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ORIGINAL ARTICLE

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Photoinhibition in common atlantic macroalgae measured on site in Gran Canaria

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Abstract The photosynthetic quantum yield was analysed in four common atlantic macroalgae, the Rhodophytes *Gelidium arbuscula* and *Halopithys incurvus* and the Phaeophytes *Halopteris scoparia* and *Lobophora variegata* in Gran Canaria, Canary Islands at their growth site. The fluorescence parameters were measured using a portable pulse amplitude modulated (PAM) fluorometer (PAM 2000) instrument and a diving PAM under water without removing the thalli from their growth sites. Solar radiation was monitored continuously above and under water during the whole experimental period using two three-channel dosimeters (European light dosimeter network; ELDONET) (Real Time Computer, Möhrendorf, Germany). These instruments measure solar radiation in three wavelength ranges, ultraviolet (UV)-A, UV-B and photosynthetic active radiation (PAR). In all four algae the effective photosynthetic quantum yield decreased significantly from the optimal values measured after dark adaptation due to exposure to 15 min solar radiation, but at least partially recovered subsequently in the shade within several hours. Increasing the exposure period to 30 min intensified the photoinhibition. In some algae no recovery was observed after this treatment and in others no significant recovery could be detected. Exposure to unfiltered solar radiation caused a significantly higher photoinhibition than PAR-only radiation or PAR plus UV-A. A substantial inhibition was found in all algae at their growth sites in the water column when the sun was at high angles, as measured with the diving PAM.

Keywords *Gelidium arbuscula* · *Halopythis incurvus* · *Halopteris scoparia* · *Lobophora variegata* · Pulse amplitude modulated fluorescence

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Introduction

About 50% of the primary biomass production on the earth is based on aquatic ecosystems (Houghton and Woodwell 1989; Siegenthaler and Sarmiento 1993). Most of the aquatic productivity is due to phytoplankton, however, macroalgae play an important role, especially in coastal areas. In addition to biomass productivity, macroalgal forests serve as breeding grounds for fish, mollusks and crustaceans. Macroalgae also have significant economic potentials, being used in the production of food for humans and animals, fertilizers and cosmetics, to name only a few.

Light is probably the most decisive factor in the coastal environment which determines the vertical distribution of macroalgae (Lüning 1985). Sessile algae face a serious stress when exposed to unfiltered solar irradiation and have been found to respond to this with reversible photoinhibition (Franklin and Forster 1997; Häder et al. 1998). Recent research has identified several other targets of short-wavelength solar radiation: damage to the water-splitting site and the reaction centre of photosystem II as well as cellular membranes (Murphy and Vu 1996). Another important target is the DNA where exposure to solar ultraviolet (UV)-B radiation induces mainly thymine dimers which cause mutations and permanent damage if not removed by the repair-enzyme photolyase. This enzyme is activated by long UV-A and blue light (Sommaruga et al. 1996).

During events of photoinhibition the photosynthetic electron transport in photosystem II is actively decreased (Trebst 1991) to protect the photosynthetic apparatus from excessive solar energy. The underlying biochemical mechanism is radiation-induced damage to the D1 protein which is subsequently removed by a protease. During the recovery period the lost protein is replaced by newly synthesized D1.

Early investigations of photosynthesis in macroalgae have been restricted to spectroscopic and gas exchange measurements (Field et al. 1989). Since the 1980s the development of pulse amplitude modulation (PAM)

fluorescence has facilitated and supplemented the analysis of important ecophysiological data (Briantais et al. 1986; Schreiber and Bilger 1987, 1993; Krause and Weis 1991). While most fluorescence techniques allow only the measurement of steady state parameters, PAM fluorescence measurements permit the analysis of adaptive processes in the photosynthetic and the physiological status of the photosynthetic apparatus by a non-invasive technique.

Recent miniaturization and development of a computer-based PAM fluorometer allows the application of the equipment in the field (Schreiber et al. 1986). The easily portable instrument can be employed at the growth site to determine key photosynthetic parameters (Schreiber and Bilger 1993; Schreiber et al. 1994). In the past few years another instrument, the diving PAM, has been developed for measurements under water, allowing the user to analyse subtidal species at their growth site in the water column.

The measured fluorescence parameters can be used for the subsequent quenching analysis based on the assumption that two parallel processes reduce the fluorescence: photochemical and non-photochemical quenching. The first indicates the use of the radiation energy in the photosynthetic apparatus while the latter is thought to be due to the build-up of charge and the pH gradient across the thylakoid membrane (Schreiber et al. 1995; Krause and Weis 1991).

The photosynthetic quantum yield can be determined using empirical equations developed by Genty et al. (1989) and Weis and Berry (1987) for which no knowledge of the dark fluorescence parameters, initial fluorescence in the dark-adapted state, when all reaction centres are open (F_o) and maximal fluorescence in the dark-adapted state when all reaction centres are closed (F_m), is necessary. The validity of this approach has been demonstrated by parallel gas exchange measurements (Schreiber and Bilger 1993).

The aim of the present paper was to analyse the photosynthetic quantum yield in common atlantic macroalgae on site and determine the degree of photoinhibition during exposure to solar irradiation. In addition, the photosynthetic quantum yield was followed during the daily cycle at the growth site of the algae. The relative contributions of photosynthetic active radiation (PAR), UV-A and UV-B are quantified.

