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SEASONAL VARIATION OF PHOTOSYNTHETIC PERFORMANCE AND LIGHT ATTENUATION IN *ULVA* CANOPIES FROM PALMONES RIVER ESTUARY[1]

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ABSTRACT

The primary production of Ulva *populations relies on their photosynthetic performance, which is dependent on the light availability under natural conditions. This study concerns the light attenuation characteristics in* Ulva *canopies and the seasonal photosynthetic performance of two different species (*Ulva rotundata *Blid.,* Ulva curvata *(Kütz.) De Toni) blooming in the Palmones river estuary. Light within canopies differed from that reaching the surface. Light availability was reduced through the water column (at high tide) and* Ulva *canopies. In addition, light was spectrally filtered. As a result, the photosynthetically usable radiation (PUR) was further attenuated through* Ulva *canopies, increasing the photosynthetically active radiation/PUR ratio. The muddy sediment deposited on and between the* Ulva *thalli also drastically restricted the light availability. Thick* Ulva *mats are frequently found covering the intertidal mudflats, and therefore, thalli within these mats may be subjected to steep light gradients. As a consequence, individual* Ulva *growth rates cannot be extrapolated to estimate the primary production of* Ulva *canopies. Interspecific differences were observed for light-saturated photosynthetic rates (P_{max}) and light compensation points (L_{CP}), with* Ulva curvata *generally displaying higher values than did* U. rotundata. *For both species, maxima were recorded in winter for P_{max}, quantum yield, chlorophyll content, and absorptance, whereas minima were found in summer. Dark respiration (R_d) was not seasonally affected, and a maximum L_{CP} was found in summer. To extrapolate these data to field situations, the temperature dependence of photosynthesis should be considered. The Q_{10} values were 2.44 for R_d and 1.79 for P_{max}, whereas the photosynthesis rate at subsaturating light levels was unaffected. The Q_{10} values showed an enhanced respiratory rate in summer and a minimum in winter, whereas the seasonal differences on P_{max} were damped.*

Key index words: canopy; light attenuation; PAR/PUR ratio; photosynthesis; Ulva

The estuary of the Palmones river is a eutrophic coastal ecosystem with a green tide episode dominated by *Ulva* species (Hernández et al. 1997). Light availability and thermal stress have been proposed as the bottom-up factors (sensu Menge 1992) controlling *Ulva* biomass (Hernández et al. 1997). Light availability is considered to be the most important variable controlling the abundance and primary production of the aquatic macrophytes. The growth and photosynthetic characteristics of the two dominant *Ulva* species in the estuary as a function of growth irradiance has been assessed in laboratory studies (Pérez-Lloréns et al. 1996). However, little is known about the photosynthetic characteristics of these species on a seasonal cycle, where additional forcing functions such as nutrient availability, temperature, or emersion may control the success of these species via their photosynthetic performance.

On a seasonal cycle, irradiance of the estuary follows an obvious bell-shaped pattern (Hernández et al. 1997). However, the actual light experienced in nature by the algae may differ, because tidal mixing and wind-driven water movements result in a highly variable underwater photic environment. Tides cause benthic populations to be covered with a changing depth of water. However, little attention has been paid to the impact of tides on light availability (Dring and Lüning 1994, Zimmerman et al. 1994, Koch and Beer 1996). Superimposed on this is a self-shading effect as a consequence of the dense growth of these sheet-like species. In the estuary, *Ulva* populations are arranged in a canopy with a variable number of layers. The upper *Ulva* thalli will reduce considerably the amount of light reaching the bottom layers. In addition, *Ulva* blades are not optically neutral because they preferentially absorb the blue and red regions of the light spectrum. Thus, a green-enriched spectrum under the *Ulva* canopies would be expected. Such a change of spectral composition will reduce the photosynthetically usable radiation (PUR) (Morel et al. 1987) within the canopy. Sediment also causes light attenuation as a variable amount of mud is deposited on and between *Ulva* thalli at low tide.

The aim of this study was to assess the propagation of light within *Ulva* canopies, as well as to follow the seasonal variation of the photosynthetic performance of *Ulva* species in the estuary. These results will allow us to compare the natural assemblage with

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the results obtained in the laboratory with *Ulva* cultured under different irradiances (Pérez-Lloréns et al. 1996).

