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Interactive effects of ultraviolet radiation and salinity on the ecophysiology of two Arctic red algae from shallow waters

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Abstract

In a comparative ecophysiological study the abundant red macroalgae *Devaleraea ramentacea* (L.) Guiry and *Palmaria palmata* (L.) O. Kuntze from shallow waters of the Arctic Kongsfjord (Spitsbergen) were exposed to hyposaline and hypersaline media in combination with and without UV-radition to evaluate the interactive effects of both environmental parameters on optimum quantum yield of photosynthesis, as well as on the physiological capability to synthesise and accumulate photoprotective mycosporine-like amino acids (MAAs). While *D. ramentacea* exhibited euryhaline features and acclimated well to the UV radiation applied, *P. palmata* can be characterised as stenohaline plant because of its high mortality already under mild hyposaline conditions (15 PSU). In addition, the latter species showed a limited ability to acclimate to changing PAR/UV radiation pointing to a relatively low physiological plasticity. Both species synthesised and accumulated MAAs after UV treatment. However, only in *D. ramentacea* a correlation between increasing MAA concentration and decreasing photosynthetic sensitivity under UV was observed. All ecophysiological data well correlate with field observations where both red algal species co-exist in the same shallow water habitat of the Kongsfjord. However, while *P. palmata* becomes more often greenish, sometimes slightly bleached over the summer months, *D. ramentacea* appears much more healthy and hence unstressed under the prevailing environmental factors.

Key words

Arctic, *Devaleraea ramentacea, Palmaria palmata*, MAAs, mycosporine-like amino acids, photoinhibition, photosynthesis

Introduction

The Arctic Kongsfjord on Spitsbergen is a marine coastal ecosystem which has intensively been studied over the last years as model for global change (Hanelt *et al.*, 2001 and references therein). A typical feature of the fjord is a well structured phytobenthic community down to depth of almost 40 m (Hop *et al.*, 2002) that plays an important role in primary production being a food source for herbivores and detrivores, as well as nursery area and habitat for fish and invertebrates (Lippert *et al.*, 2001). Marine macroalgae of such high latitudes are exposed to seasonally fluctuating environmental factors such as solar radiation and temperature, as well as to long periods of ice cover (Hanelt *et al.*, 2001; Hop *et al.*, 2002).

Compared to the „ozone hole" over Antarctica which is known since the 70ies (Smith *et al.*, 1992), the increase in ozone depletion over the Arctic represents a more recent phenomenon (Wängberg *et al.*, 1996; Rex *et al.*, 2000; Hanelt *et al.*, 2001). As a consequence of ozone springtime reduction in the polar regions UV-radiation particularly of the UVB-waveband (280-320 nm) markedly rises. Although the biological consequences of changes towards higher doses of UV-radiation in marine ecosystems are not fully understood, many phototrophic organisms living in the intertidal as well as in the upper subtidal zone of the coasts are strongly affected (Franklin & Forster, 1997).

The macroalgal species *Devaleraea ramentacea* (L.) Guiry and *Palmaria palmata* (L.) O. Kuntze are the most abundant Rhodophyta in the upper sublittoral of the Kongsfjord. While the first species represents one of the few endemics of the Arctic region, the latter one occurs from temperate to cold waters of the Atlantic ocean, and exhibits on Spitsbergen its northern distribution limit. In spring/summer both organisms are often exposed to high solar radiation, and hence their photophysiology and protecting strategies avoiding or counteracting UV-induced damage has been studied in great detail (Hanelt *et al.*, 1997; Aguilera *et al.*, 1999, 2002; Karsten & Wiencke, 1999; Karsten *et al.*, 1999, 2001). From these studies it could be concluded that *D. ramentacea* and *P. palmata* are capable to physiologically acclimate to diurnally changing solar radiation due to dynamic photoinhibition, i.e. the up- and down-regulation of photosynthesis in response to the respective prevailing low and high visible light, as well as UV conditions (Hanelt, 1998). In addition, to prevent UV-photodamage these macroalgal species are biochemically capable to synthesise and accumulate UV-absorbing substances, the so-called mycosporine-like amino acids

(MAAs) (Dunlap & Shick, 1998; Karsten & Wiencke, 1999; Karsten *et al.*, 1999). As passive sunscreens MAAs preferentially absorb UV photons in the spectral range of 310-360 nm followed by dissipating the absorbed radiation energy in form of harmless heat and fluorescence without generating photochemical reactions (Bandaranayake, 1998; Cockell & Knowland, 1999), and thereby protecting, at least partially, photosynthesis and growth of phototrophic organisms (Garcia-Pichel *et al.*, 1993; Neale *et al.*, 1998).