Materials and methods

Measurement of solar radiation

Solar radiation was measured during the experimental period in three wavelength bands (UV-B, 280–315 nm; UV-A, 315–400 nm; PAR, 400–700 nm). For this purpose a three-channel filter instrument (European light dosimeter network, ELDONET; Real Time Computer, Möhrendorf, Germany) was used, located on the roof of a nearby institute (Häder et al. 1999). This dosimeter automatically determines the irradiance in each channel at 1-s intervals and calculates the averages over 1-min intervals. A parallel instrument was located in the water column at 6 m depth to record the underwater irradiances and calculate the transmission in the three individual bands. All data are transferred to the central server of the ELDONET server in Pisa (Marangoni et al. 2000) where they can be seen and downloaded by any interested user.

Plant material

Specimens of a number of atlantic macroalgae were used for the experiments. Common species were selected which inhabit the tidal and subtidal zone: the red algae *Gelidium arbuscula* and *Halopithys incurvus* and the brown algae *Lobophora variegata*, and *Halopteris scoparia.* The analyses were carried out on mostly sunny days in October 1997 on an east-facing rocky shore (Arinaga) of Gran Canaria, Canary Islands (27.0°N, 16.5°W).

Measurements of PAM fluorescence

The basis of PAM measurements is the determination of key florescence parameters. As a starting point the background chlorophyll fluorescence signal, F_o, is induced by a weak red light source in a dark-adapted specimen. Under these conditions the photosystem II reaction centres are open. Subsequently the photosystem II reaction centres are closed by a saturating white light pulse which induces maximal fluorescence (F_m). When these measurements are performed on light-adapted specimens a F_o' value is found which may be either higher or lower than in the dark-adapted specimens and a maximal fluorescence (F_m') which is usually lower than F_m.

Two portable pulse amplitude modulated fluorometers (PAM 2000 and diving PAM; Walz, Effeltrich, Germany) were employed to analyse the photosynthetic quantum yield on site (Schreiber et al. 1986). In the first set of experiments the thalli were selected immediately before the analysis and placed into custom-made UV-transparent Plexiglas holders (GS 2458; Röhm and Haas, Darmstadt, Germany) with open sides to allow unrestricted water flow past the specimens. Four replicates were used for the same species with at least eight independent thalli: The first set of experimental devices allowed unfiltered solar radiation to reach the specimens. The second set was covered with UV cut-off filter foils which removed short-wavelength radiation <320 nm (Montagefolie, no. 10155099; Folex, Dreieich, Germany) and a third set was covered with filter foils which removed all UV radiation <395 nm (Ultraphan UV Opak; Digefra, Munich, Germany). The transmission spectra of these filter foils can be found in Figueroa et al. (1997). A final set was subjected to the same experimental conditions except the exposure period to solar radiation. All sample holders with the selected specimens were placed in shallow water on site in the shade for 30 min. Subsequently, the thalli were exposed to solar radiation for different times. Then the samples were returned to the shade to allow them to recover from photoinhibition. The photosynthetic parameters were determined and the quantum yield calculated in all experimental sets after the dark period, after the exposure time and at predetermined times during recovery for up to 6 h. We used the same protocol for measuring the yield in brown and red algae in contrast to Hanelt (1998) who suggested a different protocol for red algae which includes a far red pulse before the measurement is made. However, the intention of this study was to investigate the performance of the algae under natural conditions where they do not encounter a far red pulse.

Simultaneously, a diver determined the PAM fluorescence parameters in specimens of the same species at their growth site under water using a diving PAM (Waltz). Specimens were selected and tagged in preparation of the measurements carried out every 2 h spaced over the day in order to study the natural daily course of photoinhibition in specimens at their growth site.

Statistics

A minimum of eight independent measurements were carried out for each sample, and mean values and SD were determined. All experiments were repeated several times throughout the experi-