MATERIALS AND METHODS

Field sampling. Plant material (*Ulva rotundata* and *Ulva curvata*) for light attenuation, photosynthesis, absorptance, and pigment measurements was collected at low tide in the Palmones river estuary (southern Spain), kept cool in darkness, and transported to the laboratory in a polyethylene icebox within 4 h of sampling. Some thalli were kept in liquid nitrogen for analysis of tissue C–N content (Perkin-Elmer C-N-H 240-C analyzer; Norwalk, CT). For detailed information on the seasonal variation of physicochemical and biological variables in the estuary, see Hernández et al. (1997).

Light attenuation. The light attenuation caused by water was monitored during one tidal cycle, where high water occurred in the early afternoon, in April 1994. Time series of photon fluence rate (PFRs) in air and in water were recorded with two spherical quantum sensors (LiCor Li 193SA; Lincoln, Nebraska) at 15-min intervals and stored in a LiCor LI-1000 radiometer. The height of the water column over the submerged sensor, placed 5 cm above the sediment surface, was monitored with a metric scale placed adjacent to the sensor. The attenuation coefficient of water column (K_w) was calculated according to Beer's Law, using the recorded differences in photon fluence rates between the two sensors and the depth of the water column.

Laboratory measurements of light attenuation by *Ulva* canopies were carried out from March 1994 to December 1994. Measurements were performed by placing a variable number of either *U. rotundata* or *U. curvata* layers (usually seven to eight) over a flat quantum sensor (LiCor LI 192SB) connected to a LiCor LI-1000 radiometer. A fluorescent white light source was placed perpendicular to the canopy. The light attenuation followed an exponential curve. The attenuation coefficient (K_u, layer^{-1}) was computed from the slope of the regression line $\ln I/I_o = -K_u \cdot$layer, where I_o corresponds to the incident light and I to the irradiance reaching the detector after passing throughout different *Ulva* layers. The regression coefficient (r^2) was always about 0.96.

Wide band absorptance (400–700 nm) was measured with an integrating sphere (LiCor Li-1800-12) connected to a LiCor Li-1800 UW spectroradiometer, using one to three *Ulva* layers with similar chlorophyll concentrations. The absorptance spectrum of the structural components of the thalli was measured in *Ulva* discs after extraction for 24 h in *N*, *N*-dimethyl formamide (DMF). Wide band absorptance data versus chlorophyll concentration are from Pérez-Lloréns et al. (1996).

The PUR was calculated according to Morel et al. (1987) using A (λ) as a weighting function describing the probability that a photon of a given wavelength will be absorbed by the thallus. The dimensionless variable was derived from the absorption spectrum of *Ulva* by dividing the spectrum by the maximal absorption (A_{max}). For *Ulva*, A_{max} occurs *in vivo* at $\lambda = 440$ nm. The spectrally averaged photosynthetically active radiation (PAR)/PUR ratio was calculated in the PAR range (400–700 nm).

To assess the effect of muddy sediment on the light within the *Ulva* canopy, sediment at different dilutions (from 0% to 30% sediment dry weight (DW) in water, as normally found in the estuary) was paintbrushed between *Ulva* layers and the attenuation coefficient through *Ulva* canopies was determined as described above.

Photosynthetic measurements. The seasonal variation of the photosynthetic performance was monitored from July 1994 to May 1995. Prior to the measurements, discs of 10-mm diameter were excised from *Ulva* thalli and maintained overnight in dim light (Philips TLD 36W/54; Germany) at a constant temperature (15° C) in artificial seawater (Woelkerling et al. 1983). Oxygen evolution was measured with a Hansatech polarographic O_2 electrode (Hansatech Ltd.; Norfolk, U.K.) at 15° C. Photosynthesis–PFR curves were performed in triplicate at 12 PFRs from 0 to 1750 μmol photons·m^{-2}·s^{-1} (measured with a radiometer LiCor Li-1000 with a cosine collector, LiCor LI 192SA). *Ulva* discs were held perpendicular to the light field (high-intensity light source LS2, Hansatech Ltd.) with a nylon hook through the capillary of the plunger of a 3-mL reaction vessel. Photosynthetic parameters, light-saturated photosynthetic rate (P_{max}) and photosynthetic efficiency (α) were estimated from the hyperbolic tangent model of Jassby and Platt (1976), because it showed the best fit for *Ulva* species (Pérez-Lloréns et al. 1996). The light compensation point (L_{CP}) was calculated as dark respiration (R_d)/α. Quantum yield for oxygen evolution (ϕ) was calculated as α/absorptance.