The motivation for the present study was the field observation that in shallow waters of the Kongsfjord during the summer season thalli of *P. palmata* often looked rather greenish, sometimes slightly bleached compared to the mainly, although not always red-coloured *D. ramentacea* from similar locations. Although intuitively radiation stress seemed to be the responsible factor, earlier results indicated a relative high photosynthetic tolerance of *P. palmata* under increasing natural PAR and UV-doses (Hanelt *et al.*, 1997; Karsten *et al.*, 2001). Since the large discharge of melting water into the fjord can locally and temporary decrease the seawater salinity down to 23 PSU (Hanelt *et al.*, 2001) and because of the fact that subtidal red algae are generally stenohaline (Kain & Norton, 1990), we assumed that this abiotic factor may act as additional stressor on the macroalgal physiology. Therefore, in a comparative study we exposed *D. ramentacea* and *P. palmata* under controlled conditions on Spitsbergen to hyposaline and hypersaline media in combination with and without UV-radition to evaluate the interactive effects of both environmental parameters on photosynthetic performance, as well as on the ability to synthesise and accumulate MAAs.

Materials and methods

Algal material and study site

The red macroalgae *Devaleraea ramentacea* (L.) Guiry and *Palmaria palmata* (L.) O.Kuntze preferentially grow in shallow waters at the study site in the Kongsfjord (Ny-Ålesund, Spitsbergen, 78°55.5´ N; 11°56.0´ E). Both species are typically attached to coarse gravel and single rocks on sandy sediments in the fjord or occur as epiphytes on rhizoids of kelps such as *Laminaria saccharina* (L.) Lamour.. In the Kongsfjord *D. ramentacea* typically grows in depths from 1 m down to 8 m, while *P. palmata* is found slightly deeper from 2 m to 10 m. All algal samples were collected from healthy

looking, dark red plants at 3-5 m by SCUBA diving and kept in black bags to avoid exposure to higher solar irradiances prior laboratory experiments.

Radiation and salinity experiments

Thalli of both species were cut at 3-4 cm from the apical part using a razor blade to get almost homogeneous pieces of the same age class for the exposure experiments. All plantlets were kept 24-36 h in running seawater at 3-5°C and dim light conditions (< 5 μmol PAR $m^{-2}s^{-1}$) to minimize potential wound healing responses. Afterwards algae were treated with hypo- and hypersaline media in combination with PAR and PAR+UV exposure over a period of 4 days. Hypersaline media of 50 PSU were prepared by freezing-out fresh water from fully marine fjord water. The dilution of fjord water with MilliQ water resulted in a hyposaline solution of 15 PSU. Salinity was checked using a refractometer. All salinity treatments were carried out in 300 ml glass containers. These vessels were irradiated from the top with 30 μmol PAR $m^{-2}s^{-1}$, 6.7 W m^{-2} UV-A (320-400 nm) and 0.25 W m^{-2} UV-B (280-320 nm). As radiation source a combination of Philips daylight fluorescence tubes and Q-Panel UV-A-340 fluorescence tubes (Q-Panel Company, Cleveland, Ohio, USA) was used. Radiation measurements were carried out with a Li-Cor LI-190-SB cosine corrected sensor connected to a Li-Cor LI-1000 datalogger (Lambda Instruments, Lincoln, Neb., USA) for PAR, and with a RM-21 broad-band UV radiometer (Dr. Gröbel, Ettlingen, Germany). While half of the containers (15, 34 and 50 PSU) were exposed to the full radiation spectrum, the other half was kept under a specific filter foil to cut-off UV-A+B (PAR treatment) (400 nm cut-off; Folex PR, Folex, Dreieich, Germany). All thalli were exposed to 24 h PAR per day, while supplemented UV-radiation was applied for only 10 h per day resulting in a 10 h UV treatment interval followed by a 14 h recovery period. Temperature was kept constant at approximately 5°C. As physiological fitness parameter photosynthetic performance was measured always 8 h after on-set, as well as 7 h after off-set UV-radiation. After 1, 2 and 4 days treatment with the different salinity and radiation combinations samples for MAA analysis were taken.

Photosynthesis

After sampling algal thalli were kept for 5-10 minutes inside a light-tight box. Afterwards photosynthetic activity was determined in this container by measuring

variable chlorophyll-fluorescence of photosystem II using a portable pulse amplitude modulated fluorometer (Diving-PAM, Walz, Effeltrich, Germany). The main application of the Diving-PAM is the determination of effective PS II quantum yield by the saturation pulse method ($\Delta F/F_m'$ = effective quantum yield of an irradiated sample, $\Delta F = F_m' - F_t$, Genty *et al.*, 1989). However, if determined in the dark, as undertaken in the present study, the effective quantum yield equals the optimum quantum yield which was calculated as the ratio of variable to maximum fluorescence F_v/F_m. Minimal fluorescence (Fo) was measured with a pulsed measuring beam (approximately 0.3 μmol photons m^{-2} s^{-1}, 650 nm), followed by short pulses of saturating white light (0.4-0.8 s, 1000-5000 μmol photons m^{-2} s^{-1}) to record Fm ($F_v = F_m - F_o$) (Hanelt, 1998). F_v/F_m values of both red algal species acclimated for 24-36 h to the dim light conditions in the laboratory were characteristic for photosynthetically non-inhibited plants and consequently set to 100% (=control). While *D. ramentacea* exhibited a maximum F_v/F_m value of 0.65±0.02 (n=6), *P. palmata* showed F_v/F_m value of 0.59±0.03 (n=9). All data recorded are expressed in relation to the respective value.

