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K. Bischof · D. Hanelt · C. Wiencke

UV-radiation can affect depth-zonation of Antarctic macroalgae

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Abstract Due to depletion of stratospheric ozone over polar regions of the Northern and Southern Hemispheres UV-B-radiation has increased at the surface of the earth. Measurements of variable chlorophyll fluorescence were conducted to document UV-induced photoinhibition of photosystem II in cultivated macroalgae with different depth distributions in Antarctica. The reactions during artificial UV-exposure were observed on a short time scale (hours) and in light–dark cycles over several days. The nine species of investigated macroalgae show great differences in UV-tolerance of the photosynthetic process. Photosynthesis of the studied green algae was inhibited to a minor degree, while the brown algae showed an intermediate inhibition of photosynthesis. The response of the studied red algae varied with species. The differences in the degree of inhibition and recovery of photosynthetic efficiency and capacity indicate that UV-radiation is one important factor affecting the vertical distribution of macroalgae in nature.

Introduction

Macroalgae of high latitudes are well adapted to the low-light conditions prevailing under ice-cover in winter and at a low solar angle (Kirst and Wiencke 1995). Their lower depth-distribution limit is mostly determined by the degree of shade adaptation. In contrast, the upper depth-distribution limit is partially determined by the ability to tolerate high light stress (Hanelt 1996; Hanelt et al. 1997a). Previous investigations on photoinhibition of photosynthesis of Antarctic macroalgae focussed on the effects of high photosynthetically active radiation (PAR). In these studies inhibition of photosynthesis and recovery from light stress in accordance to depth distribution of macroalgal species has been documented by chlorophyll fluorescence studies as well as by measurements of oxygen production (Häder et al. 1996; Hanelt et al. 1997a).

Seasonal depletion of stratospheric ozone over the Northern and Southern Hemispheres results in increasing solar UV-B-radiation at the earth's surface (Lubin and Frederick 1989; Wängberg et al. 1996). Over Antarctica more than a 50% reduction of ozone is expected every spring (Karentz 1994). Macroalgae of polar regions may be sensitive to shifts in the irradiation and light climate due to global changes. Eulittoral species become fully exposed to natural sunlight during low-tide. Sublittoral species are partially protected by the water column which absorbs the shorter wavelengths. Although UV-B-radiation is more strongly absorbed than PAR even in clear Antarctic waters, biologically relevant intensities of UV-B-radiation may penetrate the water column down to 10–30 m depth (Karentz 1989). Therefore, increasing solar UV-radiation may be harmful, especially to polar species (Holm-Hansen et al. 1989, 1993).

UV-B-radiation and high PAR exert similar effects on photosynthesis, but with different molecular mechanisms (Larkum and Wood 1993; Neale et al. 1993). While high PAR results in an increase of oxidative stress on proteins of the reaction-centre of photosystem II (PS II), UV-B-radiation predominantly damages DNA and proteins by the formation of thymine dimers and the splitting of disulfide and peptide bonds (Karentz et al. 1991). However, there is evidence that the D1-protein in the reaction centre of PS II is one of the major targets for UV-B-radiation (Neale et al. 1993; Long et al. 1994). If a protein of the photosynthetic complex is affected, photoinhibition of photosynthesis is induced. In that case, it should be defined that photoinhibition is a reversible protecting mechanism, whereas photodamage is irreversible or only reversible on a long time scale (Krause and Weis 1991; Osmond 1994).

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K. Bischof (✉) · D. Hanelt · C. Wiencke
Alfred Wegener Institute for Polar and Marine Research,
D-27515 Bremerhaven, Germany

In the study presented here the specific UV-sensitivity of photosynthesis was studied in the laboratory under artificial radiation. In cultivated Antarctic macroalgal species, inhibition and recovery of photosynthesis after exposure to simulated solar UV-radiation were monitored to test whether a genetically fixed UV-tolerance occurs, and whether it shows relation to the depth distribution on the shore.

Materials and methods

Plant material and culture conditions

Nine different macroalgal species originally isolated on King-George-Island (Antarctica) were investigated (see Table 1). These isolates were kept in stock-cultures in the Alfred Wegener Institute (Bremerhaven, Germany). Plants raised from stock-cultures were cultivated at 0 °C and 8 to 15 μmol photons m^{-2} s^{-1} provided by daylight-fluorescent tubes (Osram L58/W19) under 18 h light:6 h dark photocycles. The algae were kept in glass vessels filled with filtered sea water (0.2-μm membrane filters, Sartorius Sartobran) which was changed every 2 weeks. The medium was enriched with nutrients after Provasoli (1968). Water motion was provided by aeration.

UV-experiments

Samples were exposed to artificial UV-radiation produced by Q-Panel UVA-340 fluorescent tubes (Cleveland, USA), emitting a spectrum similar to solar radiation in the range 295 to 340 nm. Comparative radiation measurements were conducted with a Spectro 320 D spectroradiometer (Instrument Systems, Germany) (see Fig. 1). In the experiments, radiation in the UV-range was measured with a RM-21 broad band radiometer (Dr. Gröbel, Ettlingen, Germany). In three different experimental setups, the algae were exposed to different doses of UV by varying the irradiance or the duration of exposure. To minimise inhibition of photosynthesis due to white light, background PAR was adjusted to 20 μmol photons m^{-2} s^{-1}. The different conditions of exposure to UV are listed in Table 2. Recovery of photosynthesis was investigated after the end of UV-exposure. At the end of Setup III the algae were exposed to normal culture conditions as described above. Each experiment was performed four times; mean values and standard deviations (SD) were calculated.