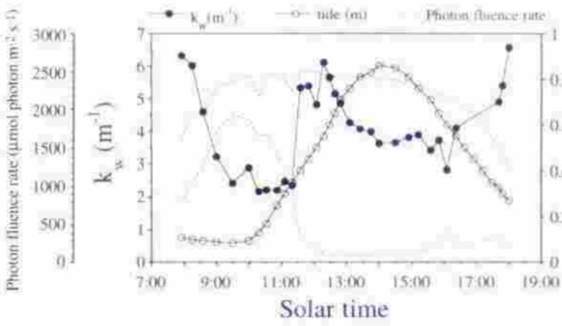

FIG. 1. Daily variation of tidal elevation, incident and underwater scalar irradiance, and light attenuation coefficient of the water column (K_w).

Absorptance measurements and chlorophyll determinations were carried out after every P–PFR curve. Pigments were extracted from fresh discs (10 mm diameter) in 4 mL of DMF, kept in darkness overnight at 4° C, and determined according to Porra et al. (1989). Absorptance (A) was estimated as: $A = 1 - 10^{-OD}$, where OD is the optical density (absorbance) of the discs at 678 nm measured in a spectrophotometer (Hitachi U-1100) with the opal-glass technique (Shibata 1959). Wide band absorptance (400–700 nm) was calculated with the calibration functions obtained in a previous study (Pérez-Lloréns et al. 1996). The short-term effect of temperature on the photosynthetic rate at light saturation (810 μmol photons·m^{-2}·s^{-1}) (P_{max}), at a subsaturating light level of 42 μmol photons·m^{-2}·s^{-1} (P_{subsat}) and R_d, was measured. *Ulva rotundata* thalli collected in November (mean temperature ca. 18° C) were maintained for 24 h at 15° C and subjected to a wide range of temperatures (from 10 to 30° C). The influence of temperature on photosynthetic parameters was calculated from the Arrhenius equation, and the Q_{10} values were computed (Price and Stevens 1982). The seasonal P_{max} and R_d data were corrected by temperature.

Statistical analysis. Seasonal differences of photosynthetic parameters, chlorophyll, and absorptance between species were analyzed for significance by a two-way analysis of variance (ANOVA). Multiple *post hoc* comparisons were done by the Tukey test (Zar 1984). The minimum significant differences (MSD) were calculated for the seasonal variation of the parameters (Fry 1993). In all cases the significance level was set at 5% probability.

RESULTS

Light attenuation. The light attenuation by the water column is shown in Figure 1. Although the tidal amplitude is low (about 1 m) and the estuary is shallow (1.5 m mean depth), underwater light was greatly reduced as a consequence of a high K_w, which, in turn, varied throughout the day. Midday K_w values were lower than those in the morning and at dusk because of the upward bias in K_w caused by low sun angles. Tidal movements also resulted in higher K_w values than those recorded at high water. The mean K_w was about 4 m^{-1}.

Downward photon irradiance was further attenuated as it passed through the thick *Ulva* mats. The mean values of K_u in *Ulva* canopies ranged from 0.2 to 0.5 layer^{-1} (Fig. 2). The seasonal trend of the attenuation coefficient for *U. rotundata* (which mainly occurs in

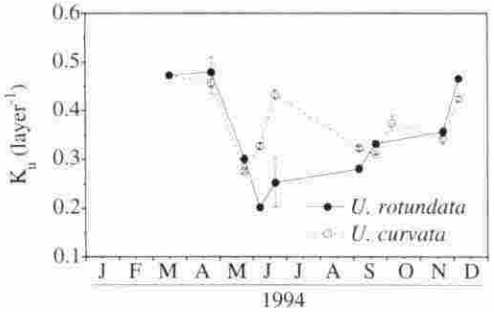

FIG. 2. Seasonal variation of the light attenuation coefficient (K_u) through *Ulva* canopies. *Ulva rotundata* was collected from the mudflat of Palmones river estuary, and *U. curvata* was collected from the main flume.