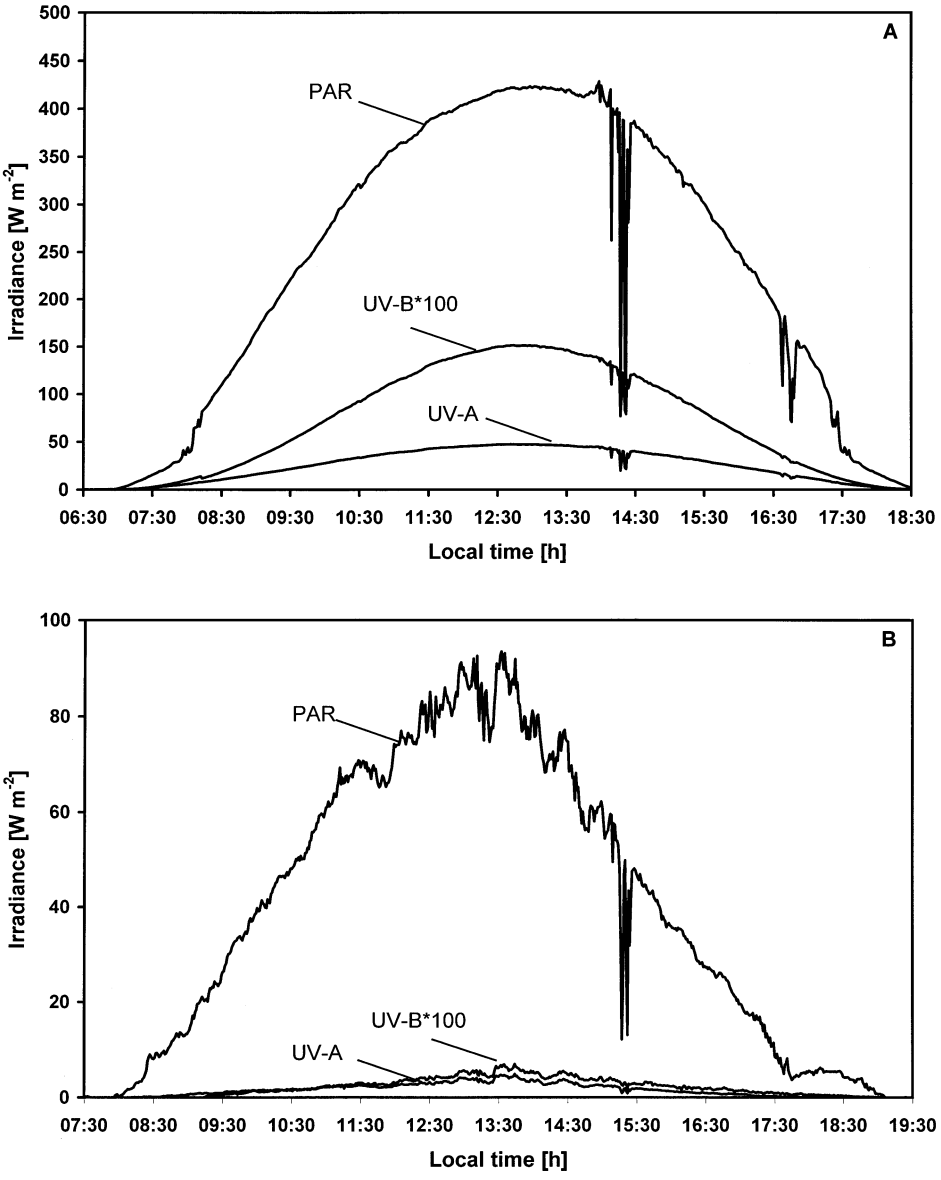


Fig. 1 Representative solar radiation for the measurement period in the photosynthetic active radiation (PAR) (400–700 nm), ultraviolet (UV)-A (315–400 nm) and UV-B (280–315 nm) wavelength ranges measured on 18 October 1997 in Gran Canaria, Canary Islands above (**A**) and 4–6 m below (**B**) the water surface depending on the tide

mental period. Student's *t*-tests were performed to determine statistically significantly differences between the different treatments (295-nm or 320-nm cut-off filters) and the 395-nm control.

Results

Figure 1 shows the solar irradiance on a representative day during the measurement period (18 October 1997) in the three channels. With the exception of a few scattered clouds in the afternoon the sky was blue throughout the day with maximal irradiances of about 420 W m^{-2} in the PAR region, 47 W m^{-2} in the UV-A and about 1.5 W m^{-2} in the UV-B region above water (Fig. 1A). The underwater irradiance at noon was about 90 W m^{-2} PAR, 5 W m^{-2} UV-A and about 0.06 W m^{-2} in the UV-B wavelength band (Fig. 1B).

The common Rhodophyte *Gelidium arbuscula* was found in mixed stands with other red, brown and green algae on rocky substrates in the intertidal zone sometimes above water at low tide. The optimal quantum yield was determined as about 0.65 after 30 min dark adaptation (Fig. 2A). When exposed to unfiltered solar radiation the quantum yield declined to about 0.3 after 15 min of exposure during solar noon in shallow water. The photosynthetic quantum yield recovered slowly, and the initial values were not reached even after 6 h in the shade. Exclusion of the UV bands resulted in a slightly more pronounced photoinhibition during exposure and recovery, but this was only in a few cases statistically significant. In a second experiment specimens were exposed for 30 min to solar radiation (Fig. 2B). After this treatment photoinhibition was even more pronounced and the recovery was likewise very limited at the end of the 6-h measurement period. In this experiment the exposure to unfiltered solar radiation had a significantly higher effect (as shown by the Student's *t*-test) than the PAR-only treatment which was even noticeable throughout