MAA extraction and analysis

After sampling, plants were oven-dried at 50°C, and then stored in sealed plastic bags under cool, dry and dark conditions until analysis. Samples (4-5 replicates) of about 10-20 mg dry weight (DW) were extracted for 1.5-2 h in screw-capped centrifuge vials filled with 1 mL 25% aqueous methanol (v/v) and incubated in a waterbath at 45°C. After centrifugation at 5000 g for 5 min, 700 μL of the supernatants were evaporated to dryness under vacuum (Speed Vac Concentrator SVC 100H). Dried extracts were re-dissolved in 700 μL 100% methanol and vortexed for 30 s. After passing through a 0.2 μm membrane filter, samples were analysed with a Waters HPLC system according to the method of Karsten *et al.* (1998a), modified as follows. MAAs were separated on a stainless-steel Phenomenex Sphereclone RP-8 column (5 μm, 250 x 4 mm I.D.) protected with a RP-8 guard cartridge (20 x 4 mm I.D.). The mobile phase was 5% aqueous methanol (v/v) plus 0.1% acetic acid (v/v) in water, run isocratically at a flow rate of 0.7 ml min^{-1}. MAAs were detected online with a Waters photodiode array detector at 330 nm, and absorption spectra (290-400 nm) were recorded each second directly on the HPLC-separated peaks. Identification was done by spectra, retention time and by co-chromatography with standards extracted from the marine red

macroalgae *Chondrus crispus* Stackhouse (Karsten *et al.*, 1998) and *Porphyra umbilicalis* (L.) Kützing, as well as from ocular lenses of the coral trout *Plectropomus leopardus* (Lacepède, 1802), kindly sent by Dr. David Bellwood, James Cook University, Townsville, Australia. Quantification was made using the molar extinction coefficients given in Karsten *et al.* (1998b).

Statistics

Mean values and standard deviation per treatment were calculated. Statistical significance of differences in photoinhibitory response in plants kept under different salinities and radiation scenarios was tested by one-way analysis of variance (ANOVA) followed by a multi-range test using Fisher's protected least significant difference (LSD) according to Sokal & Rohlf (1981). Calculations were done using the program InStat (GraphPad, San Diego, USA).

Results

During the course of the experiment the optimum quantum yield (F_v/F_m) of the control thalli of *Devaleraea ramentacea* (34 PSU, PAR) remained always high exhibiting values between 86 and 98% of the maximum, i.e. of non-inhibited plants (Fig. 1). Algae treated with 15 PSU showed a slight, but significant decrease in F_v/F_m ($p<0.01$) down to 76% of the control over the first 39 h, followed by some recovery resulting in 87% of non-treated samples at the end of the experiment. In contrast, in plants kept at 50 PSU F_v/F_m much stronger and continuously declined to 58% of the optimum after 39 h ($p>0.01$) (Fig. 1). Afterwards optimum quantum yield gradually increased up to 76% of the control.

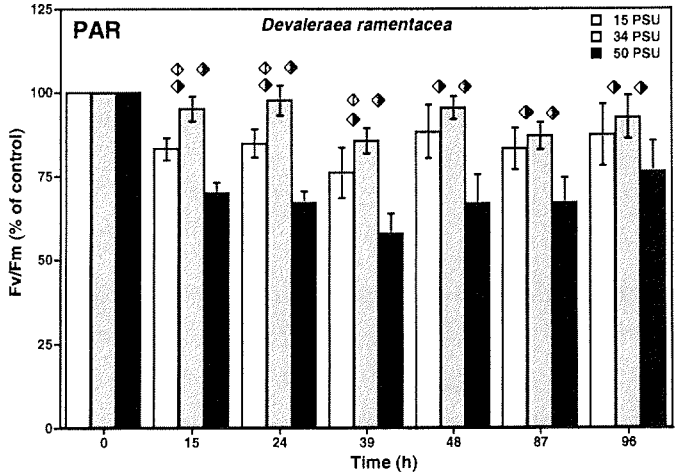

Figure 1: Changes in photosynthetic optimum quantum yield (F_v/F_m) of *Devaleraea ramentacea* under various salinity conditions (15, 34, 50 PSU) and visible light (PAR) over the course of 96 h. F_v/F_m of non-inhibited plants was determined as 0.65±0.02 and standardized to 100%. Given are the mean values±SD (n=10). Significant differences ($P < 0.01$) among samples under various salinity treatments are marked with squares: 15 PSU versus 34 PSU (white–pointed triangle), 15 PSU versus 50 PSU (white-black triangle), 34 PSU versus 50 PSU (pointed-black triangle).