the intertidal mudflats) coincided with the seasonal variation of chlorophyll (Hernández et al. 1997, Fig. 8). For *U. curvata* (which mostly grows subtidally at the main flume), a less obvious pattern was observed in summer, as these algae are usually under lower light intensities. The light attenuation caused by the structural components (measured in DMF-treated translucent *Ulva* thalli) was much lower than that of intact *Ulva* thalli (0.077 and 0.458 layer^{-1}, respectively). Chlorophyll concentration can also be used to assess the light attenuation by the canopy. The absorptance was a saturation function of the chlorophyll concentration (Fig. 3), indicating self-shading among pigments at high chlorophyll concentrations. The parameter A_0 ($A_0 = 1 - T_0$), was 0.11, which indicates the absorptance due to structural components of the thalli (Markager 1993). DMF-treated thalli showed a similar value (about 0.08).

Besides light attenuation, the spectrum was altered as light was selectively absorbed by the canopy. The absorptance spectra, and the resulting spectral irradiance under one, two, and three layers of *Ulva* are shown in Figure 4. Blue and red absorption by chlorophylls was enhanced relative to green wavelengths, as the number of layers increased (Fig. 4A), modifying the spectral composition of the light (Fig. 4B). The light was impoverished in blue and red wavelengths, whereas the green band was little affected. As a result of the preferential light absorption, the ratio PAR/PUR increased through the canopy (Fig. 5). For the incident light, the lowest PAR/PUR ratios were found in the blue region (PAR/PUR = 1 at $\lambda = 440$ nm *in vivo*), whereas they were higher in the green region of the spectrum (Fig. 5A). In addition, the PAR/PUR ratios were higher as light passed through *Ulva* layers, especially at blue and red wavelengths (Fig. 5A). The spectrally averaged PAR/PUR ratio (between 400 and 700 nm) was 2.65 for one *Ulva* thallus, increasing exponentially as a function of the number of layers in the canopy (Fig. 5B).

At low tide, mud deposition within *Ulva* canopies caused a further light reduction. The K_u increased linearly as a function of the sediment load between *Ulva* layers (Fig. 6). The K_u data shown previously (Fig. 2) were obtained in the laboratory from clean material where the mud was removed. This is not a real situation in the field, where the mud is deposited irregularly on and among the *Ulva* sheets. Some estimations of K_u through *Ulva* canopies were performed in the field. In this case, as the *Ulva* thalli were bounded by a muddy layer of estuarine water, the estimated attenuation values were higher than those estimated at the laboratory (0.755 versus 0.444 layer^{-1}). In an extreme situation, when a spot of sediment was deposited over

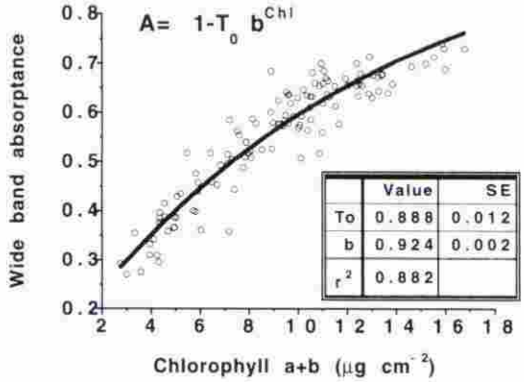

FIG. 3. Wide band (400–700 nm) absorptance of *Ulva* thalli as a function of total chlorophyll concentration on areal basis. Data were taken from Pérez-Lloréns et al. (1996).

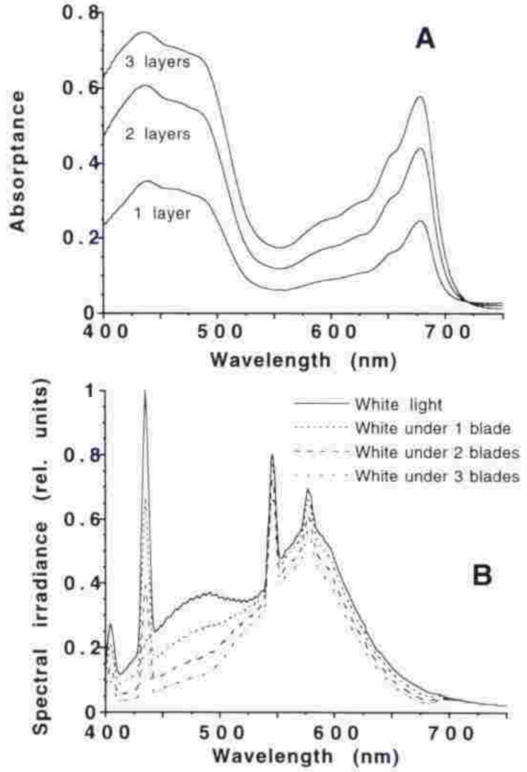

FIG. 4. A) Absorptance spectra of one, two, and three layers of *Ulva*. B) Spectral distribution of a white light source (Silvania F18/GRO fluorescent lamp) under a different number (zero to three) of *Ulva* layers.