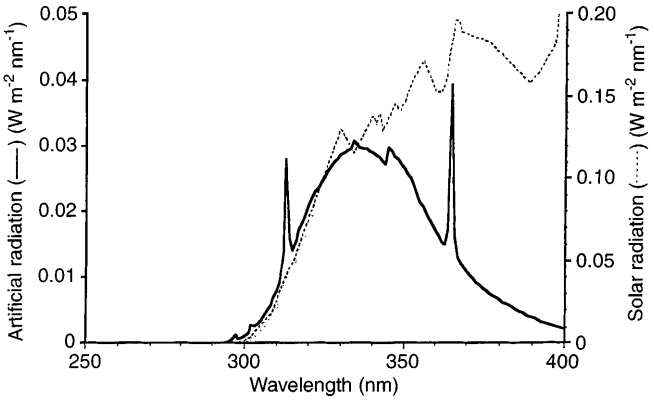

Fig. 1 Spectra emitted by artificial radiation with Q-Panel UVA-340 tubes compared with the solar spectrum of Bremerhaven, Germany. Measurements were carried out with a Spectro 320 D (Instrument Systems, Germany) spectroradiometer

Measurements of photosynthesis

Photosynthetic activity was determined by measuring variable chlorophyll-fluorescence of PS II with a PAM-2000 device (Walz, Effeltrich, Germany). Optimum quantum yield (i.e. excitation capture by open PS II centres) was calculated as the ratio of variable to maximum fluorescence (F_r/F_m) of the dark-acclimated plant. Small pieces cut from the thalli were fixed to the end of the fiberoptics of the instrument and incubated in a sea water cuvette cooled to 0 °C by a surrounding water jacket. Temperature was controlled by a cryostat. After application of a 5 s far-red pulse (30 μmol m^{-2} s^{-1} at 735 nm) to reoxidise the electron transport chain, the samples were kept in darkness for 5 min to extinguish energy-dependent fluorescence quenching (qE) and quenching by state transitions (qT). Then minimal fluorescence (F_o) was measured with a pulsed measuring beam (approximately 0.3 μmol m^{-2} s^{-1}, 650 nm). Afterwards short pulses of saturating white light (0.4 to 0.8 s, 1500 to 10 000 μmol m^{-2} s^{-1}) were provided to determine F_m. Each measurement was repeated three times.

To monitor changes in photosynthetic efficiency as well as in photosynthetic capacity, photosynthesis versus irradiance curves (*P-I* curves) were determined. Samples were irradiated with increasing irradiances of actinic red light (650 nm, 3.5 to 350 μmol m^{-2} s^{-1}). Every 30 s, a saturating pulse was applied to measure effective quantum yield of photosynthesis ($\Delta F/F_m'$) before actinic irradiation was increased again. Relative electron transport rates (ETR) were calculated by multiplying quantum yield with photon irradiance as described by Schreiber et al. (1994): rel. ETR $= \Delta F/F_m' \cdot$ PAR. These were plotted against irradiance of actinic light, and photosynthetic efficiency (corresponding to α, initial

Table 1 Investigated species and their depth distribution (after Delaca and Lipps 1976; Lamb and Zimmermann 1977; Zielinski 1990; Klöser et al. 1996)

Species	Depth distribution
Chlorophyta	
Enteromorpha bulbosa (Suhr) Montagne	Intertidal
Acrosiphonia arcta (Dillwyn) Agardh	Intertidal
Rhodophyta	
Phycodrys austrogeorgica Skottsberg	Middle–lower subtidal
Delesseria lancifolia (Hooker) Agardh	Middle–lower subtidal
Gymnogongrus antarcticus Skottsberg	Upper–lower subtidal
Iridaea cordata (Turner) Bory	Upper subtidal
Phaeophyta	
Desmarestia anceps Montagne	Upper–lower subtidal
Desmarestia antarctica Moe and Silva	Upper–middle subtidal
Himantothallus grandifolius (A. and E.S. Gepp) Zinova	Middle–lower subtidal

Table 2 UV-exposure experiments

Setup	Radiation conditions	Investigated species
I	1 h 7 W m^{-2} UV-A + 0.2 W m^{-2} UV-B 1 h 2 W m^{-2} UV-A + 0.06 W m^{-2} UV-B (recovery observed during 48 h in 20 μmol m^{-2} s^{-1} white light)	*Acrosiphonia arcta* *Enteromorpha bulbosa* *Desmarestia anceps* *Desmarestia antarctica* *Himantothallus grandifolius* *Delesseria lancifolia* *Gymnogongrus antarcticus* *Iridaea cordata* *Phycodrys austrogeorgica*
II	5 h 7 W m^{-2} UV-A + 0.2 W m^{-2} UV-B (recovery observed during 70 h in 20 μmol m^{-2} s^{-1} white light)	*Acrosiphonia arcta* *Desmarestia anceps* *Delesseria lancifolia* *Gymnogongrus antarcticus*
III	5 h 7 W m^{-2} UV-A + 0.2 W m^{-2} UV-B (during 5 d from 10:00–15:00, 20 μmol m^{-2} s^{-1} white light from 6:00–24:00, darkness from 0:00–6:00; postculture in dim white light)	*Acrosiphonia arcta* *Desmarestia anceps* *Gymnogongrus antarcticus*

slope under light-limited conditions) and capacity (corresponding to gross P_{max}, under saturating light) were determined.

