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Effects of solar radiation on photoinhibition and pigmentation in the red alga *Porphyra leucosticta*

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ABSTRACT: The effect of solar radiation on photosynthesis, quantum yield of fluorescence and pigmentation under solar radiation in a laboratory system and in the natural habitat during a daily cycle was investigated in the red eulittoral alga *Porphyra leucosticta*. Optimal (F_v/F_m) and effective ($\Delta F/F_m'$) quantum yield of fluorescence, photosynthetic efficiency and maximal photosynthesis were drastically reduced by UV-B (280–315 nm) radiation in algae transferred from the laboratory (grown in white light) to solar radiation for 3 h. The absorptance due to chlorophyll and biliproteins (phycoerythrin and phycocyanin) increased after 3 h of incubation in photosynthetically active radiation (PAR, 400–700 nm) and PAR+UV-A (315–400 nm) whereas no changes were observed under PAR+UV-A+UV-B. In the field, the effective quantum yield and oxygen production decreased at noon during a daily cycle, indicating photoinhibition. When solar UV-A and UV-B radiation was removed by means of selective filters, the average effective quantum yield increased by 28 ± 2% SD. Chlorophyll and biliprotein concentration presented a daily pattern which was affected by UV radiation. Both chlorophyll and biliprotein contents were reduced at noon, followed by recovery in the afternoon, but only when UV radiation was cut off. The difference between the maximal and minimal chl *a* concentration during the daily cycle was greater in the presence of UV radiation, but the difference for phycoerythrin and phycocyanin was greater under PAR alone. These results seem to indicate that the accumulation of pigments is affected by solar radiation, with short-term changes induced by UV light. The ecological relevance of the daily variations of photosynthesis and pigmentation under solar radiation is discussed.

KEY WORDS: Biliproteins · Chlorophyll · Daily cycle · PAM fluorescence · Photosynthesis · *Porphyra leucosticta*

INTRODUCTION

Thinning of the ozone layer results in increased levels of ultraviolet (UV) radiation at the earth's surface (Häder 1996). Consequently, at present there is a great concern about the possible impact that increasing UV radiation may have on natural ecosystems, especially on marine systems (Worrest 1982, Smith et al. 1992, Prézelin et al. 1994).

Evaluating the effect of UV-B on algal photosynthesis is crucial for understanding the flow of carbon in the ocean in a scenario of global climate change (Häder & Worrest 1991, Häder 1996). A decrease of phytoplankton productivity by enhanced UV-B can be due to a direct effect on the carbon assimilation system (Lesser et al. 1994, Schofield et al. 1995) or nitrogen assimilation (Behrenfeld et al. 1995), or to DNA damage (Buma et al. 1993) or inhibition of motility (Ekelund 1990, Häder & Liu 1990).

Benthic macroalgae, in contrast to phytoplankton, are fixed and restricted to their growth site and thus have no opportunity to avoid high levels of visible light (PAR, wavelength λ = 400–700 nm) or UV radiation by vertical migration, as do phytoplankton. This evidence suggests that sublittoral macroalgae may show a lower

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tolerance to environmental stress, particularly to high irradiances and to UV radiation, while supralittoral or intertidal algae should be more adapted to cope with higher UV levels at the surface. In the field, strong sunlight depresses the photosynthetic activity of marine macroalgae, causing dynamic photoinhibition (Hanelt 1992, 1996). Photoinhibition of photosynthesis results from excessive excitation of the photosynthetic apparatus (Osmond 1994). It is a reversible process which inactivates PSII when incident light exceeds the electron transport capacity. The functional consequences of photoinhibition are a decrease of the quantum yield, a decline in the convexity of the light response curve and a decreased rate of light-saturated photosynthesis, showing the inextricable link between dark and light reactions of photosynthesis (Osmond 1994).

Photoinhibition affects complex biophysical, biochemical, physiological and ecological processes, which can be defined by their differing relaxation times, ranging at least 15 orders of magnitude in size and time (Osmond 1994). With regard to these different scales, photoinhibition has been investigated both in the laboratory with controlled nutrient status of the plants and temperature, and under natural conditions, using fluorescence induction kinetics (Büchel & Wilhelm 1993).

Photosynthetic activity in the field follows a diurnal pattern so that the lowest levels occur usually between noon and afternoon (Hanelt 1992, Henley et al. 1992, Hanelt et al. 1994). Recent investigations have described higher reduction of photosynthetic capacity in subtidal than in intertidal algae when exposed to full sunlight (Maegawa et al. 1993, Forster & Lüning 1996). This depletion of the photosynthetic capacity is followed by a decrease of the growth rate, increasing pigment photobleaching and tissue damage in some brown and red macroalgae from shaded and deep areas after sun exposure (Lüning 1980, Kain 1987, Wood 1987).

In this study, the effects of solar radiation on pigmentation, oxygen production and quantum yield of fluorescence in the red eulittoral macroalga *Porphyra leucosticta* Thur in Le Jol. during a daily cycle in its natural environment and under short exposure (3 h) to solar radiation in a laboratory system are analyzed.

MATERIALS AND METHODS

Algal material and pretreatment. ***Laboratory system:*** Thalli of *Porphyra leucosticta* were collected on the coast of Lagos (Málaga, southern Spain) and transported to the laboratory in an icebox. Prior to the exposure to solar radiation, algae were precultivated for 2 d in the laboratory at 17 ± 1°C in aerated 5 l beakers containing Provasoli's enriched seawater. Algae were illuminated by Day-light white fluorescent lamps (Osram-DL 18W) at an irradiance of 120 µmol m^{-2} s^{-1} in a light/dark regime of 12 h/12 h.

Field experiments: Algae were collected from their natural habitat and kept for at most 5 min in a dark box to avoid solar interference before the measurements. The box contained seawater collected from the field to maintain the same temperature as in the natural system.

