



Revista Chilena de Historia Natural

ISSN: 0716-078X

editorial@revchilhistnat.com

Sociedad de Biología de Chile

Chile

RAUTENBERGER, RALF; MANSILLA, ANDRÉS; GÓMEZ, IVÁN; WIENCKE,
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Magellan (Chile)
Revista Chilena de Historia Natural, vol. 82, núm. 1, 2009, pp. 43-61
Sociedad de Biología de Chile
Santiago, Chile

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Photosynthetic responses to UV-radiation of intertidal macroalgae from the Strait of Magellan (Chile)

Respuestas fotosintéticas a la radiación UV en algas intermareales del Estrecho de Magallanes (Chile)

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ABSTRACT

For the first time, the photosynthetic performance of field-grown macroalgae from the Magellan Strait was evaluated with respect to their photoadaptation in the field and acclimation potential to ultraviolet radiation. Five macroalgal species were collected in the eulittoral and the upper sublittoral: *Ulva intestinalis*, *Porphyra columbina*, *Adenocystis utricularis*, *Desmarestia confervoides* and *D. ligulata*. Photosynthesis vs. irradiance (P-I) curves of macroalgae cultivated in the laboratory under low white light intensities more than a week were used to assess the acclimation potential to irradiance conditions in the field. Both, photosynthetic parameters referred to as maximum electron transport rate (ETR_{max}) and light saturation points of photosynthesis (I_k) were species-specific and did not correlate with the position on the shore. I_k ranging between 80 and 215 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ was indicative of moderate sun-adaptation in all studied species. The acclimation potential to UV-radiation was determined as the extent and the rates (m_{inh}) of PSII inhibition (resulting from decreased maximum PSII-quantum yield (Fv/Fm)) after four hours of UV-exposure and as the subsequent rates of recovery (m_{rec}) in dim PAR. The results suggest that photosynthesis of each species during UV-exposure was transiently down regulated rather than damaged. Furthermore, no reductions in ETR_{max} were detected after 4 h exposure to UV-A and UV-B-radiation, and consequently the Calvin cycle could not be affected. Thus, Fv/Fm was a more sensitive parameter than ETR_{max} explaining the photosynthetic UV acclimation. Both, the rates of inhibition and the rates of recovery were not correlated with the morpho-functional groups of macroalgae nor to their vertical distribution. Thus, although the capacity to acclimate to UV-radiation varied among the different species, data suggest that such responses are based on metabolic adjustments or possibly photoprotective strategies. In conclusion and taking into account the light adaptation characteristics, all species collected in the midlittoral and the upper sublittoral at the Strait of Magellan seem to be well acclimated to UV-B doses occurring at their habitat, which might be a pre-requisite to withstand enhanced solar UV-B during ozone depletion or summertime irradiance conditions.

Key words: UV-radiation, macroalgae, photosynthesis, photoacclimation, Strait of Magellan.

RESUMEN

La actividad fotosintética de algas provenientes del Estrecho de Magallanes fue medida por primera vez con el propósito de determinar su fotoadaptación en terreno y su potencial de aclimatación a la radiación ultravioleta. Cinco especies fueron recolectadas desde la zona eulitoral y sublitoral superior: *Ulva intestinalis*, *Porphyra columbina*, *Adenocystis utricularis*, *Desmarestia confervoides* y *D. ligulata*. Curvas de fotosíntesis versus irradiancia (P-I) medidas en algas cultivadas en el laboratorio por más de una semana fueron usadas para determinar la aclimatación potencial de las algas en su hábitat. Tanto las capacidades fotosintéticas, determinadas a través de la tasa máxima de transporte de electrones (ETR_{max}), como los puntos de saturación de fotosíntesis (I_k) fueron especies-específicas, no observándose correlaciones con la distribución vertical de

las algas. Valores de I_k con rangos entre 80 y 215 $\mu\text{mol m}^{-2} \text{s}^{-1}$ indicaron una moderada adaptación a la luz en todas las especies estudiadas. La aclimatación a la radiación UV fue determinada a través del grado de disminución del rendimiento cuántico máximo del PSII (Fv/Fm) y su subsiguiente tasa de recuperación. Los resultados sugieren que bajo exposición a la radiación UV, la fotosíntesis no es dañada sino más bien regulada a la baja de forma transitoria. Además, no se observaron reducciones en ETRmax después de 4 h de exposición a la radiación UV-A y UV-B, y por consiguiente el ciclo de Calvin pudo no ser afectado. De este modo, Fv/Fm fue un parámetro mucho más sensitivo que ETRmax para explicar la aclimatación de fotosíntesis a la radiación UV. Tanto las tasas de inhibición como las tasas de recuperación no estuvieron correlacionadas con grupos morfofuncionales ni con la distribución vertical. Por tanto, aunque la capacidad para aclimatar a la radiación UV varió entre las diferentes especies, los resultados sugieren que estas respuestas están basadas en ajustamientos metabólicos o posiblemente estrategias fotoprotectoras. En conclusión, y tomando en cuenta las características de adaptación a la luz, todas las especies colectadas en el mesolitoral y sublitoral del Estrecho de Magallanes están bien aclimatadas a las dosis de UV-B que ocurren en su hábitat, lo cual es un prerequisite para tolerar aumentos de UV-B durante disminución de ozono o durante condiciones de alta radiación en verano.

Palabras clave: radiación UV, macroalgas, fotosíntesis, fotoaclimatación, Estrecho de Magallanes.

INTRODUCTION

Chemical processes in the stratosphere over Antarctica lead to an annual depletion of ozone concentration in austral springtime since 1979 (Farman et al. 1985). When the ozone concentration in the air-column falls below the threshold of 220 Dobson Units, the so-called ozone hole develops (Stolarski et al. 1990). Ground-based measurements revealed a dramatic springtime loss of total ozone by $\approx 30\%$ over Antarctica in 1979 compared with normal conditions (Farman et al. 1985). As soon as the polar vortex over the Antarctic breaks down in late spring, the ozone-poor air mass may move towards the southern tip of South America (Thompson 1991, Casiccia et al. 2003). Several times, the area of the Antarctic ozone hole has reached record sizes of more than 28 million km^2 , e.g., in the years 1998, 2000, 2003 and 2006 (Newman et al. 2007). Since the beginning of the 1990s, in September and October the Antarctic ozone hole has transiently extended as far north as to the southernmost regions of South America, e.g., Ushuaia (in 1990) and Punta Arenas (in 1993) (Casiccia et al. 2003). The most important consequence of low stratospheric ozone concentrations is the increase of solar UV-B-radiation on the Earth's surface (Casiccia et al. 2003), which is also affecting to aquatic environments (Tedetti & Sempéré 2006).

Irradiance conditions in aquatic environments depend on multiple factors such as optical properties of the water body, the time of day, season and cover of the sky by clouds

(Kirk 1994). Thus, marine organisms are exposed to rapidly changing irradiance conditions. In the case of (adult) macroalgae, which are strictly sessile, diverse metabolic mechanisms (e.g., photoacclimation and inhibition of photosynthesis) have been identified as a way to avoid impairments induced by UV-radiation (reviewed by Bischof et al. 2006).

Although various studies have hitherto investigated the response of macroalgae to UV-radiation in relation to their vertical distribution in temperate and polar regions (Bischof et al. 1999, Gómez et al. 2004, Rautenberger & Bischof 2006), no information is available about photoadaptation and acclimation potential of photosynthesis to UV-radiation of adult macroalgae occurring at Strait of Magellan (Mansilla et al. 2006) or southernmost Patagonia (Rautenberger & Bischof 2006), a region especially affected by transient Antarctic ozone hole (Casiccia et al. 2003).