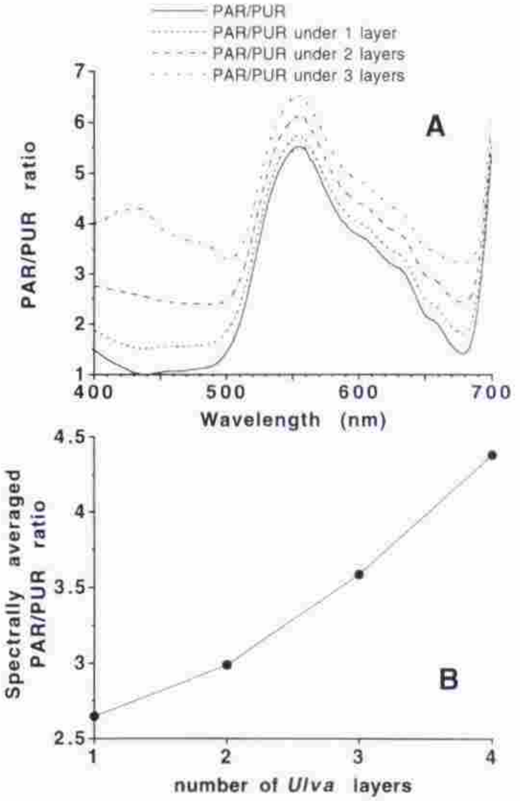

FIG. 5. A) Spectral distribution of the PAR/PUR ratio reaching an *Ulva* thalli and under a canopy of different numbers of *Ulva* layers. B) Spectrally averaged (400–700 nm) PAR/PUR ratio as a function of the number of *Ulva* layers in the canopy.

a blade (about 30% DW sediment), K_u was 4 times greater than without sediment (Fig. 6).

Photosynthetic performance. The P_{max} and L_{CP} showed significant interspecific differences ($P < 0.05$), with *Ulva curvata* generally displaying higher values than those of *U. rotundata* (Fig. 7, Table 1). No significant differences were found between species for chlorophyll content and absorptance (Fig. 8). Both species showed significant seasonal variations of P_{max}, ϕ, L_{CP},

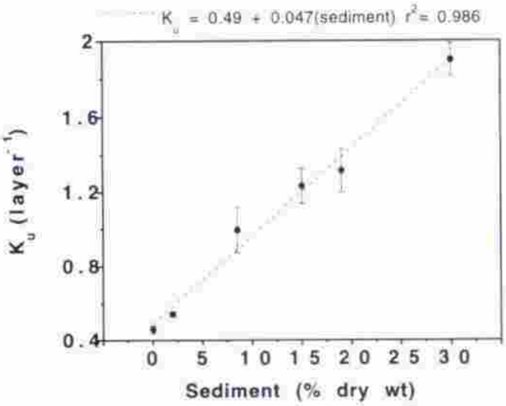

FIG. 6. Light attenuation coefficient through *Ulva* canopies as a function of the mud concentration (% dry weight sediment) deposited between the *Ulva* layers.