Experimental procedure. ***Laboratory system:*** Algae were transferred from the laboratory to transparent Plexiglas tanks with circulating water (17 ± 2°C) and exposed for 3 h (12:00 to 15:00 h local time) to solar radiation. Fluorescence parameters and oxygen production were determined at initial time and after 3 h exposure to full solar radiation (PAR+UV-A+UV-B), solar without UV-B radiation (PAR+UV-A) and solar without UV-A and UV-B radiation (PAR). In order to cut off UV-A and UV-B radiation (PAR treatment), Ultraphan filters (Digefra GmbH, Munich, Germany) with transmission at $\lambda > 395$ nm were used. In order to cut-off only UV-B radiation (PAR+UV-A treatment), Folex filters (Folex GmbH, Dreieich, Germany) with transmission at $\lambda > 320$ nm were used. The transmittance of the filters is shown in Fig 1 Because these filters absorb 10% of PAR radiation, a neutral filter (1 layer of plastic net with 2 × 2 mm of mesh size) was placed on the top of the bath for the PAR+UV-A+UV-B treatment, to obtain the same irradiance among the treatments. In order to investigate the effect of the dose of solar radiation on the photosynthetic metabolism, an additional Plexiglas tank covered with several neutral filters to obtain about 150 µmol m^{-2} s^{-1} of solar radia-

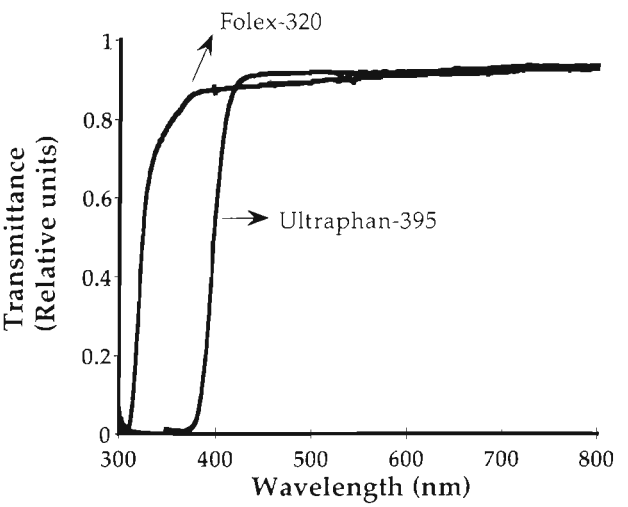

Fig. 1 Transmittance (relative units) of the filters used to remove UV-B (Folex-320) and both UV-A and UV-B radiation (Ultraphan-395)

tion was used (LL, low light treatment). The experiment was carried out twice during the same time periods on subsequent days.

Field system: The natural daily photoinhibition was determined by collecting, every hour from sunrise to sunset, thalli of algae exposed to full solar radiation (PAR+UV-A+UV-B) and of algae covered with Ultraphan filters cutting off UV-A and UV-B radiation (PAR).

Fluorescence measurements. In both laboratory and field experiments, the fluorescence parameters were estimated immediately after harvesting by means of pulse amplitude modulated fluorescence (PAM 2000; Waltz, Effeltrich, Germany) according to Schreiber et al. (1986, 1995). First, the optimal quantum yield according to Krause & Weis (1991) was calculated as F_v/F_m where $F_v = F_m - F_0$ (see Table 1 for an explanation of all symbols and abbreviations used in this paper). The algae were incubated for 15 to 30 min in darkness after harvesting. The initial fluorescence (F_0) is induced by low irradiation pulses in dark-adapted samples. Following a single saturating flash, maximal fluorescence, F_m, is detected. The effective quantum yield was calculated from $\Delta F/F_m'$ where $\Delta F = F_m' - F_t$, with F_t being the current steady-state fluorescence and F_m' the maximal fluorescence in the light-adapted state (Genty et al. 1989). $\Delta F/F_m'$ was determined at 20 to 30 µmol m^{-2} s^{-1} irradiance by covering the algae to avoid solar interference during the measurements.

Oxygen exchange measurements. ***Laboratory system:*** Photosynthetic determinations were conducted at time = 0 and after 3 h exposure to solar radiation by measuring oxygen evolution using Clark-type electrodes (YSI 5331) in a 7 ml chamber illuminated by halogen lamps (Schott KL-1500). Maximal photosyntehtic rate (P_{max}), photosynthetic efficiency (α) and the light compensation point for photosynthesis (LCP) were determined as described by Figueroa et al. (1995). At least 3 replicates were used in each treatment and the experiments were repeated 2 times.

Field system: Net photosynthesis and dark respiration were determined as oxygen exchange at discrete time intervals under solar irradiance. Epiphyte-free algae were incubated in cylindrical glass bottles of 250 ml volume for 15 to 20 min. To prevent carbon limitation, 5 mM of sodium bicarbonate was added to the seawater at the beginning of the measurements. Temperature was controlled by placing the bottles in aquaria continuously pumped with seawater. Respiration was estimated as oxygen depletion in dark bottles. O_2 concentration in the seawater was estimated at the beginning and at the end of the experiments by means of a Crison OXI-92 oxygen electrode.

Pigment analysis. Chl *a* was extracted with 90% pH-neutralized (sodium carbonate) acetone for 24 h at 4°C in the dark and after grinding the thalli in a mortar. Its concentration was determined spectrophotometrically by using the equation of Jeffrey & Humphrey (1975). Phycoerythrin (PE) and phycocyanin (PC) were extracted at 4°C in 0.1 M phosphate buffer (pH 6.5) containing 10 mM EDTA-Na_2 and 4 mM phenylmethylsulphonylfluoride. Biliprotein concentration was determined spectrophotometrically using the equations of Beer & Eshel (1985). In the case of the laboratory system, the absorptance of the thalli at the maximal absorption of chl *a* (680 nm), phycocyanin (624 nm) and phycoerythrin (566 nm) was calculated according to Figueroa et al. (1995). The absorptance was determined by using a Li Cor spectroradiometer model Li-1800UW supplied with a Li-1800-12 integrating sphere. Absorptance was determined as: $A = 1 - T - R$ where T is transmittance and R is reflectance of the wet thallus.

