comparison to plants grown at 5 °C (Fig. 5B). Similarly, *Gymnogongrus antarcticus* acclimated to 5 °C and 0 °C (Fig. 5C).

*K. antarctica* did not show any acclimation of the respiratory metabolism to the growth temperature, i.e. respiration rates of individuals cultivated at 0 and 5 °C were similar at these temperatures (Fig. 6A). In contrast, the other investigated algae partially acclimated respiration rates to higher growth temperature. In *B. callitricha*, rates of respiration were, overall, lower in 5 °C-grown than in 0 °C-grown plants (Fig. 6B). Additionally, respiration rates in the 5 °C-grown plants were less sensitive to changes in temperature. The net effect was that respiration rates were similar in plants growing at 0 °C and 5 °C at the respective growth temperature. Similarly *Gymnogongrus antarcticus* exhibited acclimation of dark respiration to 5 °C, but not to 10 °C, and *P. ahnfeltioides* to 5 and 10 °C (Fig. 6C, D).

### Daily metabolic carbon balance

Daily carbon balance was calculated for 0 °C of plants grown at 0 °C (Table 4). For *Gymnogongrus antarcticus* and *Gigartina skottsbergii* the highest daily carbon balance was calculated based on fresh and dry weight, reaching values of 3.1 mg C $g^{-1}$ FW $day^{-1}$ and 30.7 mg C $g^{-1}$ DW $day^{-1}$, followed by *B. callitricha*, *P. ahnfeltioides* and finally *K. antarctica*.

### Chlorophyll *a* content

Chlorophyll *a* contents varied greatly between species (Table 5). The lowest concentrations were found in *P. ahnfeltioides* with 0.12 mg Chl *a* $g^{-1}$ DW and the highest in *Gymnogongrus antarcticus* with 2.61 mg Chl *a* $g^{-1}$ DW.

Significant differences in chlorophyll *a* content within one species grown at different temperatures were found only in *B. callitricha*. Plants grown at 0 °C had with 1.09 mg Chl *a* $g^{-1}$ DW about twice the concentration of chlorophyll *a* based on dry weight compared to the plants grown at 5 °C (0.59 mg Chl *a* $g^{-1}$ DW). On a chlorophyll *a* basis, $P_{max}$ values of this species are similar for plants growing at 0 and 5 °C (64.1 ± 25.4 μmol $O_2$ $mg^{-1}$ Chl *a* $h^{-1}$ and 65.1 ± 16.0 μmol $O_2$ $mg^{-1}$ Chl *a* $h^{-1}$, respectively).

## Discussion

### Temperature adaptation and acclimation of growth

The temperature-growth patterns of temperature-acclimated plants of *Gigartina skottsbergii*, *B. callitricha*,

**Table 3** (Net)photosynthetic capacity:dark respiration (*P*:*R*) ratios of algae cultivated at optimal growth temperatures. Data represent means ± SD of three measurements

| Algal species | Growth temperature [°C] | Experimental temperature | | | | | |
|---|---|---|---|---|---|---|---|
| | | 0 °C | 5 °C | 10 °C | 15 °C | 20 °C | 25 °C |
| *Ballia callitricha* | 0 | 4.1 ± 1.3 | 2.3 ± 0.6 | 1.7 ± 0.4 | 1.2 ± 0.5 | 0.8 ± 0.4 | 0.1 ± 0.2 |
| *Gigartina skottsbergii* | 0 | 9.1 ± 2.2 | 7.6 ± 0.5 | 5.8 ± 0.5 | 4.6 ± 0.8 | 2.5 ± 0.5 | 0.6 ± 0.3 |
| *Gymnogongrus antarcticus* | 5 | 11.6 ± 1.9 | 7.5 ± 2.9 | 5.3 ± 1.5 | 3.6 ± 2.0 | 3.5 ± 2.5 | 3.3 ± 1.6 |
| *Kallymenia antarctica* | 5 | 3.1 ± 1.5 | 2.6 ± 1.0 | 2.2 ± 0.8 | 2.4 ± 0.9 | 1.7 ± 0.3 | 1.2 ± 0.3 |
| *Phyllophora ahnfeltioides* | 10 | 10.8 ± 2.4 | 7.1 ± 1.8 | 4.3 ± 1.5 | 3.0 ± 0.9 | 2.4 ± 0.2 | 1.4 ± 0.7 |