Optimal quantum yield (F_v/F_m) differs between algal classes (Büchel and Wilhelm 1993). The reasons are probably the different pigment contents and construction of the photosynthetic apparatus in these groups. Therefore the means of the measured values of unstressed controls were normalised to 100%, allowing a better comparison between samples from different algal groups.

Results

First experimental setup

In all species the degree of inhibition of photosynthetic efficiency was dependent on the dose of the respective UV-radiation. Figure 2 illustrates the changes in F_v/F_m after exposure for 1 h to two different irradiances. All samples exposed to 7 W m^{-2} UV-A plus 0.2 W m^{-2} UV-B (high dose) were more strongly inhibited than those exposed only to 2 W m^{-2} UV-A plus 0.06 W m^{-2} UV-B (low dose). The two green algae *Enteromorpha bulbosa* and *Acrosiphonia arcta* showed small responses to UV-radiation. In general the brown algae tested were more sensitive than the green algae. Within the brown algae photosynthetic efficiency of *Desmarestia antarctica* was least affected. In the red algae a very heterogeneous response to UV-exposure was found. In *Iridaea cordata* lower irradiances of UV-radiation resulted in a similar decrease in F_v/F_m to that in the green algae. *Gymnogongrus antarcticus* exhibited much lower F_v/F_m values after exposure. *Delesseria lancifolia* and *Phycodrys austrogeorgica* were the most sensitive plants tested here. In *D. lancifolia* photosynthetic efficiency at lower irradiance was depressed to 32% and down to 4% at higher irradiance. In *P. austrogeorgica* F_v/F_m values after exposure were at 24% of the controls at lower and about 1% at higher UV-irradiance.

To distinguish between regulating mechanisms (dynamic photoinhibition) and photodamage in the photosynthetic apparatus the course of recovery was observed, as shown for four species in Fig. 3. Within

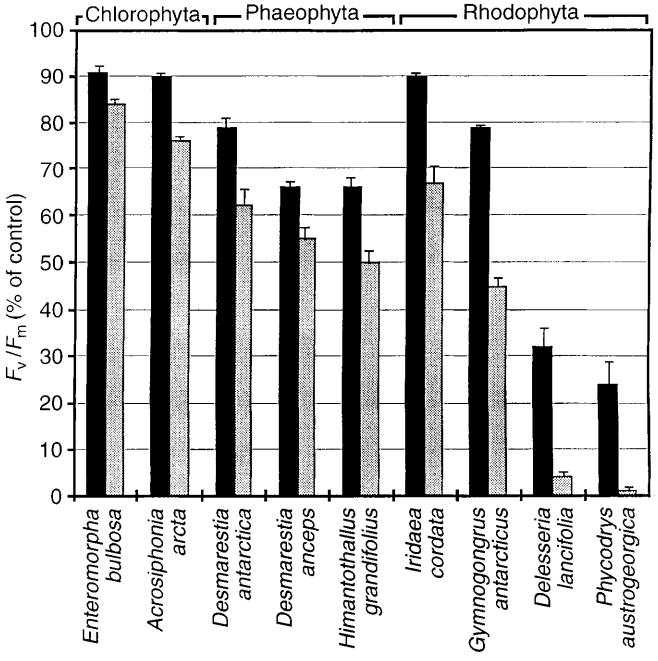

Fig. 2 Changes in variable to maximum fluorescence (F_v/F_m) after 1 h of UV-exposure (*filled bars* 2 W m^{-2} UV-A + 0.06 W m^{-2} UV-B; *shaded bars* 7 W m^{-2} UV-A + 0.2 W m^{-2} UV-B)

48 h F_v/F_m in *Acrosiphonia arcta* and *Desmarestia anceps* recovered completely from both UV-treatments. *A. arcta* exposed to the low UV-dose for 1 h recovered already within 24 h. After 48 h of recovery *Gymnogongrus antarcticus* exhibited F_v/F_m values of 90% of controls after 1 h of exposure to the high UV-dose, while individuals exposed to the lower irradiance had fully recovered. In *Delesseria lancifolia* exposed to low and high UV-doses recovery was still incomplete after 48 h.

Analysis of the *P-I* curves revealed differences in the degree of inhibition in photosynthetic capacity (P_{max}) and photosynthetic efficiency (α). Figure 4 shows the

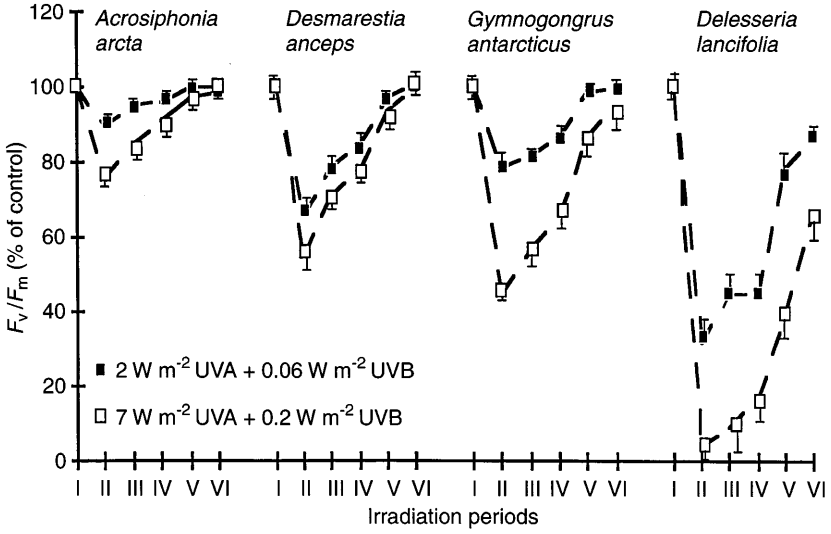

Fig. 3 Changes in F_v/F_m during exposure and recovery periods (*I* start; *II* 1 h exposure; *III* 1 h recovery; *IV* 2 h recovery; *V* 24 h recovery; *VI* 48 h recovery)