The goal of this study was to examine the light adaptation status of macroalgal assemblages of the Magellan region, which may be primary targets of enhanced solar UV-B radiation with important consequences for the whole coastal ecosystem (Häder et al. 2007). An experiment to evaluate UV-susceptibility of photosynthesis of macroalgae growing at Strait of Magellan was conducted. This study represents a first attempt in order to gain insights into potential mechanisms of photobiological acclimation and tolerance in macroalgal assemblages exposed naturally to enhanced UV-B radiation.

MATERIAL AND METHODS

Algal material and experimental conditions

Five different macroalgal species (Table 1) from the tidal zone of the Strait of Magellan were collected at Punta Santa Ana (53.50° S, 70.93° W) during late austral summer on 16th and 29th March 2005 (Fig. 1). Immediately after sampling, specimens were transported in a cooled and dark box to the laboratory of the Department of Science and Natural Resources of the Institute of Patagonia at the Universidad de Magallanes in Punta Arenas (Chile). Macrothalli were raised in air-bubbled Provasoli enriched seawater (Provasoli 1968) in a climate room at 8 ± 1 °C with artificial radiation of $20 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ PAR (provided by one True Light Natural Daylight fluorescent tube, Osram, Germany). The temperature of the cultivation room was set up to the water temperature of the Strait of Magellan during summer according to the Meteorological Service of the Chilean Navy (www.shoa.cl/cendhoc/atlas/index.htm). Macroalgae were cultivated in the laboratory between eight and 13 days until experimentation. However, *Desmarestia ligulata* was used for UV-experiment one day after sampling. For UV-exposure experiments, algae were divided and spread out in a thin layer of macrothalli in Petri dishes to minimize self-shading. After 12 h of pre-incubation at $15 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ PAR (provided by one

True Light Natural Daylight fluorescent tube, Osram, Germany), radiation was supplemented with UV-A (provided by three UV-A-340 fluorescent tubes, Q-Panel Lab Products, Cleveland, USA) and UV-B radiation (provided by three TL20W/12RS, Philips, The Netherlands) for 4 h. By the use of different cut-off filters algae were either exposed to PAR alone (controls, $\lambda \geq 400$ nm, achieved by Ultraphan URUV, Digefra, Munich, Germany), to PAR + UV-A ($\lambda \geq 320$ nm, Folanorm SF-AS, Folex, Cologne, Germany) or to PAR + UV-A + UV-B ($\lambda \geq 295$ nm, Ultraphan URT, Digefra, Munich, Germany). The light regime of the experimental set-up during UV-exposure is summarized in Table 2 and the spectral composition in Fig. 2. In order to study effects of UV radiation (particularly UV-B radiation) on macroalgal photosynthesis exclusively, intensities of PAR were kept low at about $17 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. Under such unrealistic radiation conditions, UV-effects on photosynthesis remain unmasked by high PAR induced effects as observed under natural radiation conditions. Light intensities and UV-irradiances were measured using an UV/VIS spectroradiometer (Ramses ACC Hyperspectral Sensor, TriOS GmbH, Oldenburg, Germany). The integral dose of exposed UV-B radiation (PAR + UV-A + UV-B, unweighted) over the entire experimental time (4 h) was 25.55 kJ m^{-2} . The biologically effective dose of $0.82 \text{ kJ m}^{-2} 4 \text{ h}^{-1}$ [according to the model for generalized plant damage of Caldwell (1971)] was chosen

TABLE 1

Macroalgal species used in the experiment, morpho-functional groups and depth distribution in the tidal zone at Punta Santa Ana (Strait of Magellan) near Punta Arenas, Chile

Especies usadas en los experimentos, grupos morfofuncionales y su distribución en profundidad en la zona intermareal de Punta Santa Ana (Estrecho de Magallanes) cerca de Punta Arenas, Chile

Species	Algal class	Position on the shore” at “Punta Santa Ana	Morpho-functional group of thalli
<i>Ulva intestinalis</i> L.	Ulvophyceae	Eulittoral	Sheet-like (tubular)
<i>Porphyra columbina</i> Montagne	Bangiophyceae	Eulittoral	Sheet-like
<i>Adenocystis utricularis</i> (Bory de Saint-Vincent) Skottsberg	Phaeophyceae	Eulittoral	Leathery (saccate)
<i>Desmarestia confervoides</i> (Bory de Saint-Vincent) M. Ramírez & A. Peters	Phaeophyceae	Upper sublittoral	Terete, branched
<i>Desmarestia ligulata</i> (Lightfoot) Lamouroux	Phaeophyceae	Upper sublittoral	Leathery

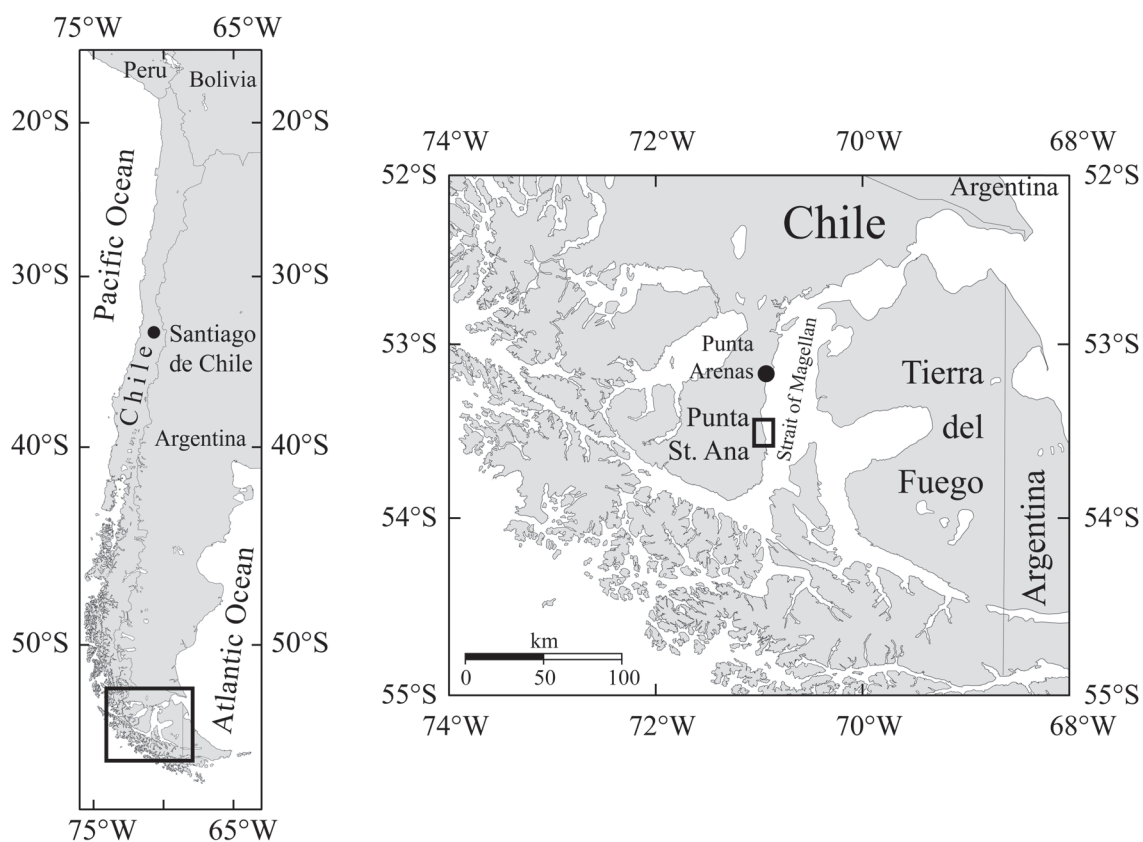


Fig. 1: Sampling site of used macroalgal species at Punta Santa Ana, 60 km south of Punta Arenas at Strait of Magellan, Chile.