F_v/F_m of *D. ramentacea* treated with salinity plus UV radiation was generally much more affected compared to the salinity only experiment (Fig. 2). Thalli kept at 15 and 34 PSU showed at the end of the first two UV exposure intervals a decline in optimum quantum yield down to 50-60% of the control. However, during each recovery period F_v/F_m increased to 75-80% of the maximum. In contrast, under hypersaline conditions photosynthesis was stronger inhibited under UV (45-50% of control; $p<0.01$) and did not show marked recovery under PAR conditions within 48 h ($p<0.01$). However, after the last interval of the UV treatment at 50 PSU F_v/F_m in *D. ramentacea* was much less affected resulting in 67% of the maximum. The final measurement of recovery at the end of the experiment clearly indicated for all salinities identical optimum quantum yields >81% of the control (Fig. 2).

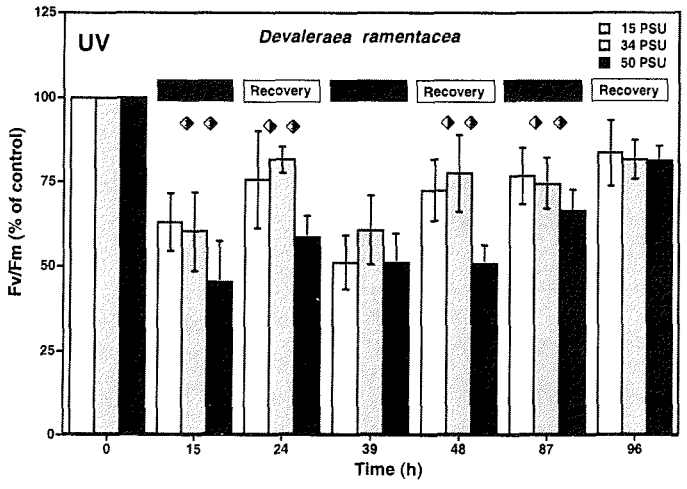

Figure 2: Changes in photosynthetic optimum quantum yield (F_v/F_m) of *Devaleraea ramentacea* under various salinity conditions (15, 34, 50 PSU) and ultraviolet radiation (UV) over the course of 96 h. F_v/F_m of non-inhibited plants was determined as 0.65±0.02 and standardized to 100%. Given are the mean values±SD (n=10). Significant differences ($P < 0.01$) among samples under various salinity treatments are marked with squares: 15 PSU versus 34 PSU (white–pointed triangle), 15 PSU versus 50 PSU (white-black triangle), 34 PSU versus 50 PSU (pointed-black triangle). The black bars indicate the 10 h UV treatment interval followed by the 14 h recovery period.

The proportional degree of photoinhibition (F_v/F_m) in *D. ramentacea* due to salinity and UV treatment is shown in Fig. 3. Under hyposaline conditions over the first 48 h 15 PSU and UV led to nearly equal photoinhibitory responses (Fig. 3A). However, after 87 and 96 h exposure, the UV effect strongly decreased resulting in only 23-28% of the total decline in optimum quantum yield. In contrast, under hypersaline conditions the UV effect on F_v/F_m in *D. ramentacea* was generally much less pronounced and continuously decreased over the course of the experiment (Fig. 3B). After 87 and 96 h treatment only the salinity factor was responsible for photoinhibition.

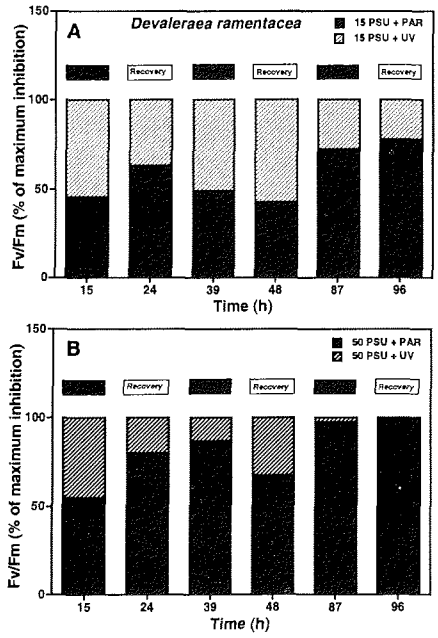

Figure 3: The effect of salinity and UV treatment on the maximum decrease in the photosynthetic optimum quantum yield (F_v/F_m) of *Devaleraea ramentacea* over the course of 96 h. From the mean value data presented in figures 1 and 2 the proportional degree of photoinhibition due to both stress factors was calculated and expressed as percentage of maximum photoinhibition. A: 15 PSU ± UV treatment; B: 50 PSU ± UV treatment.