decrease of both parameters after 1 h of exposure to 7 W m^{-2} UV-A plus 0.2 W m^{-2} UV-B. Under low UV-radiation, photosynthetic capacity in *Enteromorpha bulbosa* and *Acrosiphonia arcta* was not affected. P_{max} in *Himantothallus grandifolius* was also the same as the control value, while α decreased to 50%. P_{max} in *Desmarestia antarctica* was lowered to 88%, in *Desmarestia anceps* to 65%. In all studied red algae P_{max} had decreased after 1 h of exposure. P_{max} in *Iridaea cordata* decreased to 87% of the control, in *Gymnogongrus antarcticus* P_{max} was lowered to 76%. At the end of exposure, quantum yield of *Delesseria lancifolia* and *Phycodrys austrogeorgica* was nearly zero.

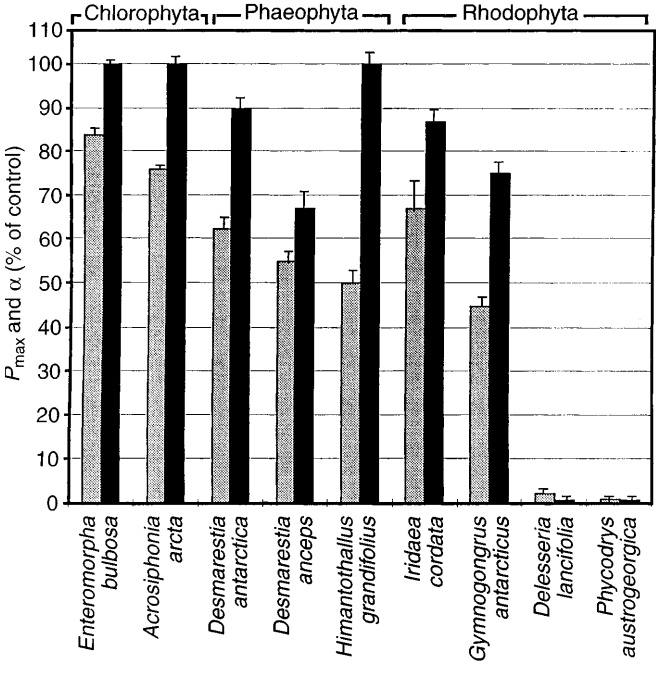

Fig. 4 Changes in photosynthetic capacity (P_{max}; *filled bars*) and (α; *shaded bars*) after 1 h of exposure to 7 W m^{-2} UV-A + 0.2 W m^{-2} UV-B

Recovery of P_{max} and α was monitored during 48 h. With the exception of *Delesseria lancifolia* and *Phycodrys austrogeorgica* recovery of photosynthetic capacity was complete within 24 h in all species (Fig. 5). *Acrosiphonia arcta* showed only a decrease in α of 22% without effects on P_{max}. With exception of two very sensitive red algae, photosynthetic capacity is less affected and recovered faster than α. In *D. lancifolia* UV-irradiation depressed P_{max} and α to a similar extent, and photosynthesis recovered subsequently in the same manner.

Second experimental setup

In this series the dose was increased by extending the exposure time to 5 h with 7 W m^{-2} UV-A plus 0.2 W m^{-2} UV-B, followed by recovery in dim white light (see Fig. 6). Photosynthetic efficiency decreased more than in the shorter exposure and did not recover completely in any of the tested species. F_v/F_m values in *Acrosiphonia arcta* changed least. In *Desmarestia anceps* F_v/F_m was more depressed than in *A. arcta* and recovery proceeded more slowly. In *Gymnogongrus antarcticus* F_v/F_m decreased to 10% within 3 h of exposure with no further decrease within the following 2 h of exposure. After 70 h photosynthetic efficiency recovered to 87%. Again, *Delesseria lancifolia* was the most sensitive species. Within the first hour of exposure photosynthetic efficiency in *D. lancifolia* was inhibited strongly to 15% and did not recover.

Figure 7 shows the changes of P_{max}. In each species, except *Delesseria lancifolia,* P_{max} decreased more slowly and to a smaller degree than the optimal quantum yield (Fig. 6). Recovery also proceeded much faster and was already complete within 20 h. Similar to the decrease in F_v/F_m, P_{max} in *D. lancifolia* was completely depressed within the first hour of treatment and did not recover at all.