Table 1. Symbols and abbreviations used in this paper

α	Photosynthetic efficiency
chl *a*	Chlorophyll *a*
F_0	Initial fluorescence in the dark-adapted state; all reaction centers are open (oxidized)
F_m	Maximal fluorescence in the dark-adapted state; all reaction centers are closed (reduced)
F_0', F_m'	The same for the light-adapted state, respectively
F_t	Current steady-state fluorescence
LCP	Light compensation point for photosynthesis
LL	Low light treatment
PAM	Pulse Amplitude Modulated fluorometer
PAR	Photosynthetically Active Radiation (λ = 400–700 nm)
PC	Phycocyanin
PE	Phycoerythrin
P_{max}	Maximal photosynthetic rate
PSII	Photosystem II
UV-A	Ultraviolet A radiation (λ = 315–400)
UV-B	Ultraviolet B radiation (λ = 280–315)
WL	Fluorescent white light

Monitoring of solar radiation and temperature ratio during the daily cycle. Solar irradiance was measured using a newly developed filter instrument (ELDONET, Real Time Computer, Möhrendorf, Germany). The dosimeter takes readings in 3 wavelength bands (UV-B, 280–315 nm; UV-A, 315–400 nm; PAR, 400–700 nm) at 1 s intervals, averages them over 1 min intervals and stores them on a computer. From these values doses are calculated on an hourly and daily basis for each channel. The temperature was continuously monitored in the field system in the air and in the surface water.

Statistics. Mean values and standard deviation were calculated from at least 8 replicates per treatment for PAM measurements and from at least 3 replicates for photosynthetic determination in independent samples for each treatment. Pigments were extracted in triplicate samples. Statistical significances of means were

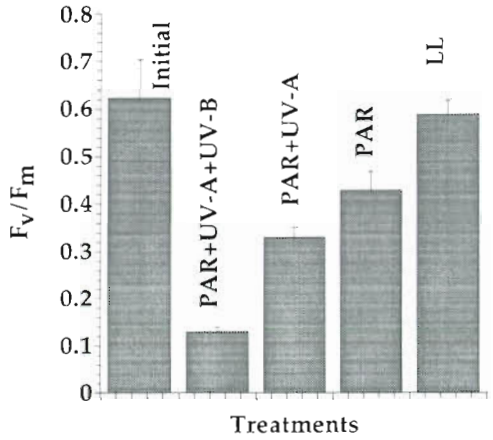

Fig. 2. Optimal quantum yield (F_v/F_m) of *Porphyra leucosticta* grown in white light under laboratory conditions (Initial) compared to the F_v/F_m of algae subjected to high levels of solar radiation (1500 to 2000 µmol m^{-2} s^{-1} of PAR) for 3 h around noon (12:00 to 15:00 h local time) in a laboratory system (PAR, PAR+UV-A and PAR+UV-A+UV-B) and to low levels of solar radiation (LL, 120 µmol m^{-2} s^{-1})

tested with a model 1 one-way ANOVA followed by a multi-range test by Fisher's protected least significance difference (LSD) (Sokal & Rohlf 1981).

RESULTS

Laboratory system

F_v/F_m drastically decreased in algae exposed for 3 h to solar radiation of 1500 to 2000 µmol m^{-2} s^{-1} and previously grown in the laboratory at 120 µmol m^{-2} s^{-1}. Nevertheless, the degree of decrease of F_v/F_m was very different in the 3 treatments, reaching 30 ± 2% in PAR, 40 ± 3% in PAR+UV-A and 82 ± 5% in PAR+UV-A+UV-B (Fig. 2). Algae exposed to the low level of solar radiation (LL) did not show any significant decrease of F_v/F_m (Fig. 2). Thus, short exposure of laboratory-adapted algae to solar radiation provoked a drastic photoinhibition. Photoinhibition was more drastic when both UV-A and UV-B were present. After an additional 12 h under low irradiance of white light (50 µmol m^{-2} s^{-1}), F_v/F_m in LL and PAR treatments recovered to the initial values (Table 2); in PAR+UV-A F_v/F_m recovered to about 90 ± 5% and PAR+UV-A+UV-B to about 75 ± 5%.

The absorptance peak due to chl *a* ($A_{chl\ a}$) increased after 3 h exposure to solar radiation in the PAR and LL treatments, compared to the initial values of laboratory-adapted algae. $A_{chl\ a}$ under PAR+UV-A+UV-B slightly decreased compared to the initial values (Fig. 3a), but it did not change under PAR+UV-A. Similar results were obtained for the maximal absorptance peaks of PE (A_{PE}) at λ = 566 nm and PC (A_{PC}) at λ = 624 nm (Fig. 3b). The highest increase of absorptance