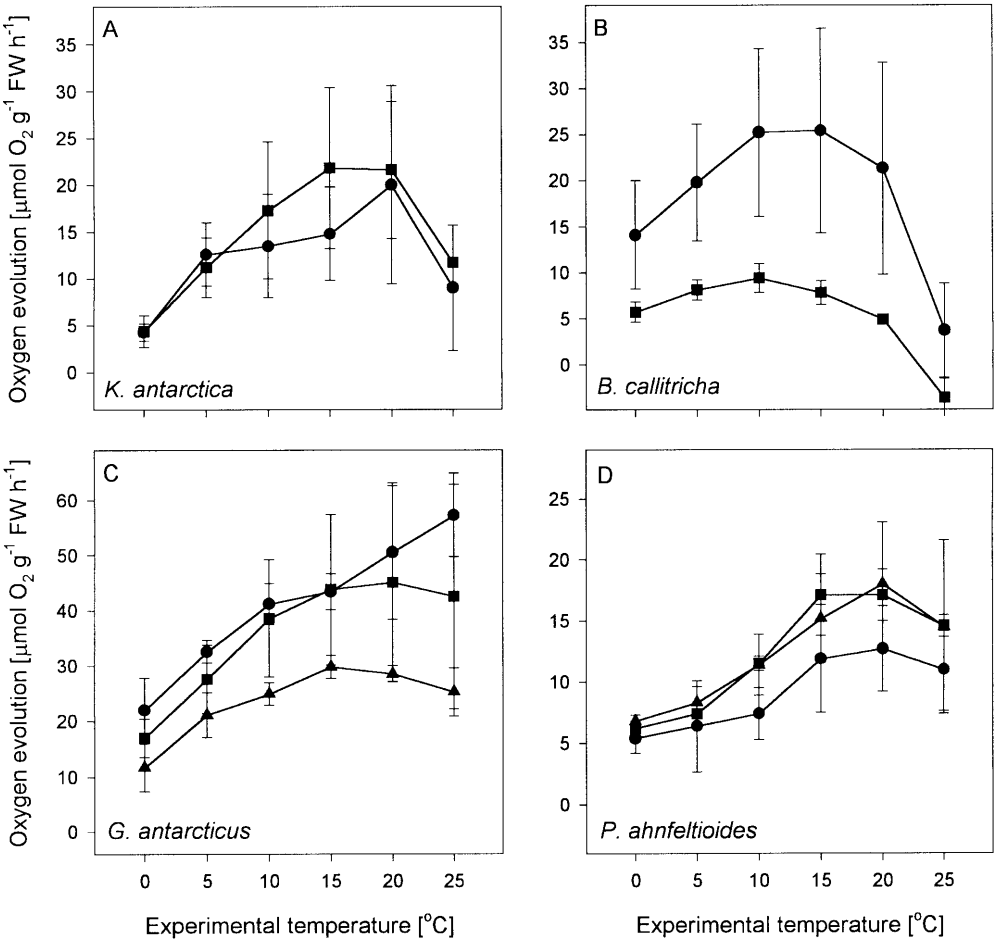


**Fig. 5A–D** Effect of temperature on (net)photosynthetic capacity of plants grown at 0 °C (*circle*), 5 °C (*square*) or 10 °C (*triangle*). Data represent means ± SD of three measurements

*Gymnogongrus antarcticus* and *P. ahnfeltioides* reported here are similar to those described earlier by Bischoff-Bäsmann and Wiencke (1996). The newly investigated species *K. antarctica* is characterised by a growth range between 0 and 10 °C and an upper survival temperature of 15 °C (data not shown), and therefore can be assigned to the eurythermal group.