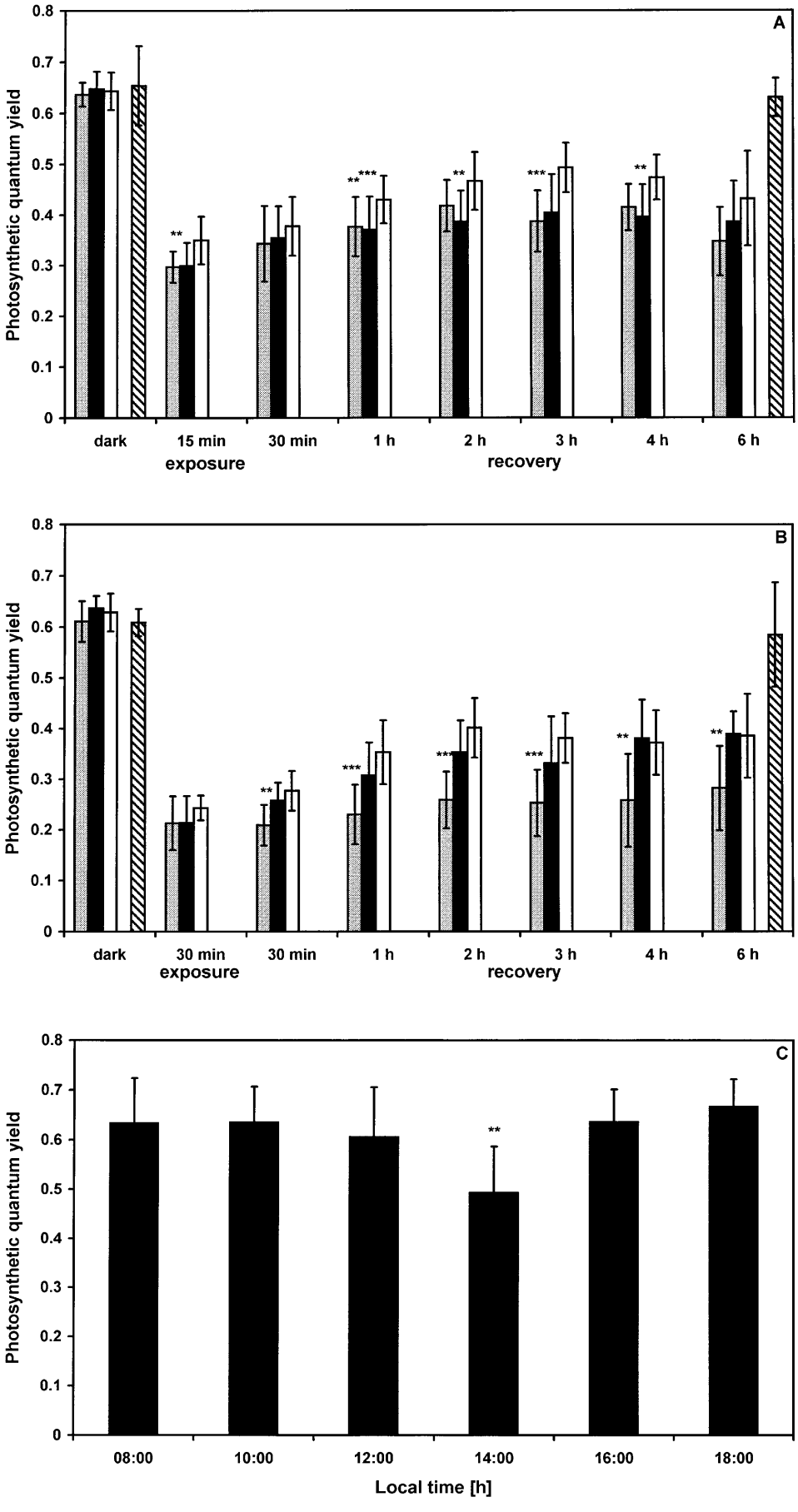


Fig. 2 Photosynthetic quantum yield of the Rhodophyte *Gelidium arbuscula* measured after 30 min dark adaptation, 15 min (**A**) or 30 min (**B**) exposure and after increasing recovery times in the shade. The specimens were exposed either to unfiltered solar radiation (*grey bars*), radiation filtered through a 320-nm cut-off filter foil (*black bars*) or filtered through a 395-nm cut-off filter foil (*white bars*). Independent controls were subjected to the same treatment except solar exposure and measured after the dark treatment and after the recovery period, respectively (*striped bars*). The values for unfiltered solar radiation and under the 320 nm cut-off filter treatments (**A** and **B**), respectively, are statistically significantly different from the corresponding PAR-only values (395 nm cut-off) in each set with $P<0.001$ (***) and $P<0.01$ (**), respectively, as indicated by Student's *t*-test. **C** Photosynthetic quantum yield measured at 2-h intervals with the diving pulse amplitude modulation (PAM) fluorometer on the same species at their growth site. For each data point eight measurements were averaged and the SD calculated (*error bar*). The measured values during the day are statistically significantly different from the first value (*same symbols* as for **A** and **B**)