Sitio de recolección de macroalgas en Punta Santa Ana, 60 km al sur de Punta Arenas en el Estrecho de Magallanes, Chile.

TABLE 2

Light regime in the experimental treatments measured by an UV/VIS spectroradiometer (Ramses ACC, TriOS GmbH, Oldenburg, Germany). Weighted UV-B irradiances were calculated by multiplying the action spectra for generalized plant damage response according to Caldwell (1971) and unweighted UV-B-radiation. Dose of unweighted and weighted UV-B-radiation during the entire experimental time of PAR + UV-A + UV-B exposure were $25.55 \text{ kJ m}^{-2} 4 \text{ h}^{-1}$ and $0.82 \text{ kJ m}^{-2} 4 \text{ h}^{-1}$, respectively. Different letters behind data represent statistically significant differences between light treatments

Condiciones de luz en los tratamientos experimentales medidos usando un espectroradiómetro UV/VIS (Ramses ACC, TriOS GmbH, Oldenburg, Alemania). Las radiaciones UV-B ponderadas fueron calculadas multiplicando el espectro de acción de la respuesta de daño generalizado en plantas de acuerdo a Caldwell (1971) y la radiación UV-B experimental.

Dosis de radiación UV-B experimentales (no ponderadas) y ponderadas durante el periodo de experimentación a exposiciones a PAR + UV-A + UV-B fueron $25.55 \text{ kJ m}^{-2} 4 \text{ h}^{-1}$ y $0.82 \text{ kJ m}^{-2} 4 \text{ h}^{-1}$, respectivamente. Diferentes letras representan diferencias estadísticamente significativas entre tratamientos de iluminación

Light treatment	PAR ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	UV-A (W m^{-2})	UV-B (W m^{-2}) unweighted	UV-B (W m^{-2}) weighted
PAR	17.4 ± 0.9^a	1.2 ± 0.0^a	0.00 ± 0.00^a	0.00 ± 0.00^a
PAR + UV-A	16.0 ± 0.9^a	9.8 ± 0.4^b	0.16 ± 0.00^b	0.00 ± 0.00^a
PAR + UV-A + UV-B	16.9 ± 0.9^a	11.6 ± 0.4^c	1.77 ± 0.01^c	0.06 ± 0.00^b

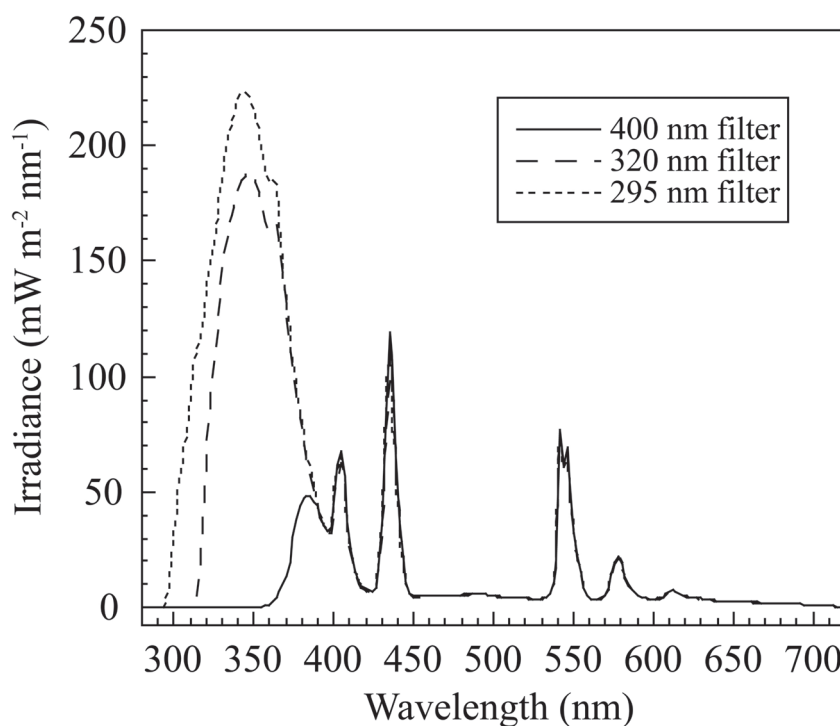


Fig. 2: Spectral composition of the experimental light regime exposed to the macroalgae. PAR alone (= control): solid line, PAR + UV-A: dashed line, PAR + UV-A + UV-B: dotted line.

Composición espectral del régimen de luz experimental al cual se expusieron las macroalgas. PAR solo (= control): línea sólida, PAR +UV-A: línea segmentada, PAR +UV-A + UV-B: línea punteada.

to simulate daily UV-B doses occurring both under ozone depletion in early spring (October) and under non depleted conditions in summertime caused by low a solar zenith angle over southernmost South America [around 31° in December, database of National Science Foundation UV Monitoring Network, USA (<http://www.biospherical.com/nsf/>)]. After UV-exposure, algae were cultivated under low PAR intensities of 20 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ for recovery. Measurements of chlorophyll *a* fluorescence were performed before (t_0), after two and 4 h of UV-exposure and after four and 24 h of recovery. The experiment performed with *P. columbina* was completed after 4 h of recovery; therefore data after 24 h of recovery are not available.

Chlorophyll *a* fluorescence measurements

Measurements of in vivo chlorophyll *a* fluorescence were performed with a portable pulse amplitude modulated fluorometer PAM-2100 (Walz GmbH, Effeltrich, Germany)

according to the protocol of Hanelt (1998). Pieces of algal material were taken from Petri dishes and samples were inserted into custom-made cuvettes filled with seawater at 8 ± 1 °C. The end of the fiber optic probe of the PAM-fluorometer was mounted to the algal samples at a distance of 5 mm. After the application of a 5 s far-red pulse, the brown and green algae were darkened for 5 min. Measuring the red alga, a second short, red, actinic pulse was given after 5 min. of dark adaptation. Basal fluorescence, F_0 , was determined by using the measuring beam and maximal fluorescence, F_m , was induced after applying a saturation pulse. Photosynthetic efficiencies were calculated according to the equation of Schreiber et al. (1994).

$$\frac{F_v}{F_m'} = \frac{(F_m' - F_t)}{F_m'} \quad (1)$$

The change of F_v/F_m over the experimental time was expressed as percentage of inhibition (%) and calculated by the formula:

$\text{m}^{-2} \text{s}^{-1}$, $n = 7$) and *D. ligulata* ($115.9 \pm 11.2 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, $n = 7$) were statistically lower than those of *U. intestinalis* and *D. confervoides* but not different among each other (Table 3).