Acclimation of growth is evident in all investigated species. The specific growth rates increase with acclimation time at optimal temperatures, whereas they decrease at sub- and supra-optimal temperatures. Moreover, growth is possible for a short time at supra-optimal temperatures under which no growth was found under long-term exposure in all eurythermal species and the stenothermal species *Gigartina skottsbergii*. The same pattern is described by Novaczek et al. (1990) for three Arctic to cold-temperate algae, where growth declined steadily at the upper temperature growth limit, approaching zero after 2–6 weeks. Physiologically this may be interpreted as a temperature-induced stimulation of growth-related enzymes, e.g. enzymes involved in remobilisation of storage compounds and respiration. Ecologically it may be an advantage in allowing intertidal individuals of these species to grow at elevated temperatures, e.g. in tide pools heated up by the sun in summer to up to 14 °C (Klöser 1994). The observed increase of growth rates after acclimation at 0 °C in *Gigartina skottsbergii* and the eurythermal species is regarded as an acclimation to the new light conditions in the experiment. Temperature effects can be excluded as the algae were pre-cultured at 0 °C.

## Photosynthetic light demands

Antarctic macroalgae are characterised by very low light demands, which is reflected by low light intensities required for light compensation and saturation of photosynthesis and high photosynthetic efficiencies at the low growth temperatures. This is described in other laboratory studies (Wiencke et al. 1993), has been measured in the field (Gómez et al. 1997) and is supported by the data presented here.

## Temperature adaptation and acclimation of photosynthesis and respiration

The photosynthesis versus temperature curves show, with the exception of *Gigartina skottsbergii*, relatively

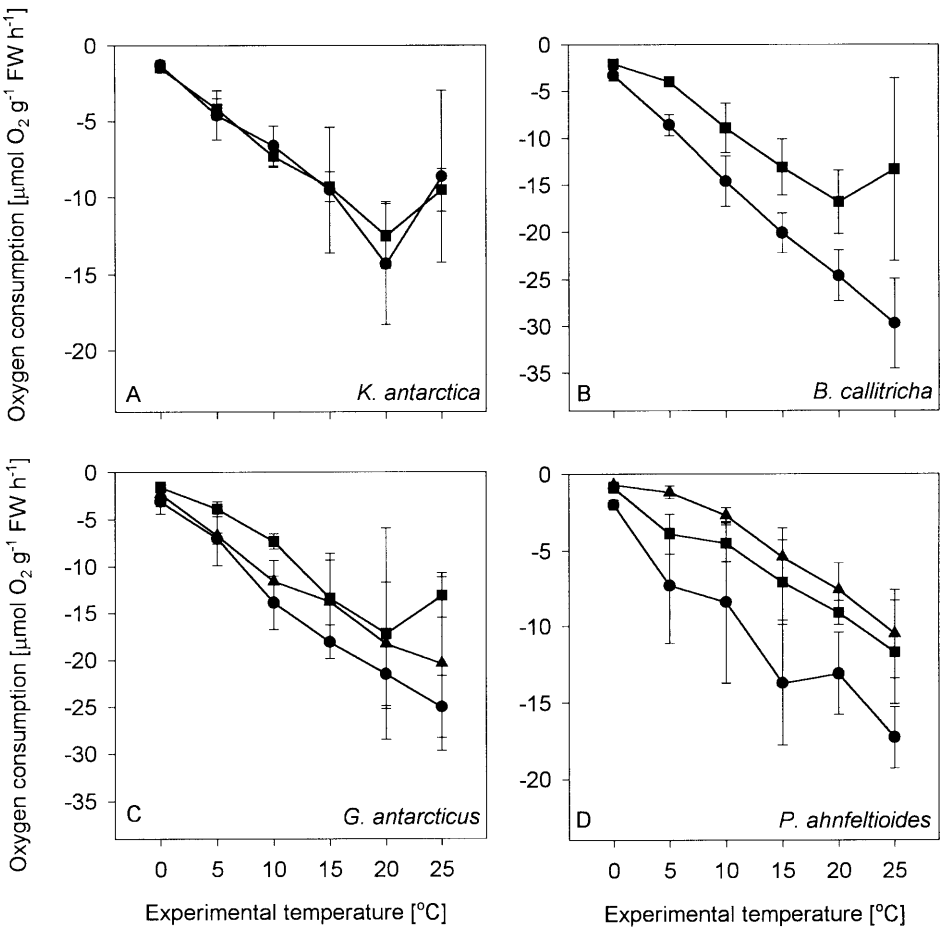


**Fig. 6A–D** Effect of temperature on dark respiration of plants grown at 0 °C (*circle*), 5 °C (*square*) or 10 °C (*triangle*). Data represent means ± SD of three measurements