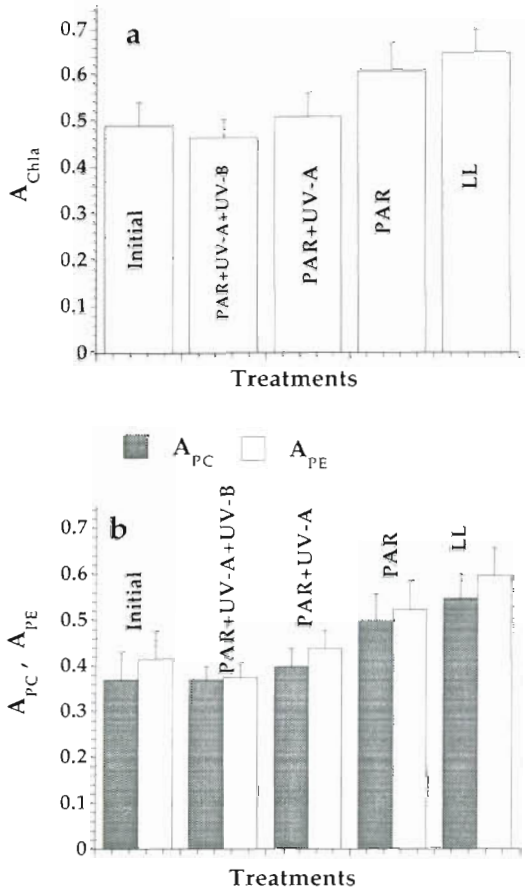

Fig. 3. Absorptance peaks (relative units) due to (a) chl *a* ($A_{chl\ a}$, 680 nm) and (b) phycocyanin (A_{PC}, 624 nm) and phycoerythrin (A_{PE}, 566 nm) of *Porphyra leucosticta* grown in white light under laboratory conditions (Initial) compared to the absorptance of algae subjected to solar radiation for 3 h around noon (12:00 to 15:00 h local time) in a laboratory system (PAR, PAR+UV-A and PAR+UV-A+UV-B)

Table 2. *Porphyra leucosticta*. Recovery of the optimal quantum yield (F_v/F_m) of algae subjected for 3 h to PAR, PAR+UV-A and PAR+UV-A+UV-B and then transferred to white light (see 'Materials and methods'). The recovery of the optimal quantum yield is expressed as a percentage of the initial quantum yield of algae grown in the laboratory before exposure to solar radiation. The recovery was determined after 3, 6 and 12 h of incubation in white light (WL) at 50 µmol m^{-2} s^{-1} irradiance

Time in WL (h)	PAR	PAR+UV-A	PAR+UV-A+UV-B
3	85 ± 8.3	65 ± 5.6	45 ± 6.0
6	99 ± 4.3	80 ± 9.0	62 ± 6.4
12	100 ± 10	90 ± 5.0	75 ± 5.0

for both chlorophyll and biliprotein pigments was observed under LL.

P_{max} increased and α decreased after 3 h exposure to solar radiation (Table 3). P_{max} increased less for PAR+UV-A+UV-B than for PAR and PAR+UV-A. On the other hand, α for PAR+UV-A+UV-B decreased more than α for PAR and PAR+UV-A (Table 3). The LCP was higher in the presence of UV-B compared to PAR+UV-A and PAR treatments.

Field system

Maximal irradiance during the daily cycle was 425 W m^{-2} for PAR, 45 W m^{-2} for UV-A and 1.2 W m^{-2} for UV-B (Fig. 4). The temperature inside of the ELDO-NET unit oscillated from 28 to 38°C but in the surface water ranged only from 16 to 18°C. PAR and temperature were identical in the zones where the experiments were conducted. Thus the possibility is excluded that the differences in the photosynthetic activity between PAR and PAR+UV-A+UV-B treatments were due to any difference in PAR and temperature at the different experimental sites.

Under full solar radiation, F_v/F_m and $\Delta F/F_m'$ presented a similar daily cycle, with a decrease from dawn to noon and recovery from noon to dusk. The decrease was smaller when UV-A and UV-B radiation were removed than under full solar radiation (Fig. 5). Maximal decrease of F_v/F_m at noon was about 11.3 ± 2% in PAR and 19.3 ± 2% in PAR+UV-A+UV-B, while the maximal decrease in $\Delta F/F_m'$ was 10.2 ± 1% in PAR and 38.7 ± 3% in PAR+UV-A+UV-B. Thus, the average decrease in effective quantum yield of about 28 ± 2% under PAR+UV-A+UV-B in natural conditions was less pronounced when UV-A and UV-B were eliminated from the solar radiation. The daily decrease of F_v/F_m was smaller than the decrease of $\Delta F/F_m'$.

The pigmentation pattern during the daily cycle was drastically affected by UV radiation (Figs. 6 & 7). Under PAR+UV-A+UV-B, chlorophyll concentration

Table 3. *Porphyra leucosticta*. Photosynthetic parameters: maximal photosynthesis (P_{max}) expressed as μmol O_2 g^{-1} FW h^{-1}, photosynthetic efficiency (α) and light compensation point (LCP) for photosynthesis (μmol m^{-2} s^{-1}) before (Initial) and after 3 h exposure to solar radiation (PAR, PAR+UVA and PAR+UV-A+UV-B) in an experimental chamber at 25°C

Treatment	P_{max}	α	LCP
Initial	129 ± 6.2	1.30 ± 0.08	27.0 ± 2.4
PAR	289 ± 9.2	0.95 ± 0.06	28.4 ± 3.0
PAR+UV-A	282 ± 8.4	0.92 ± 0.03	28.6 ± 2.5
PAR+UV-A+UV-B	219 ± 8.2	0.56 ± 0.02	33.4 ± 2.2