Photosynthetic efficiency under UV-exposure

In all examined macroalgae, both incident UV-A and UV-B radiation caused a decrease of the photosynthetic efficiencies (Fv/Fm) and, thus, an increase of inhibition of PSII. However, exposure to low PAR intensities alone (= control) did not lead to a PSII inhibition. The UV-induced increase of PSII inhibition was already observed after two hours of exposure to UV-A and UV-B radiation. At that time, no statistical differences of inhibition were detected between both UV-treatments in all species with the exception of *D. confervoides*. Photosystem II of that species was inhibited up to 7 % due to incident UV-A radiation and to 12 % due to UV-B radiation (Fig. 3). After four hours, inhibition did not increase statistically despite its prolonged exposure to UV radiation. Therefore, *Desmarestia confervoides* exhibited pronounced differences of PSII inhibition between exposure to UV-A (7 %) and UV-B

radiation (16 %). Photosystem II of *U. intestinalis*, however, showed marked differences only after four hours because of increased PSII inhibition due to prolonged exposure to UV-B radiation. PSII was inhibited by UV-A radiation up to 16 % and due to UV-B-exposure to 25 % (Fig. 4). In *D. ligulata*, inhibition increased by the factor of two from 7 % after two hours to 14 % after four hours of UV-A-exposure. However, increase of inhibition from 12 % after two hours to 26 % after four of UV-B-exposure was not significant ($P > 0.05$). Nevertheless, impinging UV-B radiation caused a statistically higher inhibition of PSII than UV-A radiation (Fig. 5). In *P. columbina* and *A. utricularis*, maximum degrees of inhibition were already reached after two hours under both UV-treatments. They did not further increase despite prolonged UV-exposure of two hours additionally. In both species, neither UV-A radiation nor UV-B radiation caused significant differences of PSII inhibition at both times. UVA and UV-B radiation inhibited PSII to 5 to 13 % in *P. columbina*, respectively (Fig. 6). In *A. utricularis*, exposure to UV-A and UV-B radiation lead to an inhibition of 15 to 26 %, respectively (Fig 7).

TABLE 3

Photosynthetic versus irradiance (P-I) parameters determined from relative maximal electron transport rate (ETR_{max}) at continuously increasing actinic light intensities measured by pulse-amplitude modulated (PAM) chlorophyll fluorescence. Tested field-grown macroalgal species were measured under unstressed conditions. Data were submitted to one-way ANOVA ($P < 0.05$, Tukey-Kramer HSD test). Different letters denote statistical differences between each species for a corresponding P-I parameter

Parámetros de curvas fotosíntesis versus irradianza (P-I) determinados a partir de la tasa máxima de transporte de electrones (ETR_{max}) durante aumento continuo de intensidades de luz actínica usando fluorescencia de clorofilas de pulso/amplitud modulada (PAM). Las mediciones de algas crecidas en ambiente natural se realizaron mientras estas no se encontraban sometidas a estrés solar. Los datos fueron tratados aplicando ANOVA de una vía ($P < 0.05$; prueba de Tukey-Kramer HSD). Diferentes letras denotan diferencias estadísticas entre cada especie para cada parámetro P-I

Species	Initial linear slope, $\alpha[(\mu\text{mol photons m}^{-2} \text{s}^{-1})^{-1}]$	Relative ETR _{max} (r.u.)	$I_k(\mu\text{mol photons m}^{-2} \text{s}^{-1})$	n
<i>U. intestinalis</i>	0.79 ± 0.06^a	136.1 ± 15.2^a	174.3 ± 23.4^a	9
<i>P. columbina</i>	0.78 ± 0.18^a	74.8 ± 7.2^c	99.3 ± 21.3^b	6
<i>A. utricularis</i>	0.80 ± 0.19^a	59.1 ± 11.2^c	80.4 ± 33.0^b	7
<i>D. confervoides</i>	0.47 ± 0.06^b	98.6 ± 18.6^b	215.0 ± 54.0^a	8
<i>D. ligulata</i>	0.55 ± 0.05^b	63.2 ± 6.3^c	115.9 ± 11.2^b	7

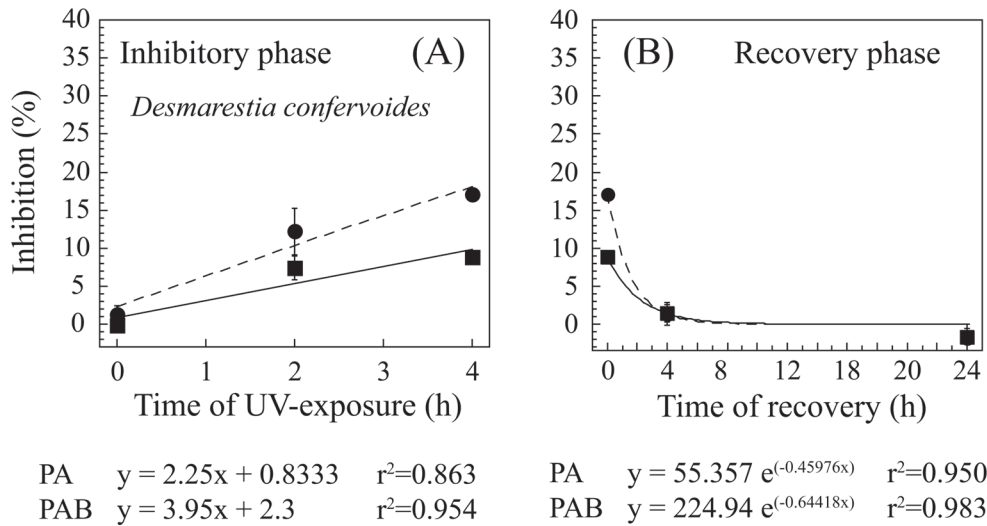


Fig. 3: *Desmarestia confervoides*. Degree of photoinhibition (A) due to PAR + UV-A (PA: solid line) and PAR + UV-A + UV-B-exposure (PAB: dashed line) and its subsequent recovery (B) up to 24 h in dim PAR. Photoinhibition data were fitted to a linear regression ($y = mx + n$), while data of recovery phases were adjusted to an exponential function ($y = a \cdot e^{(-bx)}$). Equations and coefficients of determination are shown for each phase.

Desmarestia confervoides. Grado de fotoinhibición (A) debido a la exposición a PAR + UV-A (PA: línea sólida) y PAR + UV-A + UV-B (PAB: línea segmentada) y su subsiguiente recuperación (B) a las 24 h de exposición en luz tenue. Las curvas de fotoinhibición fueron calculadas usando regresión lineal, mientras que las fases de recuperación fueron ajustadas a una función exponencial ($y = a \cdot e^{(-bx)}$). Las ecuaciones y coeficientes de determinación son indicadas para cada fase.

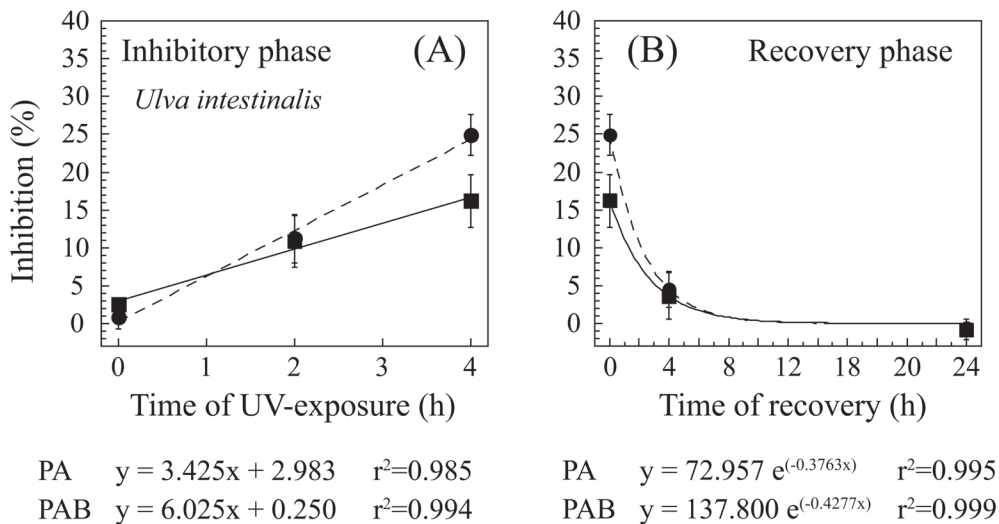


Fig. 4: *Ulva intestinalis*. Degree of photoinhibition (A) due to PAR + UV-A (= PA: solid line) and PAR + UV-A + UV-B-exposure (PAB: dashed line) and its subsequent recovery (B) up to 24 hours in dim PAR. Photoinhibition data were fitted to a linear regression ($y = mx + n$), while data of recovery phases were adjusted to an exponential function ($y = a \cdot e^{(-bx)}$). Equations and coefficients of determination are shown for each phase.