Seven different mycosporine-like amino acids (MAAs) were detected in *D. ramentacea*, namely mycosporine-glycine, shinorine, porphyra-334, palythine, asterina-330, palythinol and palythene (data not shown). Plants at the beginning of the experiment contained total MAAs of 1.2 mg g^{-1} dry weight (DW) (Fig. 4). After 1 day treatment with salinity and UV both 15 PSU samples showed a decrease in total MAAs (0.8 mg g^{-1} DW) and both 50 PSU samples an increase in total MAAs (1.5-1.7 mg g^{-1} DW). MAAs in plants kept at 34 PSU with and without UV were unaffected. While after 2 days exposure thalli at all 15 PSU and 34 PSU conditions showed unchanged total MAA concentrations, algae at both 50 PSU conditions exhibited a decrease in total MAAs (1.0-1.2 mg g^{-1} DW). A strong UV-induced increase in total MAAs was observed at the end of the experiment. Under all salinities UV-exposure led to almost doubling of the MAA contents. However, while at 15 PSU and 50 PSU 1.5 mg and 1.7 mg MAAs g^{-1} DW, respectively, were measured in *D. ramentacea*, at 34 PSU the highest total MAA concentration of 2.2 mg g^{-1} DW was determined (Fig. 4).

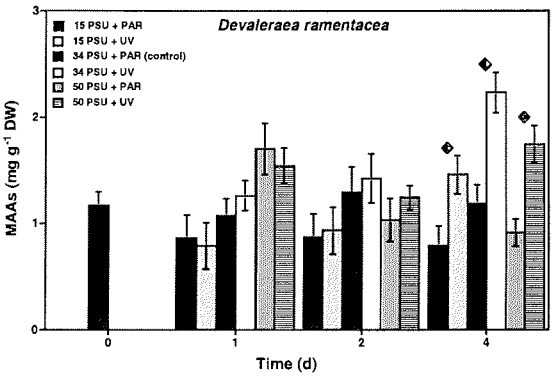

Figure 4: The interactive effects of salinity and UV treatment on the total intracellular mycosporine-like amino acid contents (MAAs) in *Devaleraea ramentacea* over the course of 96 h. Given are the mean values ± SD (n=4-5).

While in *D. ramentacea* F_v/F_m of the control conditions (34 PSU, PAR) remained unchanged over the course of the experiment, in *P. palmata* a small, but continuous decline of this parameter was observed resulting in 75-80% of the maximum (Fig. 5). Compared to *D. ramentacea*, the optimum quantum yield of *P. palmata* was much stronger affected by salinity, particularly at 50 PSU over the first 48 h ($p<0.01$) (Fig. 5). After that period F_v/F_m in algae kept at 15 PSU also strongly declined resulting in fully bleached and hence dead thalli at the end of the experiment. While after 96 h the 34 PSU samples exhibited 78%, the 50 PSU plants showed only 48% of the optimum photosynthesis (Fig. 5).

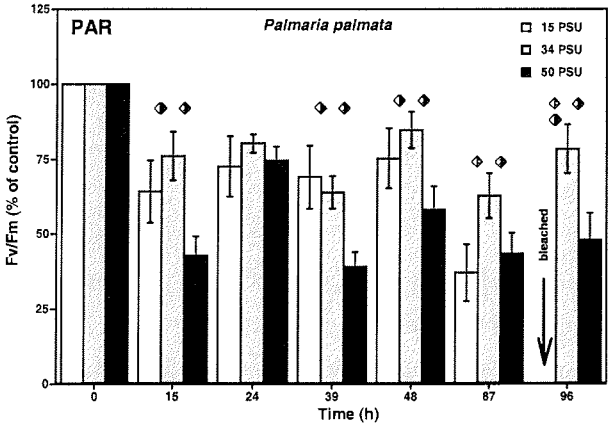

Figure 5: Changes in photosynthetic optimum quantum yield (F_v/F_m) of *Palmaria palmata* under various salinity conditions (15, 34, 50 PSU) and visible light (PAR) over the course of 96 h. F_v/F_m of non-inhibited plants was determined as 0.59±0.03 and standardized to 100%. Given are the mean values±SD (n=10). Significant differences ($P < 0.01$) among samples under various salinity treatments are marked with squares: 15 PSU versus 34 PSU (white-pointed triangle), 15 PSU versus 50 PSU (white-black triangle), 34 PSU versus 50 PSU (pointed-black triangle). Arrow indicates completely bleached (dead) thalli at 15 PSU.