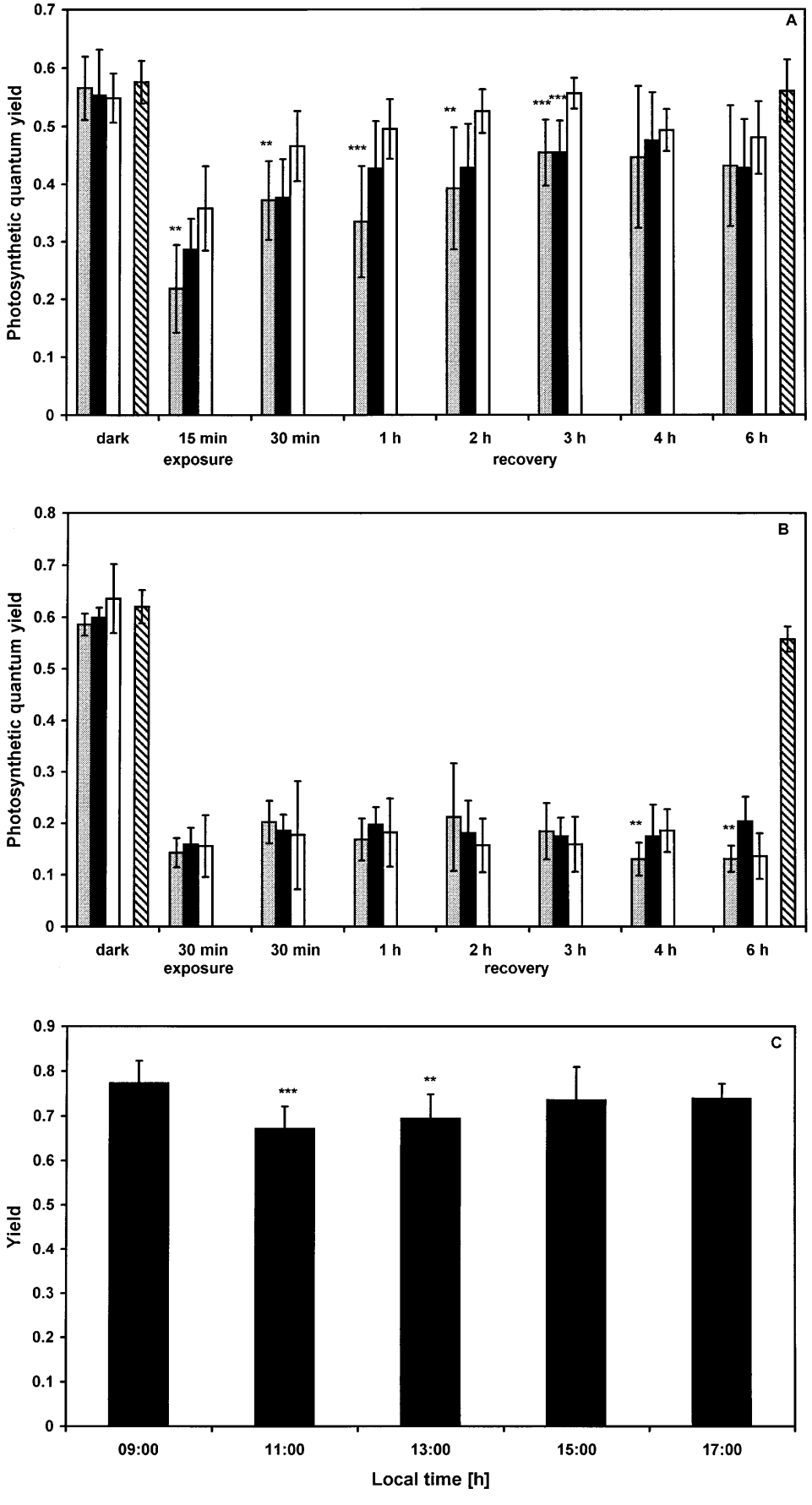


Fig. 3 Photosynthetic quantum yield of the red macroalga *Halopithys incurvus* measured after 30 min dark adaptation, 15 min (**A**) or 30 min (**B**) exposure and after increasing recovery times in the shade calculated as $(F_{m'}-F_t)/F_{m'}$; where $F_{m'}$=maximal fluorescence in the light-adapted state, F_t=current steady state fluorescence. The specimens were exposed either to unfiltered solar radiation (*grey bars*), radiation filtered through a 320-nm cut-off filter foil (*black bars*) or filtered through a 395-nm cut-off filter foil (*white bars*). Independent controls were subjected to the same treatment except solar exposure and measured after the dark treatment and after the recovery period, respectively (*striped bars*). The values for unfiltered solar radiation and under the 320 nm cut-off filter treatments (**A** and **B**) are statistically significantly different from the corresponding PAR-only values (395 nm cut-off) in each set with $P<0.001$ (***) and $P<0.01$ (**), respectively, as indicated by Student's *t*-test. **C** Photosynthetic quantum yield measured at 2-h intervals with the diving PAM on the same species at their growth site. For each data point at least eight measurements were averaged and the SD calculated. The measured values during the day are statistically significantly different from the first value (*same symbols* as for **A** and **B**)