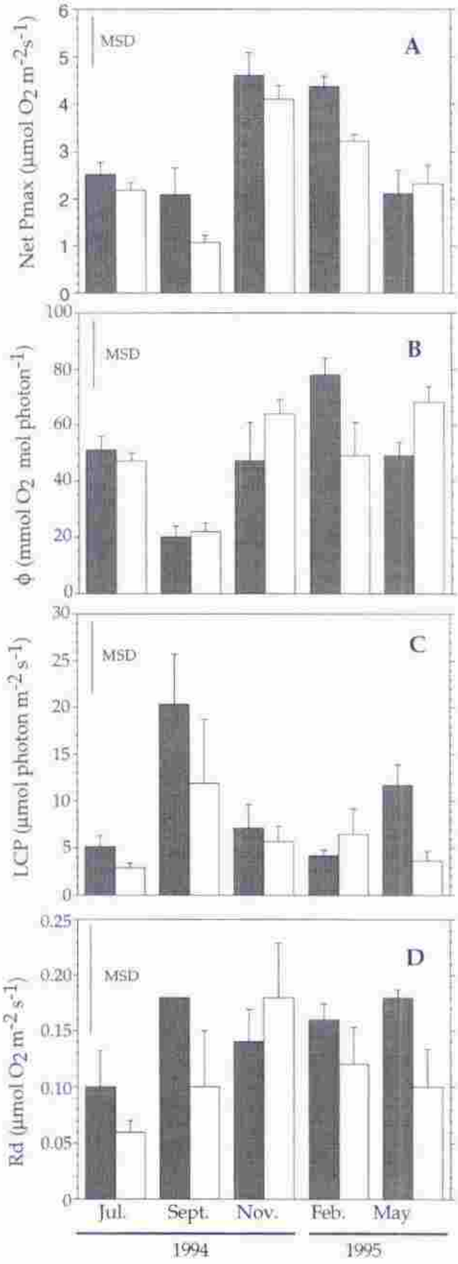

FIG. 7. Seasonal variation of A) light-saturated rate of photosynthesis; B) quantum yield; C) light compensation point; and D) dark respiration for *U. curvata* (shaded columns) and *U. rotundata* (white columns). Data are presented as means ± SE ($n = 3$). Vertical bars on the left indicate the minimum significant differences.

TABLE 1. *F-values of two-way ANOVA with replication ($n = 3$) of photosynthetic parameters, chlorophyll content, and absorptance (A) measured in the two* Ulva *species in different months. Significance levels are:* ** $P < 0.025$; * $P < 0.05$; *ns, no significant difference* ($P > 0.05$).

Source of variation	P_{max}	R_d	L_{CP}	ϕ	Chl ($a + b$)	A
A) Species	6.56**	ns	5.32*	ns	ns	ns
B) Month	22.16**	ns	6.13**	7.37**	9.36**	27.57**
A × B	ns	ns	ns	3.20*	ns	5.70**

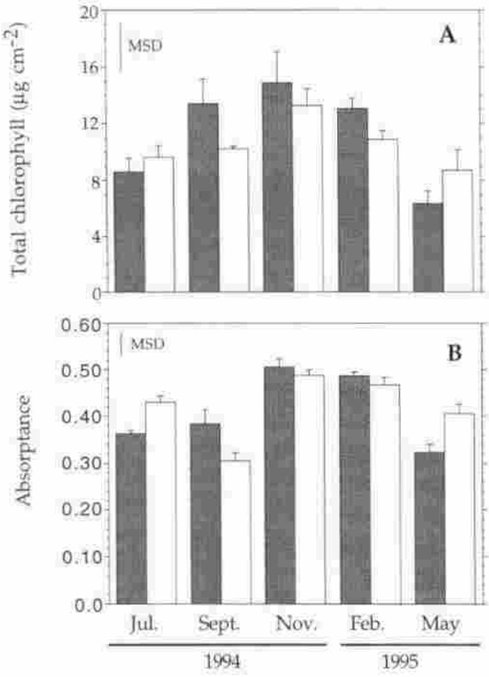

FIG. 8. Seasonal variation of A) total chlorophyll and B) absorptance for *U. curvata* (shaded columns) and *U. rotundata* (white columns). Data are presented as means ± SE ($n = 3$). Vertical bars on the left indicate the minimum significant differences.