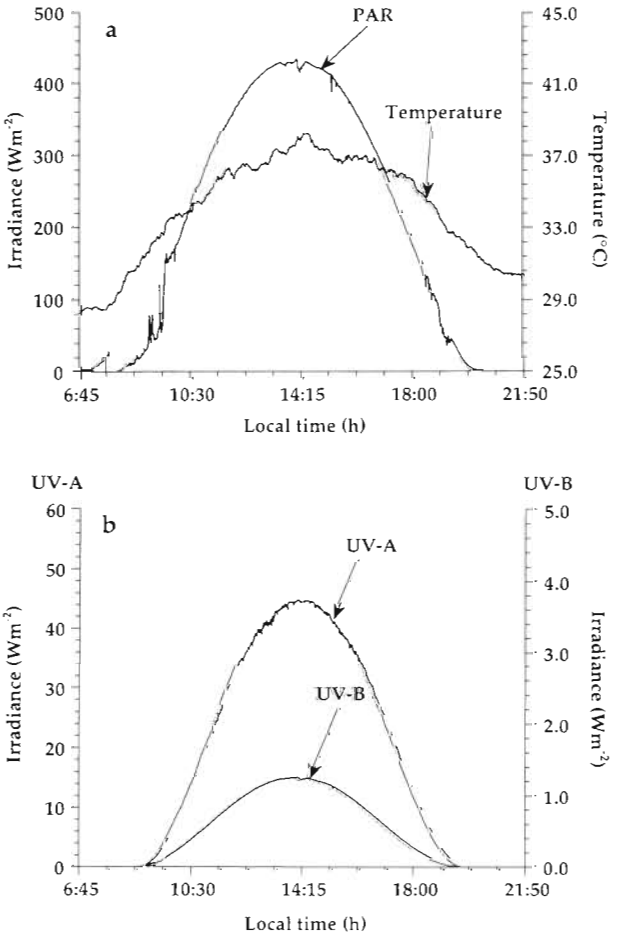

Fig. 4. Daily variations of PAR (400–700 nm), UV-A (315–400 nm) and UV-B (280–315 nm) expressed in energy units and temperature, measured in the air during one of the experimental days

did not change during the morning, decreased drastically around noon, and maintained low values for the rest of the day (Fig. 6a). However, under PAR, chlorophyll concentration increased from dawn to noon and decreased from noon to dusk (Fig. 6b). Chlorophyll concentration was significantly ($p < 0.05$) greater in the morning (7:30 to 12:00 h) that in the afternoon (13:30 to 21:00 h) in both treatments. Under PAR+UV-A+UV-B, PE concentration decreased from dawn to noon, partially recovered from noon to afternoon and decreased at dusk again (Fig. 7a). Under PAR, PE concentration increased from morning to noon and then drastically decreased with a slow recovery in the afternoon periord (Fig. 7b). PC presented the same pattern as PE and the same differences between the treatments (Fig. 7c, d). Under PAR+UV-A+UV-B, both PE and PC concentrations were significantly ($p < 0.05$) greater in the early morning (7:30 to 9:00 h) and early afternoon (15:00 to 18:00 h) than around noon

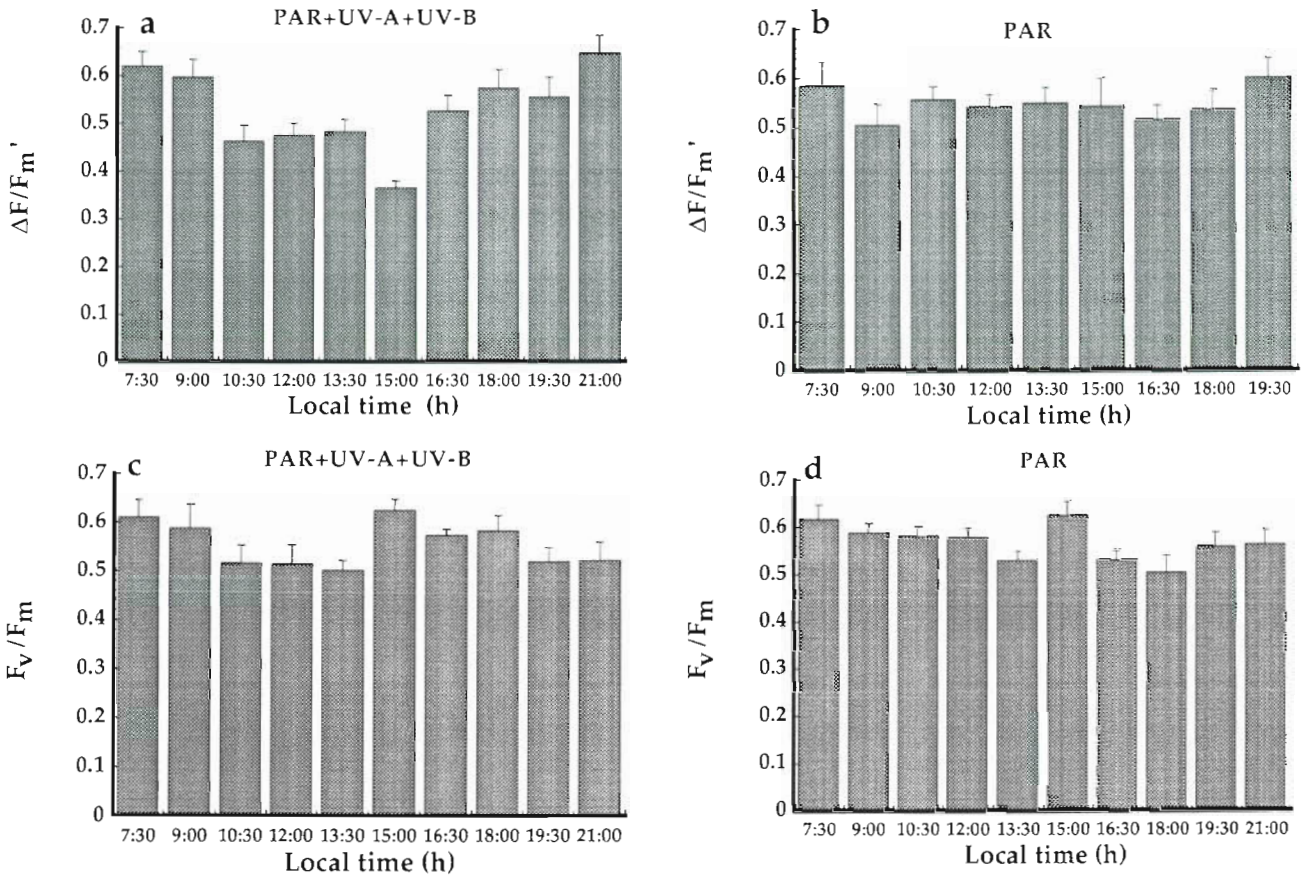

Fig. 5. Daily variations of (a, b) the effective quantum yield ($\Delta F/F_m'$) and (c, d) the optimal quantum yield (F_v/F_m) of *Porphyra leucosticta* in its natural habitat under full solar radiation (PAR+UV-A+UV-B) and without UV radiation (PAR)