Ulva intestinalis. Grado de fotoinhibición (A) debido a la exposición a PAR + UV-A (PA: línea sólida) y PAR + UV-A + UV-B (PAB: línea segmentada) y su subsiguiente recuperación (B) a las 24 h de exposición en luz tenue. Las curvas de fotoinhibición fueron ajustadas a una regresión lineal, mientras que las fases de recuperación fueron ajustadas a una función exponencial ($y = a \cdot e^{(-bx)}$). Las ecuaciones y coeficientes de determinación son indicadas para cada fase.

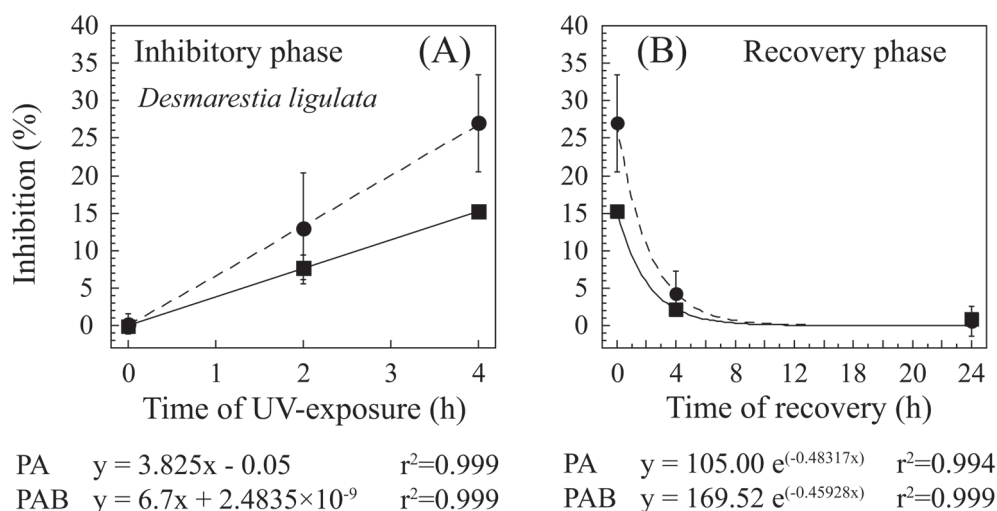


Fig. 5: *Desmarestia ligulata*. Degree of photoinhibition (A) due to PAR + UV-A (PA: solid line) and PAR + UV-A + UV-B-exposure (PAB: dashed line) and its subsequent recovery (B) up to 24 h in dim PAR. Photoinhibition data were fitted to a linear regression ($y = mx + n$), while data of recovery phases were adjusted to an exponential function ($y = a \cdot e^{(-bx)}$). Equations and coefficients of determination are shown for each phase.

Desmarestia ligulata. Grado de fotoinhibición (A) debido a la exposición a PAR + UV-A (PA: línea sólida) y PAR + UV-A + UV-B (PAB: línea segmentada) y su subsiguiente recuperación (B) a las 24 h de exposición en luz tenue. Las curvas de fotoinhibición fueron ajustadas usando regresión lineal, mientras que las fases de recuperación fueron ajustadas a una función exponencial ($y = a \cdot e^{(-bx)}$). Las ecuaciones y coeficientes de determinación son indicadas para cada fase.

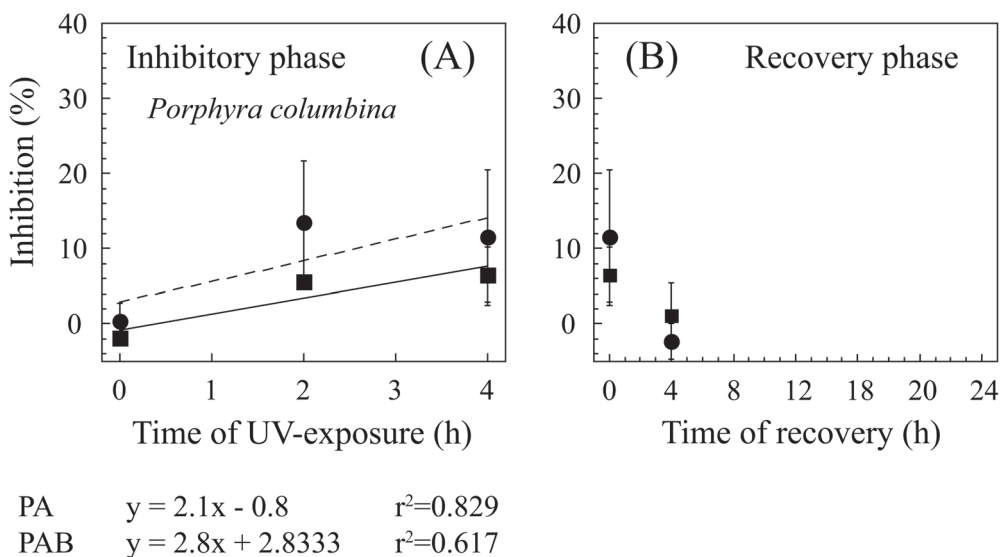


Fig. 6: *Porphyra columbina*. Degree of photoinhibition (A) due to PAR + UV-A (= PA: solid line) and PAR + UV-A + UV-B-exposure (PAB: dashed line) and its subsequent recovery (B, right). The experiment was cancelled after four hours of recovery; therefore, data of 24 hours of recovery are not available. Photoinhibition data were fitted to a linear regression ($y = mx + n$). Equation and coefficient of determination is only shown for inhibitory phase.

Porphyra columbina. Grado de fotoinhibición (A) debido a la exposición a PAR + UV-A (PA: línea sólida) y PAR + UV-A + UV-B (PAB: línea segmentada) y su subsiguiente recuperación (B) a las 4 h de exposición en luz tenue. Las curvas de fotoinhibición fueron ajustadas a una regresión lineal. Las ecuaciones y coeficientes de determinación son indicados para la fase de inhibición.