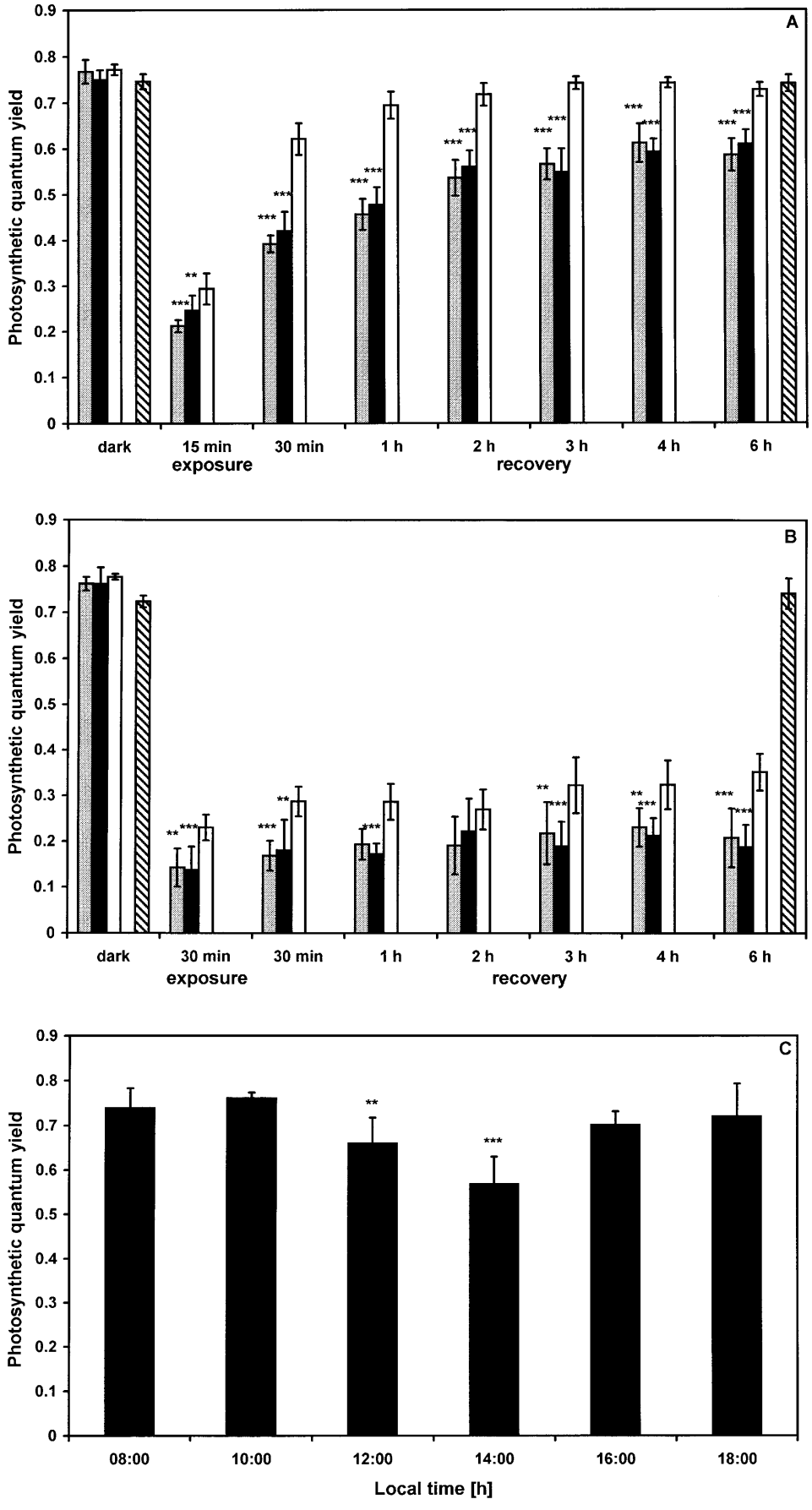
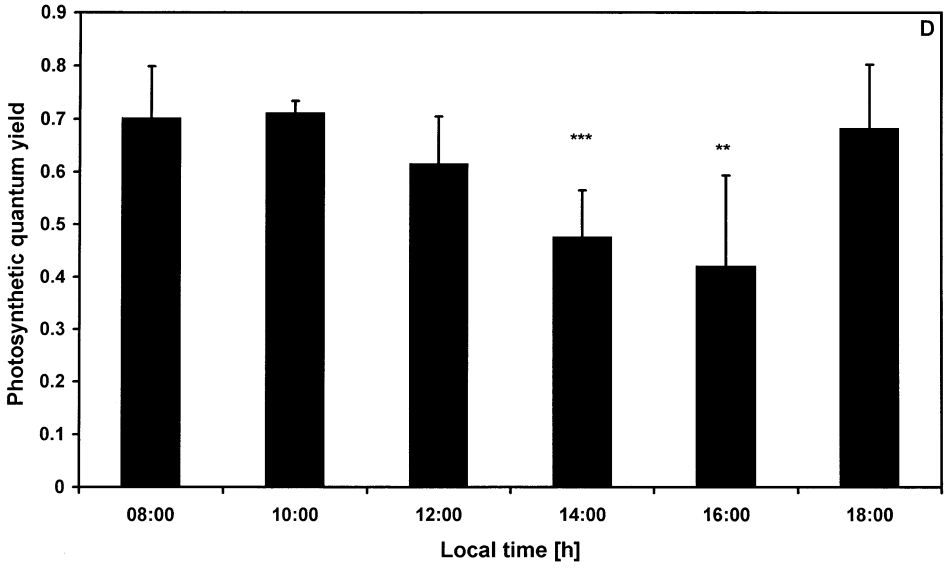


Fig. 4 Photosynthetic quantum yield of brown macroalga *Lobophora variegata* measured after 30 min dark adaptation, 15 min (**A**) or 30 min (**B**) exposure and after increasing recovery times in the shade calculated as $(F_{m'}-F_t)/F_{m'}$. The specimens were exposed either to unfiltered solar radiation (*grey bars*), radiation filtered through a 320-nm cut-off filter foil (*black bars*) or filtered through a 395-nm cut-off filter foil (*white bars*). Independent controls were subjected to the same treatment except solar exposure and measured after the dark treatment and after the recovery period, respectively (*striped bars*). The values for unfiltered solar radiation and under the 320-nm cut-off filter treatments (**A** and **B**) are statistically significantly different from the corresponding PAR-only values (395 nm cut-off) in each set with $P<0.001$ (***) and $P<0.01$ (**), respectively, as indicated by Student's *t*-test. Photosynthetic quantum yield measured at 2-h intervals with the diving PAM on the same species at their growth site at 5 m depth (**C**) and 1.5 m depth (**D**). For each data point at least eight measurements were averaged and the SD calculated. The measured values during the day are statistically significantly different from the first value (*same symbols* as for **A** and **B**)

Fig. 4 D



most of the recovery period. The exposure to PAR plus UV-A (320 nm cut-off) resulted in an intermediate result. This behaviour could be observed also throughout the recovery period.

The photosynthetic quantum yield was determined in *Gelidium* thalli at their natural growth site using the diving PAM (Fig. 2C). Thalli growing 2 m below the high water mark were measured at 2-h intervals throughout the day. The photosynthetic yield decreased from >0.63 in the morning to <0.5 during local noon and then recovered in the afternoon.

The red macroalga *Halopithys incurvus* was found attached to rocks from about 5 m depth to close to the surface. Dark-adapted specimens had photosynthetic quantum yields around 0.55 (Fig. 3A). After 15 min exposure to unfiltered solar radiation the effective yield had dropped to about 0.2, but recovered during the subsequent period to almost its initial value. A significant difference was found in this species between the PAR-treated samples and those exposed to unfiltered radiation both during exposure and the recovery period. The PAR plus UV-A treated specimens showed an intermediate behaviour. When exposed to 30 min radiation a dramatic decrease in the photosynthetic quantum yield was observed (Fig. 3B) and there was no marked recovery. *Halopithys* also showed a significant decrease in the photosynthetic quantum yield during local noon at its growth site at 2 m depth below the high water mark (Fig. 3C).