broad optima, as has been repeatedly described for seaweeds in the literature (Oates and Murray 1983; Knoop and Bate 1990). The temperature dependence of enzymatic reactions of the Calvin cycle plays an important role at sub-optimal temperatures. RuBisCO, especially, is attributed a key role (Sukenik et al. 1987). Supra-optimal temperatures result finally in structural changes or denaturation of proteins. Photosystem II is probably one of the most heat-sensitive complexes and is particularly responsible for decreasing photosynthetic rates at high temperatures (Fork at al. 1979). Furthermore, adverse temperatures lead to an impairment of membrane functions, thereby limiting the efficiency of photosynthetic electron transport carriers (Havaux 1987). Some authors especially emphasise the increasing influence of photorespiration with increasing temperatures, due to the decline in the $CO_2/O_2$ specificity of RuBisCO at higher temperatures (Berry and Björkman 1980). However, many macroalgae, including the Rhodophyta, show low rates of photorespiration, probably because of the presence of a carbon-concentrating mechanism (CCM) (Johnston et al. 1992; Kübler and Raven 1994; Mercado et al. 1997). Additionally, photorespiration is presumably not important at the low ambient seawater temperatures.

Acclimation of the photosynthetic metabolism leading to improved performances at lower temperatures has been shown for *B. callitricha* and *Gymnogongrus antarcticus* and partially for *P. ahnfeltioides*. Acclimation over a time span of several weeks may be achieved by an increase in the capacity of temperature-limited enzymatic steps in the photosynthetic process

**Table 4** Daily metabolic carbon balance of algae grown at 0 °C for 16 h under saturating light based on fresh weight (mg C $g^{-1}$ FW $day^{-1}$) and dry weight (mg C $g^{-1}$ DW $day^{-1}$) and dry: fresh weight (DW:FW) ratio (%)

| Algal species | Carbon balance based on FW | Carbon balance based on DW | DW:FW (%) |
|---|---|---|---|
| *Ballia callitricha* | 1.9 ± 0.9 | 9.0 ± 4.2 | 21.2 ± 0.6 |
| *Gigartina skottsbergii* | 3.0 ± 0.2 | 13.4 ± 0.8 | 22.2 ± 0.2 |
| *Gymnogongrus antarcticus* | 3.1 ± 0.9 | 30.7 ± 15.8 | 11.0 ± 2.1 |
| *Kallymenia antarctica* | 0.6 ± 0.2 | 4.1 ± 1.4 | 14.0 ± 1.3 |
| *Phyllophora ahnfeltioides* | 0.7 ± 0.2 | 7.3 ± 2.3 | 31.0 ± 1.0 |

**Table 5** Chlorophyll *a* content based on dry weight (mg Chl *a* $g^{-1}$ DW). Data represent means ± SD of six measurements. Significant differences at $P < 0.05$ (one-way ANOVA) are marked

| Algal species | Growth temperature (0 °C) | Chlorophyll *a* content |
|---|---|---|
| *Gigartina skottsbergii* | 0 | 0.90 ± 0.11 |
| *Ballia callitricha* | 0 | 1.09 ± 0.32* |
| | 5 | 0.60 ± 0.08* |
| *Kallymenia antarctica* | 0 | 0.73 ± 0.13 |
| | 5 | 0.59 ± 0.09 |
| *Gymnogongrus antarcticus* | 0 | 2.61 ± 0.35 |
| | 5 | 2.48 ± 0.33 |
| | 10 | 2.24 ± 0.29 |
| *Phyllophora ahnfeltioides* | 0 | 0.17 ± 0.03 |
| | 5 | 0.12 ± 0.04 |
| | 10 | 0.15 ± 0.08 |

compensating for short-term temperature effects. A similar temperature independence of light-saturated photosynthesis when measured at growth temperature has also been found by Davison et al. (1991) for the subpolar to temperate macroalga *Laminaria saccharina*.