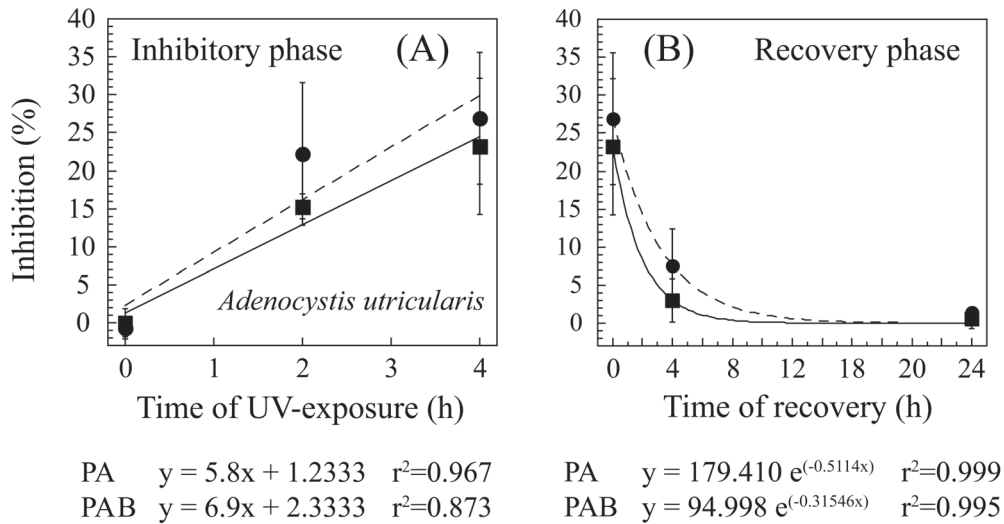


Fig. 7: *Adenocystis utricularis*. Degree of photoinhibition (A) due to PAR + UV-A (= PA: solid line) and PAR + UV-A + UV-B-exposure (PAB: dashed line) and its subsequent recovery (B) up to 24 h in dim PAR. Photoinhibition data were fitted to a linear regression ($y = mx + n$), while data of recovery phases were adjusted to an exponential function ($y = a \cdot e^{(-bx)}$). Equations and coefficients of determination are shown for each phase.

Adenocystis utricularis. Grado de fotoinhibición (A) debido a la exposición a PAR + UV-A (PA: línea sólida) y PAR + UV-A + UV-B (PAB: línea segmentada) y su subsiguiente recuperación (B) a las 24 h de exposición en luz tenue. Las curvas de fotoinhibición fueron ajustadas usando regresión lineal, mientras que las fases de recuperación fueron ajustadas a una función exponencial ($y = a \cdot e^{(-bx)}$). Las ecuaciones y coeficientes de determinación son indicadas para cada fase.

Highest rates of inhibition (m_{inh}) were detected in *A. utricularis* (UVA: 5.80 ± 1.95 , UV-B: 6.91 ± 1.91 ; $n = 3$), *U. intestinalis* (UVA: 3.30 ± 0.63 , UV-B: 6.08 ± 0.88 ; $n = 3$) and *D. ligulata* (UVA: 3.83 ± 0.38 , UV-B: 6.67 ± 1.53 ; $n = 3$) exposed to both UV treatments (Fig. 8). The other two species (*P. columbina* and *D. confervoides*) exhibited low inhibition rates of 2.17 ± 0.58 and 2.24 ± 0.05 (both $n = 3$) due to UV-A exposure and 2.75 ± 1.64 and 3.97 ± 0.25 (both $n = 3$) under UV-B radiation (Fig. 8).

After transfer to low PAR intensities close to $20 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, first inhibition of PSII decreased again quickly within four hours but, then, it slowed down within subsequent 20 hours in each species. This suggests a two stage recovery of PSII. After four hours in dim PAR, inhibition of PSII in *P. columbina* and *D. confervoides* did recover completely (= 0 % of inhibition) (Fig. 3 and 6). Although degrees of inhibition were still approximately 5% in the other three species after four hours, they required 24 hours to recover completely. Specimens of *A. utricularis* exposed to PAR + UV-A + UV-B, however, recovered to 97 % after 24 hours in comparison to control

cultures. However, rates of recovery (m_{rec}) were not statistically significant between species and UV-treatment (Fig. 9).

Photosynthesis versus irradiance (P-I) curves of UV-exposed macroalgae

Comparisons of photosynthesis versus irradiance (P-I) curves after four hours of exposure to UV-A and UV-B radiation of all examined species are displayed in Fig. 10, 11 and 12. Maximal relative electron transport rates (ETR_{max}) of controls of the chlorophyte *U. intestinalis* were 151.6 ± 8.1 r.u. ($n = 3$) but incident UV-A radiation significantly decreased relative ETR_{max} down to 121.6 ± 9.5 r.u. ($n = 3$) (Fig. 10A). Exposure of *U. intestinalis* to UV-B radiation also reduced ETR_{max} to 130.6 ± 11.4 r.u. ($n = 3$) but this reduction, however, was not statistically different to that of controls. In contrast, ETR_{max} of other four species (*P. columbina* (Fig. 10B), *A. utricularis* (Fig. 11), *D. confervoides* (Fig. 12A) and *D. ligulata*) did not change statistically due to exposure neither to PAR + UV-A nor to PAR + UV-A + UV-B.

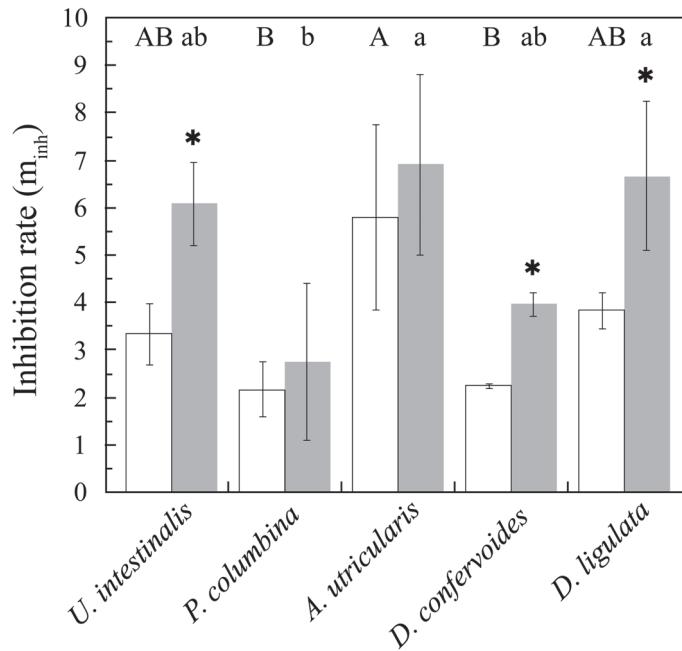


Fig. 8: Rates of inhibition of Fv/Fm (m_{inh}) in five macroalgal species after a four hours exposure to PAR + UV-A (white columns) and PAR + UV-A + UV-B radiation (grey columns). Big and small letters represent statistical differences of inhibition rate between all species exposed either UV-A or UV-B radiation. Asterisks represent statistical differences between UV-A and UV-B effects within a species.

Tasas de la fase de inhibición (m_{inh}) de cinco especies de macroalgas luego de cuatro horas de exposición a radiación PAR + UV-A (columnas blancas) y PAR + UV-A + UV-B (columnas grises). Letras grandes y pequeñas representan diferencias estadísticas en las tasas de inhibición entre todas las especies expuestas ya sea a UV-A o UV-B. Los asteriscos denotan diferencias estadísticas entre los efectos de UV-A y UVB dentro de cada especie.