Thalli of the brown macroalga *Lobophora variegata* were found in the intertidal zone down to 8 m depth. Dark-adapted specimens showed an optimal photosynthetic quantum yield of about 0.75 (Fig. 4A). After 15 min of exposure the yield had dropped in the PAR-only exposed specimens significantly to <0.3 but recovered to almost its initial value within a few hours. In the specimens treated with unfiltered solar radiation or PAR plus UV-A the yield had dropped even further and there was no complete recovery. The difference between the treatments was statistically significant during exposure and recovery. After 30 min of exposure the photoinhibition was very severe, and there was no visible recovery (Fig. 4B). The treatments under the different filters showed statistically significant results. Measurements with the diving PAM on specimens at 5 m depth revealed a significant decrease in the effective photosynthetic quantum yield during local noon (Fig. 4C). This effect was even more pronounced in specimens located at 1.5 m depth (Fig. 4D).

The common Phaeophyte *Halopteris scoparia* was found on rocky substrates in the intertidal zone but always submerged even at low water. The optimal quantum yield was recorded at about 0.75 after 30 min dark adaptation (Fig. 5A). The quantum yield decreased to about 0.25 after 15 min of exposure during solar noon when exposed to unfiltered solar radiation in shallow water. The photosynthetic quantum yields recovered to almost their initial values during a few hours in the shade. The exposure to unfiltered solar radiation had a significantly higher effect than the PAR-only treatment, at least throughout most of the recovery period. When exposed for 30 min to solar radiation the recovery was not complete at the end of the 6-h measurement period (Fig. 5B).

Using the diving PAM, the photosynthetic quantum yield was determined in specimens left at their natural growth site at 5 m depth at 2-h intervals throughout the day (Fig. 5C). The photosynthetic yield decreased only little during local noon and early afternoon and recovered later in the afternoon.

Discussion

Solar radiation in the subtropical Canary Islands is characterized by high PAR (400–700 nm) and UV (280–400 nm) components. The UV-B range (280–315 nm) was found to have high values near 1.5 W m^{-2}. Due to high transparency of the water column the penetration of