Under the salinity plus UV treatments, F_v/F_m in *P. palmata* decreased even more indicating strong interactive effects of both abiotic factors (Fig. 6). While the 34 PSU samples showed during on-set of UV radiation always declining optimum quantum yields (41-54% of the control), after off-set the UV source marked recovery occured (67-84% of the control). Algae incubated at 15 PSU plus UV also died after 87 h treatment as indicated by completely bleached tissue (Fig. 6). Thalli of *P. palmata* at 50 PSU plus UV exhibited over the course of the experiment a similar photosynthetic response compared with plants at 50 PSU without UV.

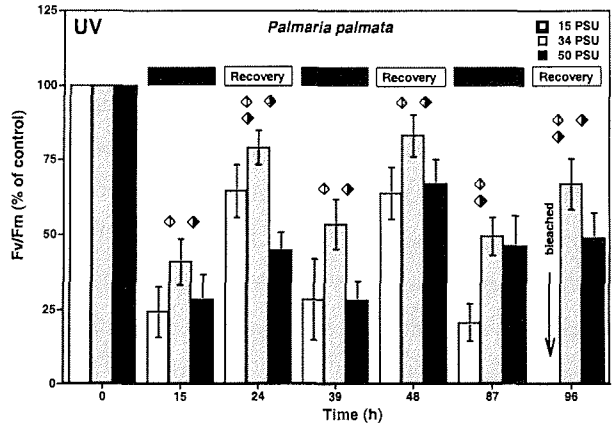

Figure 6: Changes in photosynthetic optimum quantum yield (F_v/F_m) of *Palmaria palmata* under various salinity conditions (15, 34, 50 PSU) and ultraviolet radiation (UV) over the course of 96 h. F_v/F_m of non-inhibited plants was determined as 0.59±0.03 and standardized to 100%. Given are the mean values±SD (n=10). Significant differences ($P < 0.01$) among samples under various salinity treatments are marked with squares: 15 PSU versus 34 PSU (white–pointed triangle), 15 PSU versus 50 PSU (white-black triangle), 34 PSU versus 50 PSU (pointed-black triangle). Arrow indicates completely bleached (dead) thalli at 15 PSU. The black bars indicate the 10 h UV treatment interval followed by the 14 h recovery period.

As in *D. ramentacea*, the proportional degree of photoinhibition (F_v/F_m) in *P. palmata* due to both abiotic factors was in average mainly because of salinity treatment (Fig. 7). Although at the beginning of the experiments UV radiation also led to some decrease in optimum quantum yield, this effect got weaker after 48 h.

In *P. palmata* six different MAAs were detected, namely shinorine, porphyra-334, palythine, asterina-330, palythinol and palythene (data not shown). Plants at 34 PSU plus UV showed already after 24 h a small, but significant increase in total MAA concentration ($p<0.01$) (Fig. 8). These samples continuously accumulated MAAs 2-fold over the course of the experiment. Although under hyposaline conditions total MAAs decreased at the beginning, after 48 h a significant UV-induced formation could be observed ($p<0.01$) followed by bleaching of the tissue. Under hypersaline treatment thalli of *P. palmata* exhibited after 48 h a strong accumulation of MAAs due to UV ($p<0.01$) and after 96 h a decline from 2.4 to 1.9 mg MAAs g^{-1} DW (Fig. 8).

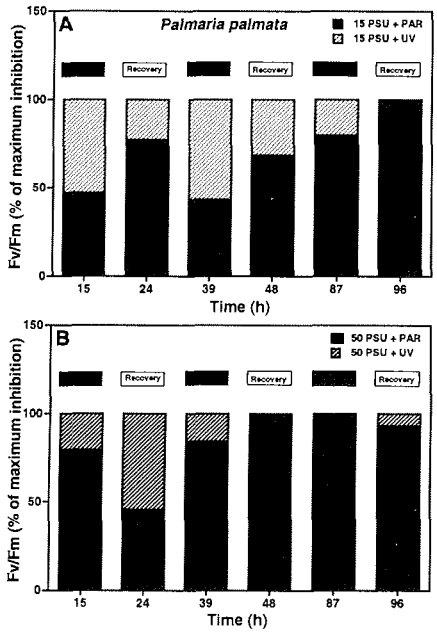

Figure 7: The effect of salinity and UV treatment on the maximum decrease in the photosynthetic optimum quantum yield (F_v/F_m) of *Palmaria palmata* over the course of 96 h. From the mean value data presented in figures 1 and 2 the proportional degree of photoinhibition due to both stress factors was calculated and expressed as percentage of maximum photoinhibition. A: 15 PSU ± UV treatment; B: 50 PSU ± UV treatment.