(12:00 to 13:30 h) and in the evening (19:30 to 21:00 h). However, under PAR, both PE and PC concentrations were significantly ($p < 0.05$) greater around noon (12:00 to 13:30 h) than in the early morning (7:30 to 9:30 h) and afternoon (15:00 to 16:30 h). A delay of 2 h in the minimal values of biliprotein content during the daily cycle was produced under PAR compared to PAR+UV-A+UV-B. The difference between the highest and the lowest concentration of chl *a* during the daily cycle was larger under PAR+UV-A+UV-B than under PAR (Fig. 6). However, the difference between the maximal and minimal concentration of PE was higher when UV was cut off from the solar radiation (Fig. 7b). Similar differences between PAR and PAR+UV-A+UV-B were observed in the case of PC.

Oxygen evolution presented a daily pattern similar to that of chlorophyll (Fig. 8). Photosynthesis under PAR+UV-A+UV-B decreased from morning to noon, presenting a slight increase in the afternoon (Fig. 8a). However, under PAR no large variations in the photosynthetic rate during the day were observed (Fig. 8b).

DISCUSSION

Benthic marine algae have to cope with extreme changes in the incident solar radiation as a result of variable weather conditions, sun angle and tidal level. In the present work, a daily cycle in the quantum yield of fluorescence and oxygen evolution of the eulittoral alga *Porphyra leucosticta* was shown. The algae were photoinhibited by excess light at noon, with a recovery of effective quantum yield and photosynthesis in the afternoon. Several authors have already described the occurrence of photoinhibition in macroalgae growing in the natural environment (Hanelt 1992, 1996). High solar irradiance reduces the photosynthetic activity of marine algae (Ramus & Rosenberg 1980, Henley et al. 1991, Hanelt et al. 1994, Häder et al. 1996, 1997a, b, Hanelt 1996) which is shown by depression of the effective quantum yield and photosynthetic O_2 production. This dynamic photoinhibition follows a diurnal pattern, so that the lowest photosynthetic activity is found at noon and in the afternoon hours (Huppertz et al. 1990, Henley et al. 1991, 1992, Hanelt 1992, 1996, Häder et al.

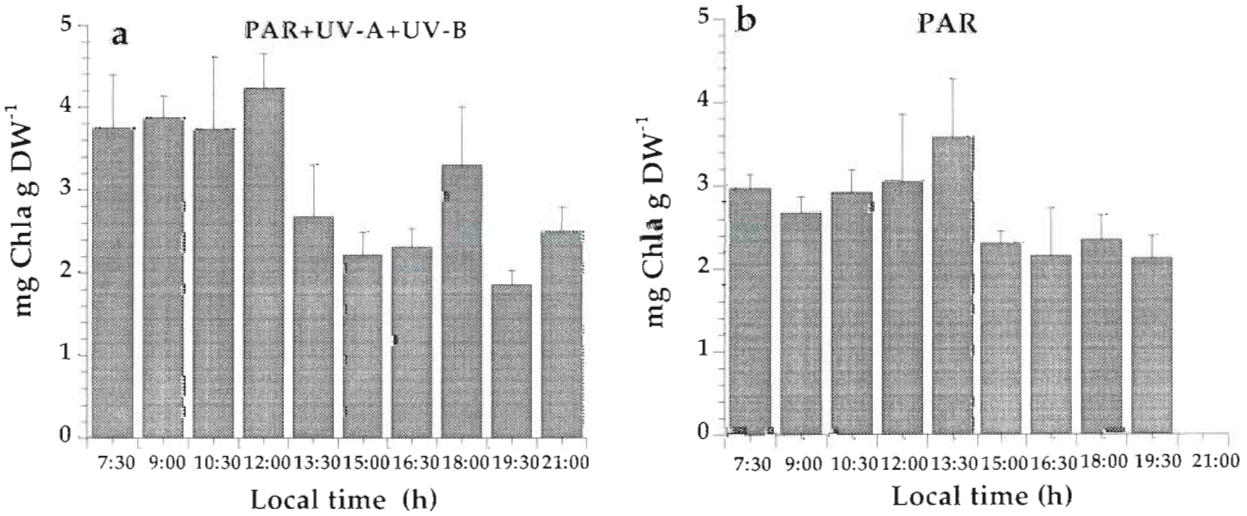

Fig. 6. Daily variations in the chlorophyll concentration (mg g^{-1} DW) of *Porphyra leucosticta* in its natural habitat, (a) under full solar radiation (PAR+UV-A+UV-B) and (b) without UV radiation (PAR)

1996, 1997a, b). *P. leucosticta* seems to be adapted to the light stress conditions in the eulittoral zone in southern Spain because it displayed dynamic photoinhibition but its quantum yield recovered in the afternoon period. However, when the algae were previously incubated for 2 d under laboratory conditions using white light lamps producing no UV radiation, exposure to full solar radiation caused high photoinhibition with a lim-