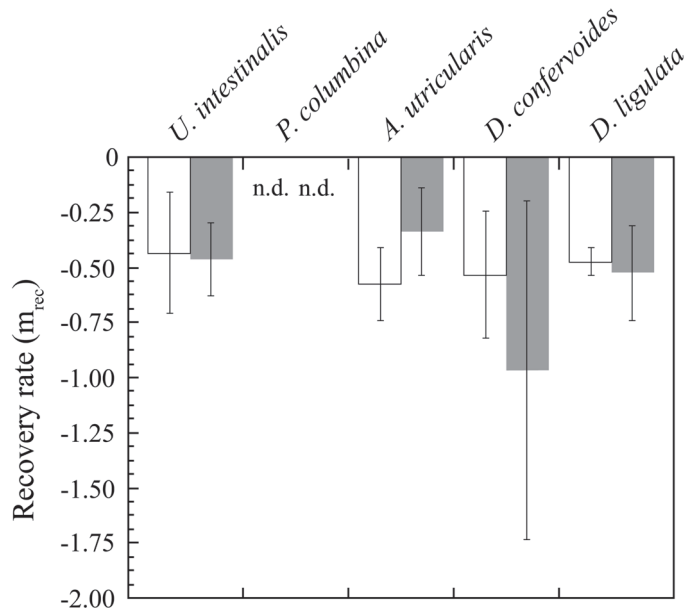


Fig. 9: Rates of recovery (m_{rec}) of five macroalgal species which were previously exposure to PAR + UV-A (white columns) and PAR + UV-A + UV-B radiation (grey columns). N.d. indicates no data after 24 h of recovery.

Tasas de la fase de recuperación (m_{rec}) de cinco especies de macroalgas que fueron previamente expuestas a radiación PAR + UV-A (columnas blancas) y PAR + UV-A + UV-B (columnas grises).

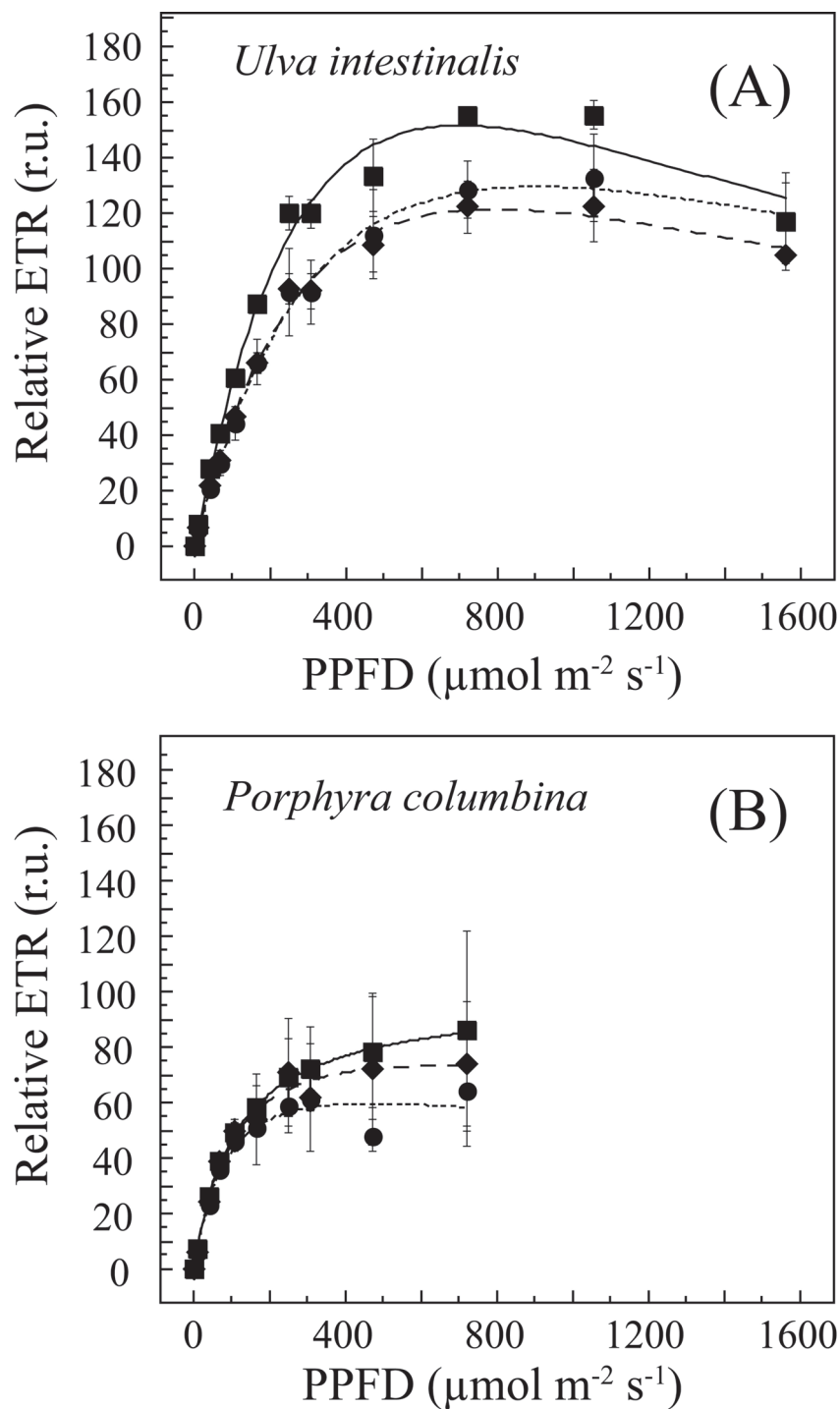


Fig. 10: Light curves of the green alga *Ulva intestinalis* (A) and the red macroalga *Porphyra columbina* (B) after four hours of exposure to low PAR (solid line), PAR + UV-A (dashed line) and PAR + UV-A + UV-B radiation (dotted line).

Curvas de luz del alga verde *Ulva intestinalis* (A) y la macroalga roja *Porphyra columbina* (B) luego de cuatro horas de exposición a baja radiación PAR (línea sólida), PAR + UV-A (línea segmentada) y PAR + UV-A + UV-B (línea punteada).

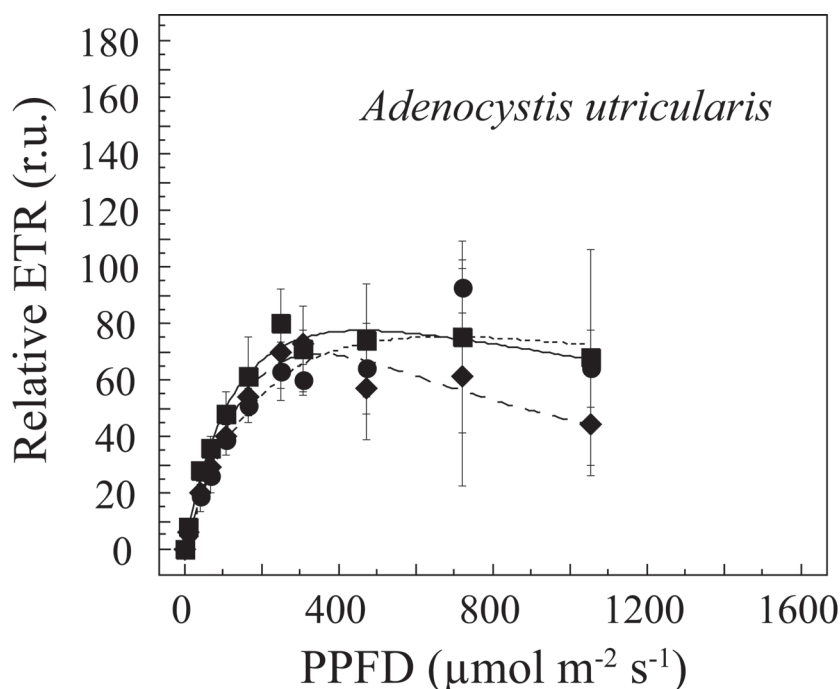


Fig. 11: Light curves of the brown alga *Adenocystis utricularis* after four hours of exposure to low PAR (solid line), PAR + UV-A (dashed line) and PAR + UV-A + UV-B radiation (dotted line).