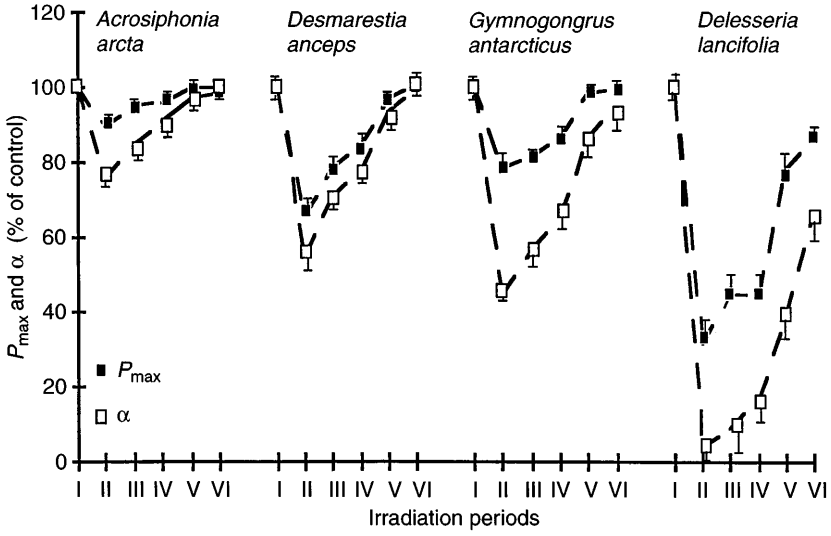

Fig. 5 Changes in P_{max} and α during exposure to 7 W m^{-2} UV-A + 0.2 W m^{-2} UV-B and recovery periods (*I* start; *II* 1 h exposure; *III* 1 h recovery; *IV* 2 h recovery; *V* 24 h recovery; *VI* 48 h recovery)

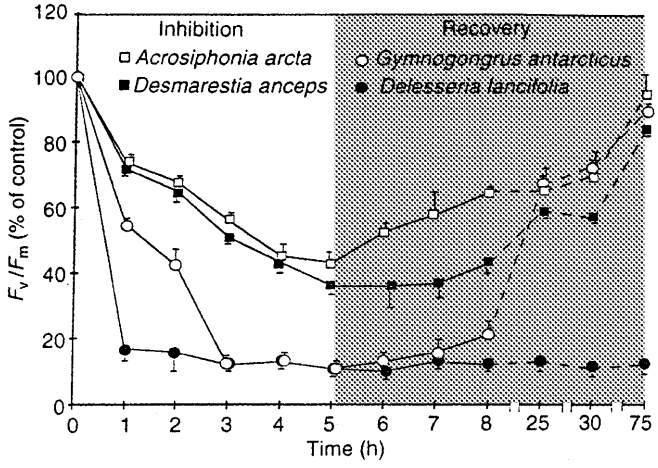

Fig. 6 Changes in F_v/F_m during 5 h of exposure to 7 W m^{-2} UV-A + 0.2 W m^{-2} UV-B and 70 h of recovery in dim white light

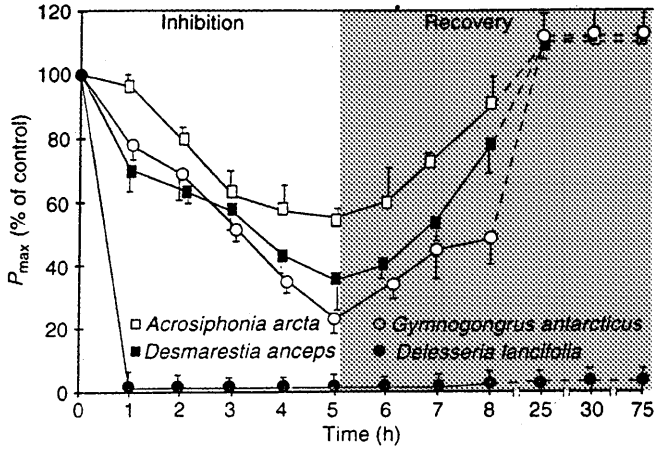

Fig. 7 Changes in P_{max} during 5 h of exposure to 7 W m^{-2} UV-A + 0.2 W m^{-2} UV-B and 70 h of recovery in dim white light

Third experimental setup

The previous experiment was repeated for five consecutive days (see Table 2), and the changes in F_v/F_m were monitored (Fig. 8). In *Acrosiphonia arcta* and *Gymnogongrus antarcticus* the amplitudes of the changes of F_v/F_m due to inhibition and recovery of photosynthesis were rather constant during the course of the experiment. After the first 5 h of irradiation F_v/F_m in *A. arcta* was depressed to 49% (Fig. 8A). By the beginning of the next exposure (after 19 h of recovery) the values had increased to 79%. Again, 5 h of irradiation lowered F_v/F_m to 49% and recovery was similar to before. *Desmarestia anceps* showed a slight decrease in photosynthetic efficiency during the time course (Fig. 8B). On the first day of treatment F_v/F_m values decreased to a lower level than in *A. arcta*. On the next morning photosynthetic efficiency recovered to 62%. The following day F_v/F_m decreased to 47% and after recovery increased to 58%. A slightly greater decrease occurred during the two following days. After recovery on the last day a level of 51% was reached. *G. antarcticus* exhibited the strongest inhibition of photosynthetic efficiency on the first day of treatment (Fig. 8C). After the first exposure F_v/F_m decreased to 13% and recovered to 37% before the next exposure. As in *A. arcta*, *G. antarcticus* showed nearly the same course of inhibition and recovery of photosynthesis during the following days.