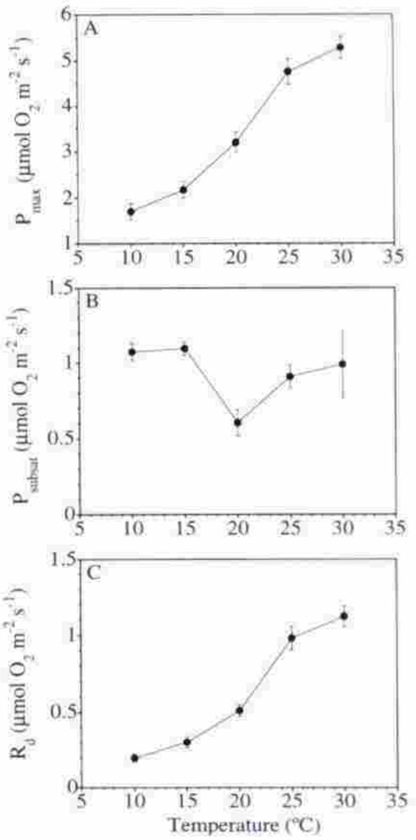

FIG. 9. Short-term effect of temperature on the rate of photosynthesis of *Ulva rotundata* at A) light saturation, B) subsaturating light level (42 µmol photons·m^{-2}·s^{-1}), and C) dark respiration. Data are presented as means ± SE ($n = 3$).

chlorophyll content, and absorptance ($P < 0.025$), while R_d was not affected (Figs. 7, 8). The highest P_{max}, ϕ, chlorophyll content, and absorptance were found in winter, and the lowest values were found in summer. In contrast, a maximum I_{CP} was measured in summer.

In the interpretation of the photosynthetic performance, the dependence of photosynthesis on temperature must be considered (Davison 1991). We assayed photosynthesis at a series of standard temperatures in *U. rotundata* grown at 18° C. The effects of temperature at light saturation, at a subsaturating light level, and on dark respiration are shown in Figure 9. The P_{max} and R_d showed a marked temperature dependence, whereas the photosynthesis rate at a subsaturating light level was unaffected. The estimated Q_{10} values were 2.44 for R_d and 1.79 for P_{max}. Photosynthetic data were corrected by the *in situ* mean temperature, which ranged from 13.8° C in February to 27.2° C in July. The seasonal trend observed for P_{max} at a standard temperature of 15° C was maintained, although the differences were damped. The R_d showed a significant maximum in summer and was minimum in winter (Fig. 10).

DISCUSSION

The primary production of *Ulva* populations depends largely on photosynthetic performance and, therefore, on the availability of light within *Ulva* canopies. Intertidal and subtidal populations are subjected to a variable light regime because they are covered by a continually changing depth of water as the tides ebb and flow. Despite a low tidal amplitude in the Palmones river estuary (about 1 m), the underwater light field was sharply reduced as denoted by the high K_w values, typical of estuarine ecosystems (Kirk 1994). K_w varied through the day. In the morning and at dusk, reflectance at the water surface increases as the zenith angle of the incident radiation changes. In addition, during the phase of tidal ebb and flow, the resuspension of bottom sediments can increase the attenuation coefficient several-fold in shallow waters (Kirk 1994). Transparency of the water column is highly variable in time and space in estuarine waters, high frequency (daily) temporal fluctuations being even more relevant than low frequency ones (Zimmerman et al. 1994). Attenuation caused by the water column will be important when high tides coincide with light periods. In contrast, when algae emerge at midday, the upper layer of the canopy is exposed to saturating irradiances but also suffers desiccation and thermal stress, especially in summer (Hernández et al. 1997).

Although light absorption by canopies is seldom measured in aquatic systems (Zimmerman et al. 1994, Davison and Pearson 1996), this process results in a further reduction of the light passing

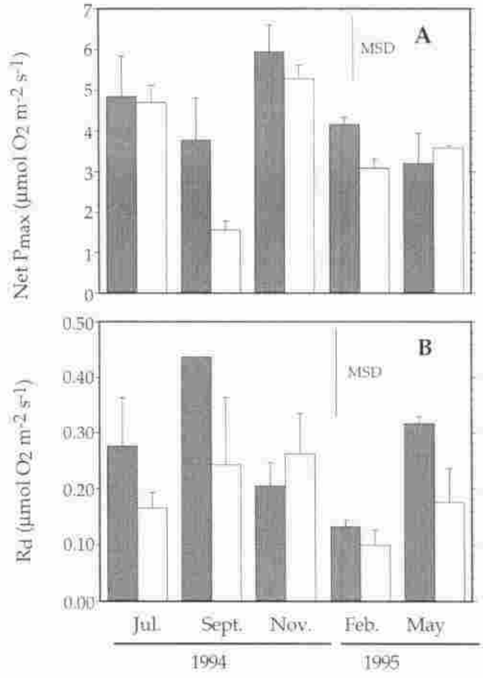

FIG. 10. Q_{10} temperature-corrected data of A) light-saturated rate of photosynthesis and B) dark respiration in a seasonal cycle for *U. curvata* (shaded columns) and *U. rotundata* (white columns). Data are presented as means ± SE (n = 3). Vertical bars indicate the minimum significant differences.

through the algal mats. K_u varied seasonally, chlorophyll being mainly responsible for light attenuation. A considerable proportion of incident light is attenuated in the canopy (K_u = 0.5 layer^{-1} means a light attenuation of about 40% layer^{-1}). On the contrary, structural components of the thalli accounted for a small proportion of light attenuation (about 8%).