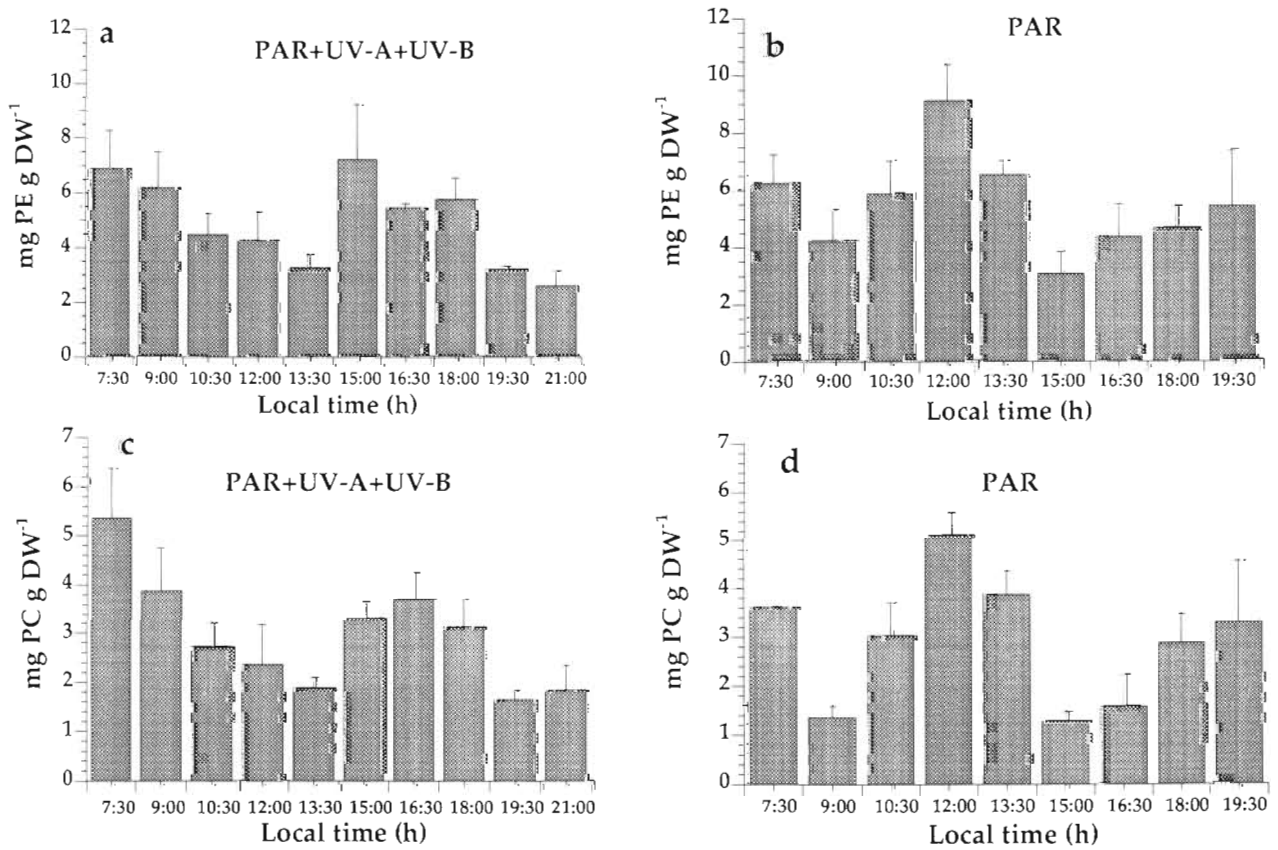

Fig. 7 Daily variations in the phycoerythrin (PE) and phycocyanin (PC) concentration (mg g^{-1} DW) of *Porphyra leucosticta* in its natural habitat (a, c) under full solar radiation (PAR+UV-A+UV-B) and (b, d) without UV radiation (PAR)

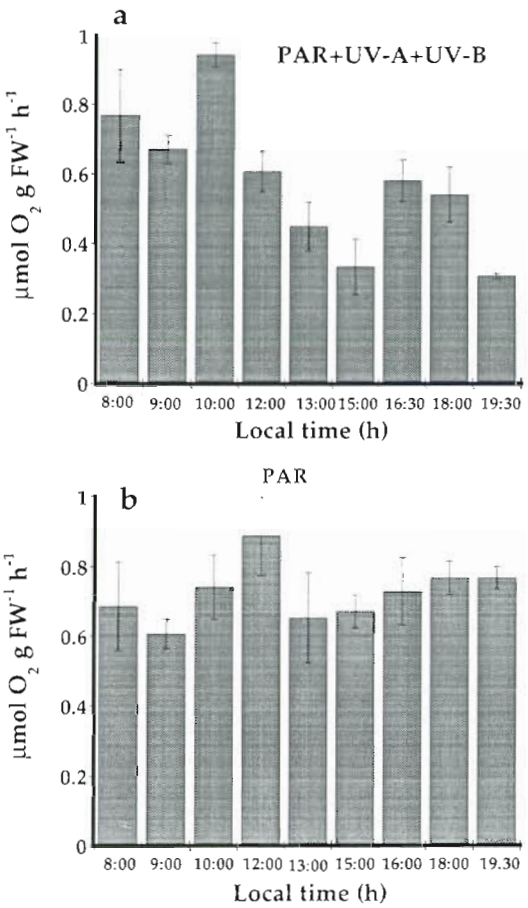

Fig. 8. Daily variations of oxygen production of *Porphyra leucosticta* in its natural habitat (a) under full solar radiation (PAR+UV-A+UV-B) and (b) without UV radiation (PAR)