Figure 9 shows that the changes in photosynthetic capacity (P_{max}) differed strongly among the three species. In *Acrosiphonia arcta* P_{max} was depressed to 40% by the end of the first exposure and then increased to 100% on the fifth day. P_{max} values during UV-irradiation on the second, third and fourth days were even higher than the initial values measured at the beginning of each day. On the last day P_{max} changed only slightly during the course of the day (Fig. 9A). In *Desmarestia anceps* P_{max} values decreased slowly during the whole time of treatment until they finally reached 50%. Again,

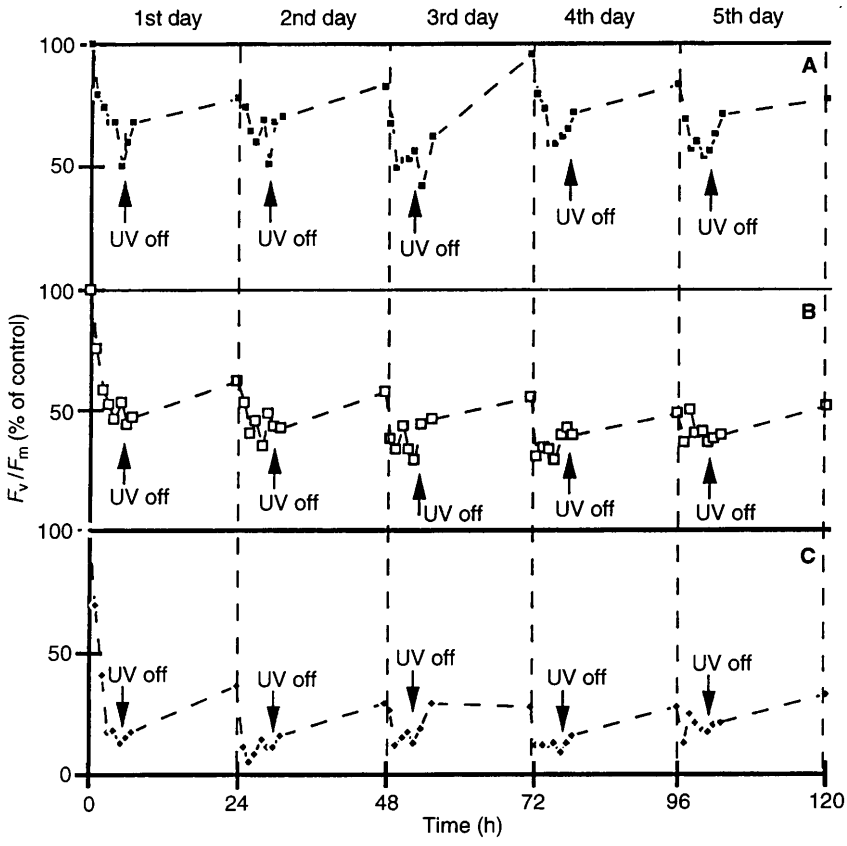

Fig. 8 *Acrosiphonia arcta* (**A**), *Desmarestia anceps* (**B**), *Gymnogongrus antarcticus* (**C**). Changes in F_v/F_m during and after a 5 h exposure to UV per day monitored for a period of 5 d; SD $\leq$ 5.8%. For further information see Table 2, Setup III

during UV-irradiation P_{max} was higher than at the beginning of each day (Fig. 9B). In *Gymnogongrus antarcticus* 5 h of UV on the first day caused a decrease of about 74%. During the whole time of treatment P_{max} did not change again significantly (Fig. 9C).

At the end of the five days all samples were transferred to standard culture conditions. *Desmarestia anceps* and *Gymnogongrus antarcticus* did not recover from the UV-treatment, the plants bleached and died, while *Acrosiphonia arcta* grew normally again.

Discussion

UV-effects on photosynthesis

Our results show that UV-radiation has the potential to impact the vertical zonation pattern through its differential effects on photosynthesis of Antarctic macroalgae. Previous studies have shown a dose-dependence of UV-induced changes in fluorescence-signals and oxygen-evolution in marine algae and seagrasses (Larkum and Wood 1993; Clendennen et al. 1996; Dawson and Dennison 1996). It is assumed that modification of the binding proteins (D_1/D_2) of the primary and secondary plastoquinone of PS II is induced by UV-radiation as a primary effect followed by a functional blocking of the primary acceptor (Renger et al. 1986).

The first experiment shows that *Enteromorpha bulbosa* and *Acrosiphonia arcta* are least sensitive. P_{max} does not decrease in either species due to UV-exposure, indicating that the PS II reaction centre (e.g. D_1-protein) is not affected. Photosynthetic efficiency (F_v/F_m) is slightly reduced but recovers completely within 24 h. Lower F_v/F_m values may indicate that excess energy is dissipated as heat in the antenna complex, resulting in a decreased quantum yield (Krause and Weis 1991). A fast recovery of photosynthetic efficiency without any change in photosynthetic capacity after exposure to high light stress has previously been defined as dynamic photoinhibition (Osmond 1994). The studied brown algal species are less tolerant to UV than the green algae, as indicated by the lower F_v/F_m values. In addition *Desmarestia antarctica* and *D. anceps* exhibit a decrease in P_{max}, which is reversible within 24 h. Reduced photosynthetic capacity is probably caused by a degradation of the D_1-protein in PS II (Mattoo et al. 1984; Ohad et al. 1984; Krause 1988).