An alternative way to estimate the light attenuation by the canopy is from chlorophyll data, considering the regression of absorptance as a function of chlorophyll concentration (Henley & Ramus 1989, Markager 1993) (Fig. 3). The curve followed a power function, indicating that there is an upper limit to light absorption (Margalef 1974). As a result, the absorptance normalized to chlorophyll concentration (spectrally averaged *in vivo* cross section, a*, in m^2·mg^{-1} chlorophyll) follows a negative exponential curve with respect to chlorophyll ($a^* = 0.010 \exp(-0.005)$, $r^2 = 0.81$), which is similar to the relationship found by Mercado et al. (1996) in *U. rigida*. This is explained on the basis of an enhanced package effect at high chlorophyll concentrations (Berner et al. 1989, Markager 1993). The lower limit (A_u = 0.11) indicated the absorptance due to the structural components of the thalli, which was close to the value reported for *U. lactuca* by Markager (0.13, 1993) and to that found in DMF-treated translucent *Ulva* discs.

Within the *Ulva* canopy, the light was not only attenuated but also spectrally filtered. The ratio PAR/PUR increased through the canopy. Thus, a lower proportion of photosynthetically usable radiation for photosynthesis by *Ulva* was available to thalli located deeper in the canopy.

The effect of sediment load is quite variable, depending on the amount of mud deposited within the canopy. Some estimates of K_u in the field were double those found in the laboratory. In addition, it was common to find some areas of the thalli completely covered by sediment spots; this almost completely occludes the light reaching lower layers. In that case, the role of heterotrophic growth on the deepest *Ulva* layers should be considered (Markager and Sand-Jensen 1990).

The field situations where a large number of *Ulva* layers form the canopy implies a steep light gradient. That may explain, in part, the observed differences between the growth rates estimated in cages and those found by biomass variation at the estuary (Hernández et al. 1997). Whether the *Ulva* sheets are permanently arranged in the same order within the canopy or are randomly mixed by tidal movements remains to be examined.

The photosynthetic performance of field material can be compared with the performance obtained in the laboratory for *Ulva* species cultured at a wide range of irradiances (Pérez-Lloréns et al. 1996). There is no reason to infer the photosynthetic performance in the field from laboratory studies, as these are performed under controlled conditions. The maximum values for P_{max} are correlated with periods of high chlorophyll and tissue N content (data not shown), whereas in spring and summer, P_{max} was lower when chlorophyll and N were low. This is in accordance with the results found in a previous study (Pérez-Lloréns et al. 1996). In fact, there was not a significant seasonal trend in chlorophyll-normalized P_{max}, except in September, when P_{max} was lower (data not shown). In summer, the lowest quantum yield and the highest L_{CP} were found in parallel with the lowest P_{max}, as was found in the laboratory under high light conditions (Pérez-Lloréns et al. 1996). The photosynthetic data corrected for Q_{10} indicated that, in natural conditions, the realized P_{max} on an areal basis was higher than that measured at standard temperature in summer, thus equalizing the seasonal differences found when photosynthesis was measured at one standard temperature. With respect to R_d, a summer maximum and a winter minimum was found when considering the temperature effects. In *Laminaria hyperborea*, temperature-adjusted RUBISCO activity was maximal in summer, whereas the maximum activity was found in spring when assayed at the same temperature (Küppers and Weidner 1980). Similarly, Hernández (1996) found significant differences in alkaline phosphatase activity in *Porphyra umbilicalis* when measured at algal mat or standard (25° C) temperature. The estimated photosynthetic performance, together with the different light attenuation processes, can be used to infer primary production in *Ulva* canopies. The photosynthetic metabolism in different light regimes within the canopy also needs further research.

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