ited capacity for recovery. Thus, it seems that in the laboratory a partial loss of the photoprotection mechanism is produced. Herbert (1990) demonstrated a high rate of repair in photoinhibited *Porphyra perforata*. Hanelt et al. (1993) found that algae which usually grow at the surface are much more resistant to photoinhibition than deep-water species or those sheltered under rocks or in caves. However, Hanelt et al. (1992) and Häder & Schäfer (1994) found no significant recovery of photosynthesis in red algae exposed to full solar radiation after excessive exposure, indicating permanent photodamage rather than photoinhibition. Nevertheless, in a previous study (Häder et al. 1997a), it has been shown that both photosynthetic O_2 production and quantum yield are recovered after 4 to 6 h in the shade in sun-adapted red algae exposed to full solar radiation. On the other hand, a clear increase in the effective quantum yield of fluorescence was observed in *P. leucosticta* when both UV-A and UV-B were removed from the solar radiation. Thus, UV radiation stresses the algae, and this radiation would be partially responsible for the dynamic photoinhibition at noon. The decrease of F_v/F_m was clearly smaller than that of $\Delta F/F_m'$. This result could be explained by the existence of a partial and rapid recovery during the 15 to 30 min incubation in darkness conducted prior to calculating F_0 and F_m. The negative effect of UV radiation on the photosynthetic metabolism in *P. leucosticta* was even stronger when the algae were previously grown in the laboratory under moderate irradiances of white light (without UV radiation). The transfer to solar radiation provokes a drastic decrease of effective quantum yield and photosynthesis but full recovery is produced under PAR and PAR+UV-A and only partial recovery under PAR+UV-A+UV-B is found. Several authors (Häder & Schäfer 1994, Gerber & Häder 1995, Herrmann et al. 1995, Hanelt 1996) have shown that even though UV-B accounts for only a very small fraction of solar radiation, it has a considerable effect on photosynthesis, inducing an important decrease of the photosynthetic O_2 production.

In addition to the daily variations in the oxygen production and yield, the photosynthetic pigments (chlorophyll and biliproteins) showed daily changes with drastic differences between PAR and PAR+UV-A+UV-B treatments. Short-term variations in the photosynthetic pigments have been previously shown in both laboratory (López-Figueroa & Niell 1989, López-Figueroa 1991, Rüdiger & López-Figueroa 1992) and natural conditions (Algarra et al. 1991, López-Figueroa 1992). The greater decrease of chl *a* concentration in PAR+UV-A+UV-B compared to PAR indicates that one direct effect of UV radiation on the photosynthetic metabolism is the photodamage of chl *a*. In our experimental system, absorptance by both chl *a* and biliproteins was greater under PAR than under PAR+UV-A+UV-B. However, under PAR a higher increase but also a higher decrease of PE than under PAR+UV-A+UV-B was produced. Under natural conditions, the difference between the maximal and minimal PE concentration was 6.05 ± 0.5 mg g^{-1} DW for PAR and only 4.3 ± 0.3 mg g^{-1} DW for PAR+UV-A+UV-B. Thus, the absence of UV seems to induce a higher turnover of PE. In the laboratory system, an increase in the absorptance due to PE was produced under PAR+UV-A compared to PAR+UV-A+UV-B.

The daily pattern of pigments under UV radiation suggests that they are damaged by excess light, but also that they recover during the afternoon, as both photosynthesis and effective quantum yield do. The direct relation between the daily cycle of chl *a* and biliprotein content and that of oxygen production and quantum yield suggests that the photoinhibition of *Porphyra leucosticta* in the natural enviromental can be explained in part by the changes in the pigment composition. In other words, the photodestruction of pig-

ments is a process involved in the depletion of photosynthesis at noon. The fact that the pigments recovered during the day indicates that the pigment variation could constitute a short-term process in the natural system coupled to irradiance changes. In Cyanobacteria, phycoerythrin is rapidly disassembled during exposure to UV radiation and a role in photoprotection has been suggested (Sinha et al. 1995). More investigation is necessary to determine the photoprotection systems of *P. leucosticta* against excess light under natural conditions.

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ERRATUM

Effects of solar radiation on photoinhibition and pigmentation in the red alga *Porphyra leucosticta*

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- Fig 8 on page 88 contained an error — the *y*-axis was incorrectly labelled. The corrected figure and its caption appear here. The authors apologize for any inconvenience caused.

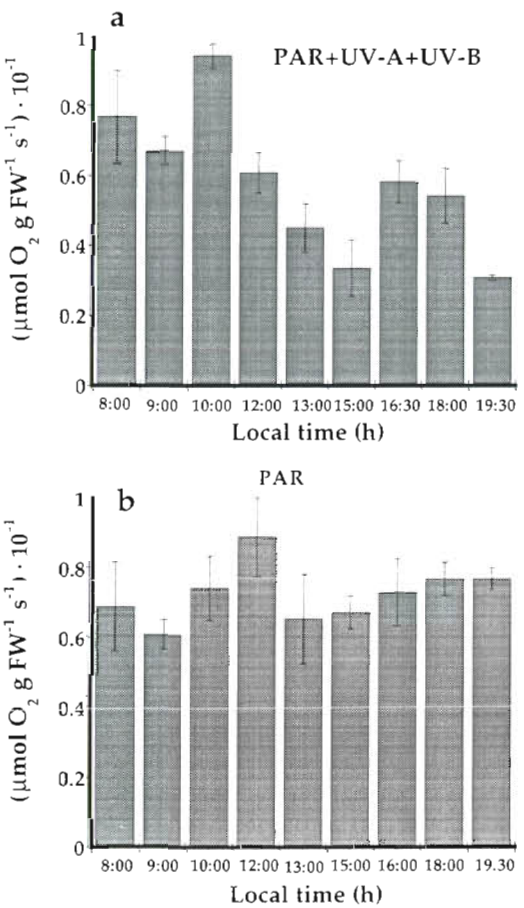

Fig. 8. Daily variations of oxygen production of *Porphyra leucosticta* in its natural habitat (a) under full solar radiation (PAR+UV-A+UV-B) and (b) without UV radiation (PAR)