In all studied red algal species both photosynthetic efficiency and capacity are reduced after UV-exposure. In *Iridaea cordata* and *Gymnogongrus antarcticus*, P_{max} values recover to the control values within 24 h but photosynthetic efficiency requires 48 h for almost complete recovery. Although reduced photosynthetic performance is based on reversible effects, the long time period required for complete recovery shows that both species are unable to protect photosynthesis sufficiently by means of dynamic photoinhibition (Osmond 1994). Damage to the photosynthetic apparatus may require a longer time for repair. In *Phycodrys austrogeorgica* and

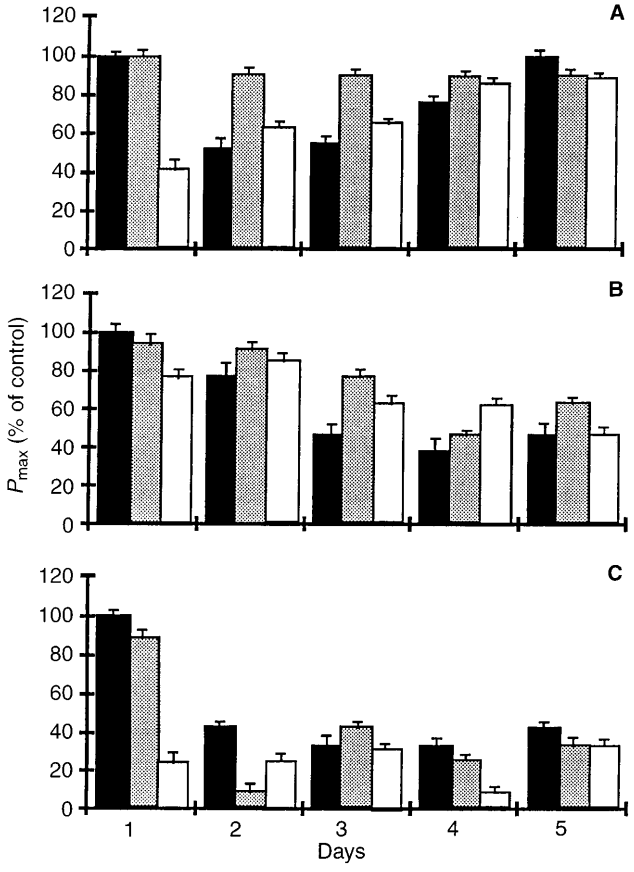

Fig. 9 *Acrosiphonia arcta* (**A**), *Desmarestia anceps* (**B**), *Gymnogongrus antarcticus* (**C**). Changes in P_{max} due to 5 h exposure to UV per day monitored for a period of 5 d. Photosynthetic capacity was determined before the start of exposure (*filled bars*), after 1 h of exposure (*shaded bars*) and at the end (5 h) of exposure (*open bars*). Exposure each day was followed by 19 h of recovery in dim white light. For further information see Table 2, Setup III

Delesseria lancifolia, UV-irradiation affects photosynthesis so strongly that photosynthetic efficiency and capacity was nearly zero and recovered to only 50% within 48 h in dim light. In addition, recovery of photosynthetic capacity was slower than that of efficiency, indicating photodamage to PS II (Aro et al. 1993).

Generally, increasing UV-dose causes a further decrease of the P_{max} values (Fig. 7). In *Acrosiphonia arcta* this is reversible within 20 h, indicating the involvement of reversible inactivation rather than damage to the reaction centre. However, as the F_v/F_m values do not fully recover within 70 h, damage to the antenna complex is more likely (see also Hanelt 1996). *Delesseria lancifolia* does not tolerate 5 h of exposure to the high UV-radiation conditions. Photosynthetic capacity is fully depressed, and even after 70 h in dim light no recovery occurs. Thus, a critical component of the photosynthetic apparatus might be completely destroyed (Andersson et al. 1992).

Restoration of high P_{max} values within the UV–light/dark cycle, as in *Acrosiphonia arcta,* shows the ability to acclimate to the UV-radiation (Fig. 9). In contrast, *Desmarestia anceps* and *Gymnogongrus antarcticus* do not show this capability. UV-induced bleaching of photosynthetic pigments, as observed in several specimens, has previously been described (El-Sayed et al. 1990; Strid et al. 1990; Holm-Hansen et al. 1993). In *Cryptomonas maculata*, Tevini (1994) found that accessory bili-proteins bleach first, followed by a degradation of carotenoids and finally of the chlorophylls.

The differences in UV-tolerance of the studied species are genetically based. Due to the cultivation of sporophytes under low-light conditions and UV-exclusion no acclimation to UV-radiation had occurred prior to the experiments. However, there is evidence that under natural conditions UV-radiation and PAR act synergistically (Neale et al. 1993; Hanelt et al. 1997b). It has been shown that the ratio between PAR and UVR in the spectra plays an important role in the inhibition of photosynthesis (Cullen et al. 1992). Plants raised under low-light conditions tend to show a greater sensitivity to UV-radiation (Teramura 1986). This is important to note when applying the results obtained by laboratory studies to field conditions. Plants could also be acclimated to low-light conditions during long-term cultivation. For this, background PAR during UV-exposure has to be adjusted to the irradiance of the culture to exclude PAR-induced photoinhibition.