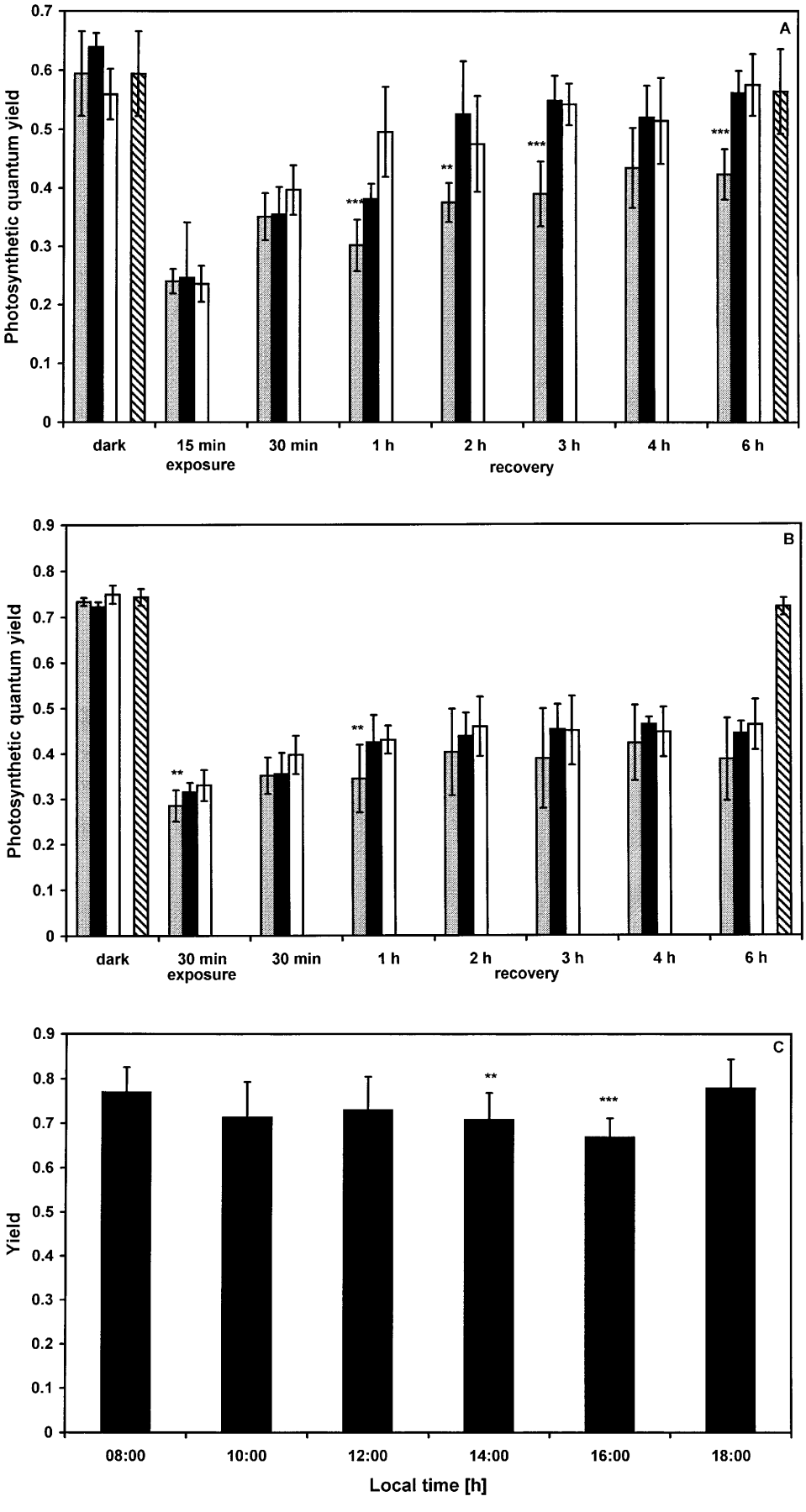


Fig. 5 Photosynthetic quantum yield of the Phaeophyte *Halopteris scoparia* measured after 30 min dark adaptation, 15 min (**A**) or 30 min (**B**) exposure and after increasing recovery times in the shade calculated as $(F_m'\text{-}F_t)/F_m'$. The specimens were exposed either to unfiltered solar radiation (*grey bars*), radiation filtered through a 320-nm cut-off filter foil (*black bars*) or filtered through a 395-nm cut-off filter foil (*white bars*). Independent controls were subjected to the same treatment except solar exposure and measured after the dark treatment and after the recovery period, respectively (*striped bars*). The values for unfiltered solar radiation and under the 320-nm cut-off filter treatments (**A** and **B**) are statistically significantly different from the corresponding PAR-only values (395 nm cut-off) in each set with $P<0.001$ (***) and $P<0.01$ (**), respectively, as indicated by Student's *t*-test. **C** Photosynthetic quantum yield measured at 2-h intervals with the diving PAM on the same species at their growth site. For each data point at least eight measurements were averaged and the SD calculated. The measured values during the day are statistically significantly different from the first value (*same symbols* as for **A** and **B**)

solar UV radiation into the water column was high and likely to affect the macroalgal populations.

The brown and red algal species used in this study are abundant on mid-Atlantic coasts and are found in the intertidal and subtidal zones on rocky shores where they are exposed to widely changing light conditions. Both the Rhodophyte and the Phaeophyte species showed a high photosynthetic quantum yield after dark adaptation. Exposure to solar radiation at the surface for as short a time as 15 min caused significant photoinhibition in all species. Recovery was only partial during the subsequent 6-h period in the shade. After exposure for 30 min the measured photoinhibition was even more pronounced and all algae failed to recover.

Similar behaviour has been found in several eulitoral Mediterranean species [Häder et al. (1996a), *Halimeda*; Häder et al. (1997a), *Caulerpa*, Häder et al. (1997b), *Cladophora*]. Surface-adapted algae recover much faster from exposure to direct sunlight than algae from a greater depth [Herrmann et al. (1995), *Ulva*; Häder et al. (1996b), *Padina*]. Ecologically more important is the finding that the photosynthetic quantum yield decreased even in thalli at their natural growth sites during or shortly after local noon. Photoinhibition was generally higher in algae growing in surface waters (1.5 m) than at deeper depths (e.g. 5 m). However, in *Lobophora* growing at 5 m depth the percent decrease was about 21%, similar to the value in *Gelidium* growing at 1.5 m. This may indicate that the red alga is more photoprotected by the production of mycosporine amino acids (MAAs) or possesses better dissipation systems for excess energy than the brown alga.

Macroalgae growing at greater depth have been found to be more sensitive to photoinhibition than surface algae (Henley et al. 1991; Häder and Figueroa 1997; Hanelt 1998), just like shade-adapted higher plants. This was attributed to better photoprotection in surface algae which seems to be genetically fixed (Hanelt 1998). There are also strong differences between different algal groups, which is also seen in this study, which could be due to different protection by MAA screening pigments or to different energy dissipation mechanisms. Judging from the presented data, in addition to white light, UV has a decisive influence on the zonation of macroalgae, and habitat choice may be governed by the degree of photoinhibition.

Photoinhibition has been found even in arctic and antarctic algae (Hanelt et al. 1994; Hanelt and Nultsch 1995; Gomez et al. 1995a, 1995b). Most of the effect is due to the white light component, but solar UV results in a significantly higher photoinhibition. Especially the short-wavelength UV-B range causes a significant enhancement of the effect even though its energetic share in the solar spectrum reaching the earth's surface amounts to <1% of the total radiation. This effect has also been found in other marine red, green and brown algae (Häder and Figueroa 1997; Häder et al. 1998) and several phytoplankton species (Jiménez et al. 1996; Figueroa et al. 1997).

Photoinhibition is considered as an active regulatory process by which the photosynthetic electron transport is reduced. The D1 protein located in photosystem II has been found to play a key role in this process (Sundby et al. 1993). During excessive solar radiation active oxygen species are generated by transfer of excitation energy from excited chlorophyll molecules to ground state (triplet) oxygen molecules (Foyer et al. 1994) giving rise to singlet oxygen which is believed to damage the D1 protein. The damaged D1 is subsequently removed by an endogenous protease.

Short-term exposure of specimens does not allow conclusions to be drawn on possible adaptation phenomena. However, the measurements with the diving PAM instrument at the growth sites indicate that all studied Rhodophyte and Phaeophyte algae are impaired by solar radiation when the sun is at high angles. This was found even for specimens growing further down in the water column. Future experiments will concentrate on transplanting specimens from deep water to habitats closer to the surface and vice versa in order to follow the photosynthetic quantum yield over longer periods of time.

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