Cultivation at different temperatures leads in none of the investigated species to an overall shift in optimum temperature of photosynthesis. This suggests that the acclimation response occurs through synthesis of higher levels of photosynthetic enzymes, instead of activation of modified enzymes with lower temperature optima, since this would shift the optimum temperature. This acclimation response might be a specific adaptation to the minimal variations in temperature in the Southern Ocean, since periodical shifts of temperature optima have been described for seaweeds native to habitats with seasonal variations in temperature (Niemeck and Mathieson 1978) and are well known in terrestrial plants (Berry and Björkman 1980).

Similarities exist between thermal acclimation of photosynthesis to sub-optimal temperatures and photoacclimation to high light. Machalek et al. (1996) described in *L. saccharina* a decrease in photosystem II reaction centre densities and a decrease in concentration of major light-harvesting pigments when grown at sub-optimal temperatures. An increase in photosystem II reaction centres is associated with an increase in chlorophyll *a* content. However, in this study chlorophyll *a* content varied significantly only in *B. callitricha*, when grown at different temperatures. Plants grown sub-optimally at 5 °C have a lower chlorophyll *a* content. In contrast, it has been reported for the red alga *Chondrus crispus* that acclimation is characterised by variations in antenna size rather than by reaction centre densities (Kübler and Davison 1995). This cannot be further discussed due to the lack of data on the light-harvesting pigments, but it might explain the similar chlorophyll *a* contents found for the other species investigated here.

In general, no temperature optimum of dark respiration was evident in the temperature range 0–25 °C, contrary to photosynthesis, showing that the respiratory process is more high-temperature resistant than photosynthesis. This has also been described for the Antarctic macroalgae *Himantothallus grandifolius* (Drew 1977) and *Ascoseira mirabilis* (Wiencke et al. 1993), as well as for terrestrial plants (Berry and Björkman 1980). Wiencke et al. (1993) found in *H. grandifolius* and *Gigartina skottsbergii* weakly expressed temperature optima for dark respiration at 10 and 15 °C, respectively. This result, however, could not be confirmed in the present study for *Gigartina skottsbergii*.

Temperature acclimation of respiration involves decreased sensitivity to changes in temperature (i.e. lower $Q_{10}$ values) and/or overall lower rates at higher temperatures. Temperature acclimation of respiration compensated short-term changes of temperature completely in *B. callitricha* and *P. ahnfeltioides* and partially in *Gymnogongrus antarcticus*.

A high temperature sensitivity of dark respiration rates was found in all species. The calculated $Q_{10}$ values show that an increase in incubation temperature from 0 to 10 °C leads to a three- to sixfold increase in respiration rates. These values are high in comparison to photosynthesis. *K. antarctica* shows, with average values of 3.5, the greatest temperature dependence of photosynthesis; the values of the other species are approximately 2.0. Similar results for other Antarctic macroalgae have been obtained by Wiencke et al. (1993).

The photosynthetic temperature responses reflect a certain degree of adaptation to the Antarctic temperature regime. Although photosynthetic rates are comparable to those of macroalgae from temperate latitudes, the optima of the stenothermal Antarctic species (10–15 °C) are situated at temperatures well below the optimum temperatures of algae from other biogeographical regions, even those from the Arctic. Optimum temperatures for photosynthesis are highest (25–35 °C) in warm-temperate/tropical species (Terrados and Ros 1992), intermediate (20–25 °C) in cold-temperate to Arctic species and lowest (10–20 °C) in Antarctic macroalgae (Drew 1977; Wiencke et al. 1993; this study).

The observed differences in the temperature-growth pattern of the stenothermal versus the eurythermal species can partly be explained by the mechanism of cold adaptation on the level of photosynthesis. The stenothermal species show a lower optimum temperature of photosynthesis than the eurythermal species. In order to balance the negative effect of low temperatures on chemical reactions, cold adaptation of photosynthesis requires either high concentrations of enzymes or synthesis of enzymes with modified properties. The degree to which the temperature optima of photosynthesis are shifted towards lower temperatures is dependent on the adaptation mechanism, as pointed out by Lüning (1990). Since an increase in enzyme concentration alone does not lead to a shift in optimum temperature, the formation of iso-enzymes is hypothesised in the stenothermal species. However, the two groups cannot be

distinguished in the temperature response of dark respiration or in temperature sensitivity ($Q_{10}$) of photosynthesis and respiration between 0 and 10 °C. Acclimation of photosynthesis and respiration to growth temperatures was found in *B. callitricha*, *Gymnogongrus antarcticus* and *P. ahnfeltioides*. In these species it is a genetically fixed response, since algae were kept for about 3 years in the laboratory at a constant 0 °C.