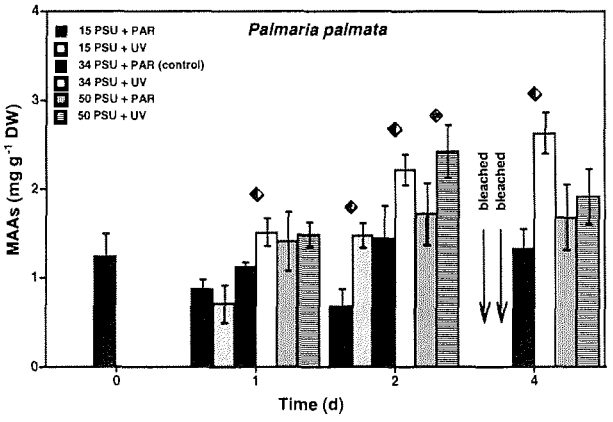

Figure 8: The interactive effects of salinity and UV treatment on the total intracellular mycosporine-like amino acid contents (MAAs) in *Palmaria palmata* over the course of 96 h. Given are the mean values ± SD (n=4-5). Arrows indicate completely bleached (dead) thalli at 15 PSU.

Discussion

On Spitsbergen solar radiation as primary environmental factor for photosynthesis and productivity of macroalgae is not only seasonally fluctuating, but also diurnally extremely variable at the earth's surface due to rapidly changing weather conditions (Hanelt *et al.,* 2001). In addition, during summer the underwater light climate of the Kongsfjord is further affected by calving glaciers and strong melting water influx resulting in increasing turbidity due to suspended particles and hence in a strong decrease of the water column transmittance (Bischof *et al.,* 1998). The irradiance *Devaleraea ramentacea* and *Palmaria palmata* were exposed to in the laboratory was much lower compared to nature. While in Arctic summer typical insolation at the earth's surface may reach 1300 μmol m^{-2} s^{-1} PAR, 19 W m^{-2} UV-A and 1.1 W m^{-2} UV-B (Bischof *et al.,* 1998), we used only 30 μmol m^{-2} s^{-1} PAR, 6.7 W m^{-2} UV-A and 0.25 W m^{-2} UV-B to simulate realistic underwater values. In the water column maximum transmittance for PAR and UV-B as expressed by the 1% depth ranges from 6.2 to 24.2 m and 3.4 to 9 m, respectively (Bischof *et al.,* 1998). Consequently, both red algal species may experience in their habitat the irradiances applied.

Macroalgae living under such fluctuating conditions need a broad physiological plasticity to acclimate to the wide range of incident solar radiation to receive on one hand side always sufficient energy for photosynthesis and on the other hand to avoid

photodamage. Shallow water and intertidal macroalgae are known to undergo dynamic photoinhibition when exposed to excessive sun light that typically occurs at midday (Häder & Figueroa, 1997; Hanelt, 1998). Dynamic photoinhibition is considered as photoprotective mechanism, which dissipates excessively absorbed energy as physiologically harmless thermal radiation (Osmond, 1994). Previous studies have shown that for the evaluation of PAR- and UV-induced inhibition of photosynthesis in macroalgae the *in vivo* chlorophyll fluorescence of photosystem II, as used in the present investigation, is a suitable method (Häder & Figueroa, 1997; Hanelt *et al.*, 1997; Hanelt, 1998; Bischof *et al.*, 1998). The optimum quantum yield (F_v/F_m) was demonstrated to be a sensitive parameter to evaluate the physiological status of the photosynthetic apparatus (Cordi *et al.*, 1997), and hence represents a measure for fitness.

The experimental set-up was designed to test the photosynthetic performance of the shallow-water species *D. ramentacea* and *P. palmata* in response to UV radiation and salinity. While in the first species the strongest photoinhibitory effect was measured under hypersaline conditions without UV (25% inhibition after 4 days), at 15 PSU only a small decrease in optimum quantum yield was observed. In strong contrast, *P. palmata* did not survive hyposaline treatment over the course of the experiment, and showed also at 50 PSU 50% inhibition in F_v/F_m. Consequently, while *D. ramentacea* can be characterised as euryhaline species, *P. palmata* exhibits rather stenohaline features. From an ecological standpoint stenohalinity with respect to growth is typical for sublittoral red algae compared to the broad salinity tolerance of intertidal species (Kain & Norton, 1990). In agreement with these authors it has to be mentioned that *P. palmata* has the main distribution in temperate/cold-temperate waters of the Northern Atlantic where it sublittorally grows in depths down to 20 m or protected as typical understorey plant of kelp forests (Irvine, 1983; Lüning, 1990). These habitats are characterised by rather stable salinity conditions which support the development of stenohaline organisms. Consequently, the strong inhibition of photosynthesis and high mortality of the Arctic isolate of *P. palmata* at 15 PSU can be explained by a limited physiological capacity to acclimate to external salinity fluctuations. In addition, the occurrence of this species at the Northern distribution limit on Spitsbergen which is characterised by extremely low water temperatures may contribute to the reduced photosynthetic tolerance. The primary metabolism of temperate/cold-temperate organisms growing under Arctic conditions is most probably slowed down according