UV-sensitivity and depth-zonation

Ecophysiological studies of the influence of different abiotic factors show a general correlation between stress tolerance and vertical distribution of marine macroalgae (Levitt 1980; Davison and Pearson 1996; Hanelt 1998). Specific UV-sensitivity of photosynthesis in Antarctic macroalgae may also be an important factor determining the upper distribution limit of individual species on the shore. Figure 10 shows the vertical distribution of the studied species on the Antarctic Peninsula. The two green algae *Enteromorpha bulbosa* and *Acrosiphonia arcta* occur in the middle and lower eulittoral (Lamb and Zimmermann 1977). These two species show nearly no negative UV-effect on photosynthesis. However, despite their great tolerance these algae are able to acclimate to UV-exposure within hours or days (see above). The habitat of the red alga *Iridaea cordata* is the upper sublittoral zone (Klöser et al. 1996) down to 20 m depth, and it also can occur in tide-pools in the eulittoral zone (Lamb and Zimmermann 1977). This plant exhibits a UV-tolerance comparable to *E. bulbosa* and *A. arcta*. The brown algae *Desmarestia antarctica* and *D. anceps* are described for the middle sublittoral zone (Klöser et al. 1996). However, *D. anceps* grows mostly in greater depths and occurs only occasionally in depths shallower than 17 m. In these depths biologically relevant doses of UV-radiation occur only in very transparent waters, under clear skies and at a high solar declination (Karentz 1989). This might explain why *D. anceps* was more sensitive to UV-radiation than *D. antarctica*.

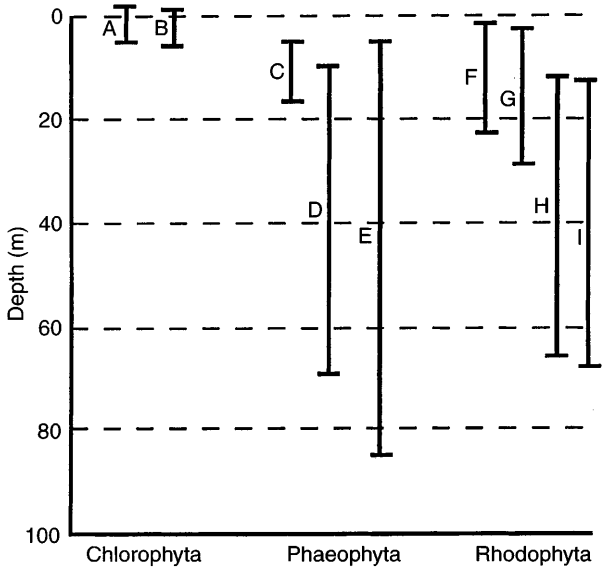

Fig. 10 Depth-zonation of the studied species at the Antarctic Peninsula (after Delaca and Lipps 1976; Lamb and Zimmermann 1977; Zielinski 1990; Klöser et al. 1996) (**A:** *Enteromorpha bulbosa*; **B:** *Acrosiphonia arcta*; **C:** *Desmarestia antarctica*; **D:** *Desmarestia anceps*; **E:** *Himantothallus grandifolius*; **F:** *Iridaea cordata*; **G:** *Gymnogongrus antarcticus*; **H:** *Delesseria lancifolia*; **I:** *Phycodrys austrogeorgica*)

Gymnogongrus antarcticus occurs from the upper sublittoral zone down to 20 m (Klöser et al. 1996), i.e. the upper distribution limit is similar to that of the brown algae *D. anceps* and *Himantothallus grandifolius*. These three species show a similar inhibition rate of photosynthesis. *H. grandifolius* was found at 5 m (Lamb and Zimmermann 1977) with the lowest depth at 90 m (Zielinski 1990). This zonation pattern is in line with its high sensitivity. The red algae *Phycodrys austrogeorgica* and *Delesseria lancifolia* are described for the middle sublittoral zone (Delaca and Lipps 1976; Zielinski 1990; Klöser et al. 1996), but they grow under canopy plants such as *D. anceps* and *H. grandifolius*. This explains their extreme sensitivity to UV-radiation. These plants may lack all protecting mechanisms against excessive radiation, because recovery from UV-exposure is poor in both species. In the field protective mechanisms against UV-radiation might not be necessary because they live in the shade of the canopy algae.

Larkum and Wood (1993) have stressed the correlation between UV-tolerance and the depth-zonation of marine macroalgae. For the vertical distribution of tropical seagrasses UV-radiation is also an important factor (Dawson and Dennison 1996). Maegawa et al. (1993) consider solar UV-radiation as one of the most important factors determining the vertical distribution of red algae in coastal ecosystems. Dring et al. (1996) showed that sensitivity to UV in red algae growing around the island of Helgoland (Germany) varies with species and depth of collection. Our previous investigations in macroalgae on the photoinhibition induced by high levels of PAR also exhibit a correlation between depth-zonation and the ability for dynamic photoinhibition (Hanelt 1992, 1998; Hanelt et al. 1993, 1994a, b, 1997a).

Macroalgae are important organisms for coastal ecosystems. As primary producers they represent the base of the food web for herbi- and detrivores (Dunton and Schell 1987), they serve as shelter for juvenile animals such as fishes and crustaceans and as habitat for many epizootic and epiphytic organisms (Iken 1996; Klöser et al. 1996). Field measurements must be conducted to investigate the impact of enhanced UV-radiation on polar coastal ecosystems. Macroalgae from the intertidal zone may be able to protect themselves against UV-radiation by synthesising and accumulating screening substances (e.g. mycosporine-like amino acids, MAA) (Sivalingam et al. 1976; Larkum and Wood 1993; Helbling et al. 1996; Karsten et al. 1998). UV-tolerance of polar macroalgae must depend on the effectiveness of protection mechanisms (MAA-synthesis, dynamic photoinhibition) and repair mechanisms (e.g. photoreactivation). Until now no data have been available on the capacity and the time scales required for development of acclimation strategies. Future studies may show whether enhanced UV-B-radiation lead to a shift in the vertical zonation patterns and species composition.

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