The obtained temperature optima of photosynthesis of all investigated Antarctic species are situated well above the ambient seawater temperature and are in all cases situated above the temperature optima of growth. Similar differences between upper temperature limits for growth and photosynthesis have been described for other macroalgae (Davison 1987; Kübler et al. 1991). This apparent contradiction shows that temperature effects on a specific physiological process (e.g. photosynthesis) do not always correspond to the temperature-growth pattern, because growth is an integration of the effect of temperature on the total metabolism.

## Daily metabolic carbon balance and *P*:*R* ratio

The temperature dependence of net photosynthesis plays an important role for the temperature tolerance of the entire organism. However, it is not solely photosynthesis but also the daily positive carbon gain that is of primary importance for the growth of the plant (Kübler et al. 1991). The increasing dark respiration rate at higher temperatures reduces the instantaneous carbon gain and should therefore be taken into consideration. The *P*:*R* ratio can provide a first valuable approximation of the instantaneous carbon gain. In all species investigated here, *P*:*R* ratios decreased continuously in the short-term experiments from about 10.0 at 0 °C to values lower than 1.0 at 25 °C. This indicates that the instantaneous carbon gain becomes negative at high temperatures. Gerard and Du Bois (1988) determined highest photosynthetic rates at 18–20 °C in short-term experiments with *L. saccharina*, but respiratory rates were still increasing at higher temperatures. These authors concluded that the resulting low *P*:*R* ratio can explain low growth rates at 20 °C. Similarly, low growth rates at higher temperatures are regarded as a result of the low *P*:*R* ratios determined in this study.

The calculated daily carbon balance estimates the carbon gain for a daily period of light-saturated photosynthesis ($H_{sat}$). Since conditions in the laboratory greatly deviate from the conditions in the field, this calculation is only a very rough assessment. The very low light demands indicated by the measured $I_k$ values ranging between 23 and 118 μmol $m^{-2}$ $s^{-1}$ lead to light-saturated photosynthesis in the field, down to a depth of 30 m during Antarctic spring (Gómez et al. 1997). Dissimilarities in the daily carbon gain on a dry weight versus fresh weight basis can be explained by differences in thallus morphologies. These differences are reflected in the dry:fresh weight ratios. Terrados and Ros (1992) gave for the Mediterranean species *Caulerpa prolifera*, for a water temperature of 30 °C and a daylength of 11 h, a daily carbon gain of 15.6 mg C $g^{-1}$ DW. In comparison, the daily carbon balance of *Gymnogongrus antarcticus* at 0 °C was estimated at 30.7 mg C $g^{-1}$ DW $day^{-1}$, twice as high as that of the Mediterranean species at 30 °C. In the Antarctic red alga *Palmaria decipiens*, a daily carbon balance of up to 3.5 mg C $g^{-1}$ FW $day^{-1}$ was measured under field conditions (Gómez et al. 1997). These results support the observation that Antarctic algae are capable of considerable primary production, in spite of the prevailing low temperatures. This is of particular relevance for survival and for compensating carbon losses in this harsh environment, with winter daylengths of only 5 h on King George Island. Additionally, ice cover leads to long twilight or even dark periods. In this context, the life strategies of Antarctic species should be remembered. Season responders like *Gigartina skottsbergii* have an opportunistic life strategy and grow whenever light conditions are favourable, whereas season anticipators exhibit a seasonal growth pattern finely tuned to the strong seasonal changes in light conditions in Antarctica (Wiencke 1990a, 1990b). Seasonal growth and photosynthetic patterns are closely related, as has been shown for *Palmaria decipiens* (Weykam and Wiencke 1996; Weykam et al. 1997), *Iridaea cordata* (Weykam et al. 1997), *A. mirabilis* (Gómez et al. 1995) and *Desmarestia menziesii* (Gómez and Wiencke 1996).

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