the Q10-rule and therefore it is reasonable to assume that acclimation responses are affected as well. This hypothesis is supported by the fact that temperature optima for photosynthesis and growth are only significantly lower in endemic Antarctic macroalgae compared to Arctic and cold-temperate species that typically exhibit strong decline of both processes with decreasing temperatures (Healey, 1972; Wiencke *et al.*, 1993, 1994; Kirst & Wiencke, 1995). Consequently, while many Antarctic seaweeds seem to be relatively strongly adapted, Arctic and cold-temperate counterparts show a much weaker adaptation to low temperatures, and hence the general fitness may be species-specifically more or less affected. Although *P. palmata* is abundant in the Kongsfjord, the data presented in combination with the observation of rather greenish, sometimes slightly bleached thalli during summer in the field indicate stressed plants. However, interactive effects of salinity and temperature must still be experimentally evaluated.

Although salinities in the upper layers of the water column does generally not decline to values lower than 23 PSU (Hanelt *et al.*, 2001), it should be mentioned that 15 PSU as tested in the present study represents a mild hyposaline stress for marine organisms. In contrast to *P. palmata* many other red macroalgae from intertidal as well as sublittoral habitats well or even preferentially grow and photosynthesise at this salinity (Bird *et al.*, 1979; Kirst, 1990; Mostaert *et al.*, 1995).

When UV-radiation was applied on top of the salinity treatment both species studied exhibited at the beginning similar photosynthetic responses, i.e. a decline of the optimum quantum yield after UV on-set followed by some degree of recovery after UV off-set. While UV-induced photoinhibition compared to the control was in *D. ramentacea* relatively small, *P. palmata* exhibited a much stronger response (Figs. 2, 6). In addition, the first species showed an increasing UV tolerance of photosynthesis over the course of the experiment, while the latter species seemed unable to photoacclimate. This confirms data of Hanelt (1998) who showed that photosynthesis of *P. palmata* collected along a depth profile in the Kongsfjord did not acclimate to the prevailing radiation gradient. Within other macroalgal species from the Arctic and Antarctica, the degree of photoinhibition is normally a function of the collecting depth, i.e. shallow-water isolates are more PAR/UV resistent than plants from deeper waters (Bischof *et al.*, 1998a, b). The difference in the acclimation potential of the photosynthetic performance between *D. ramentacea* and *P. palmata* under UV is reflected by the vertical distribution in the Kongsfjord, since the first species grows in shallower waters.

In addition, at more temperate locations *P. palmata* preferentially inhabits deeper waters than in the Arctic and hence the shallow water growth habit in the Kongsfjord appears unusual. Due to incomplete osmotic adjustment both algae may be more able to tolerate increase in UV radiation as compared to salinity change.

In recent studies, the photobiological function of MAAs as a cellular defense system against the harmful effects of UV-radiation on growth, photosynthesis and other processes has been reported for various marine phototrophic organisms (Garcia-Pichel *et al.,* 1993; Dunlap & Shick, 1998; Neale *et al.,* 1998). In a convincing bio-assay, Adams and Shick (1996) experimentally documented that UV-treated and subsequently fertilized sea urchin eggs typically show a UV-dose-dependent delay in the first cell division compared to unirradiated eggs from the same batch. The determination of the cleavage delay in eggs having different MAA contents, produced by feeding adults different macroalgal diets (with high and low MAA levels) in the absence of UV proved to be a perfect indicator for the sunscreen function of these compounds. The authors documented that the greater the MAA concentration in the eggs, the less they were affected by UV radiation. In the present study both *D. ramentacea* and *P. palmata* synthesised and accumulated MAAs over the course of the experiment in response to the UV treatment, except for those sample treated with 15 PSU. The highest MAA concentrations were usually measured at 34 PSU (Fig. 4, 8). The UV-induction data for MAAs are well supported by earlier experiments in the field, where both species were transplanted in the Kongsfjord from deeper waters to the surface, followed by exposure to natural full, as well as filtered solar radiation (Karsten & Wiencke, 1999; Karsten *et al.,* 1999). However, the most striking point is the fact that although both *D. ramentacea* and *P. palmata* form MAAs in a similar manner and concentration, this increase well correlates with the rising photosynthetic tolerance under UV in the first species only. In *P. palmata*, the optimum quantum yield under UV does not seem to benefit from higher MAA contents. These contradictory results on the potential sunscreen function of MAAs in both red algae clearly indicate species-specific physiological advantages are not solely due to the synthesis and accumulation of UV-absorbing compounds.

In conclusion, while *D. ramentacea* is able to resist different environmental stress factors in the upper sublittoral of the Arctic Kongsfjord indicating a relatively high degree of physiological plasticity, *P. palmata* exhibits a marked sensitivity against salinity and a limited capabilty to acclimate to changing PAR/UV radiation pointing to a rather inflexible metabolism.

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