Curvas de luz del alga parda *Adenocystis utricularis* después de cuatro horas de exposición a baja radiación PAR (línea sólida), PAR + UV-A (línea segmentada) y PAR + UV-A + UV-B (línea punteada).

DISCUSSION

Here, for the first time, we conducted studies on the photosynthetic performance of five field-grown macroalgal species collected at the Strait of Magellan in southernmost Chile with respect to photoadaptation to their vertical pattern of distribution and their acclimation to ultraviolet radiation. All examined species exhibited a fast acclimation to both UV-A and UV-B radiation as indicated by the fast return of decreased F_v/F_m to their initial photosynthetic efficiencies. Such high recovery rates of inhibited PSII were shown in various cold-temperate and polar macroalgae inhabiting the eulittoral and upper sublittoral in opposition to macroalgae from deeper growth sites (lower sublittoral) or the subcanopy exhibiting slower proceeding recoveries (Dring et al. 1996, Bischof et al. 1998). Down-regulation of photosynthetic efficiencies as a regulatory mechanism of photoprotection, rather than damage, is assumed due to fast kinetics of recovery after UV-exposure.

Photoadaptive characteristics of algae

P-I parameters of collected field-grown macroalgae (cultivated for 1-2 weeks in the laboratory under non-stressful conditions) give information about the state of photoadaptation, which is considered to be genetically fixed (reviewed by Bischof et al. 2006).

The results of rel. ETR suggest that photosynthetic performance is rather species-specific than a function of tidal position on the shore. A general pattern of ETR_{max} between species from the eulittoral and the upper sublittoral was absent. Studies of Gómez et al. (2004) confirm this finding as no correlation between ETR_{max} and position on the shore investigating 18 intertidal macroalgal species from the Chilean coast at Niebla (41° S, near Valdivia) was found. These authors also showed that *U. intestinalis* had higher photosynthetic capacities than *P. columbina* and *D. ligulata*. This is consistent with this study. The results suggest that thallus morphology plays an important role influencing

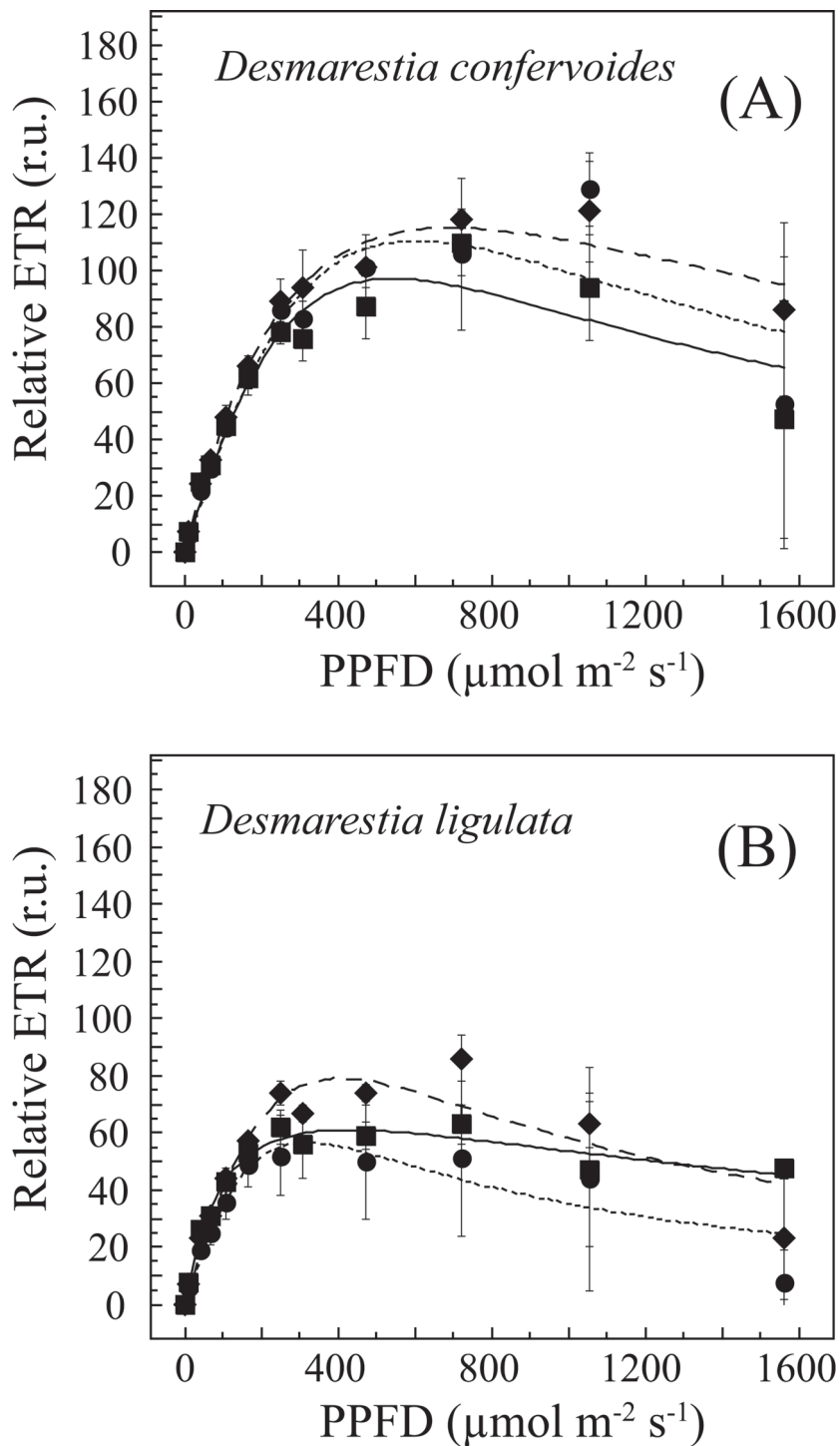


Fig. 12: Light curves of the brown macroalgal species *Desmarestia confervoides* (A) and *Desmarestia ligulata* (B) after four hours of exposure to low PAR (solid line), PAR + UV-A (dashed line) and PAR + UV-A + UV-B radiation (dotted line).

Curvas de luz de las especies de macroalga parda *Desmarestia confervoides* (A) y *Desmarestia ligulata* (B) después de cuatro horas de exposición a baja radiación PAR (línea sólida), PAR + UV-A (línea segmentada) y PAR + UV-A + UV-B (línea punteada).

photosynthetic capacity. *Ulva intestinalis* consists of a sheet-like but tubular thallus with a high content of chlorophyll *a* (Gómez et al. 2004). This thallus morph has a high surface-to-volume ratio with almost exclusively photosynthetic cells (Weykam et al. 1996). Thus, *U. intestinalis* may be classified into a group with high photosynthetic rates according to the morpho-functional model described by Littler & Arnold (1982). On the other hand, Johansson & Snoeijs (2002) found that photosynthetic capacity (based on oxygen evolution and normalized to biomass) depends on thallus morphology: thinner and filamentous species had higher rates than coarser and thicker species. Similarly, Poole & Raven (1997) outlined that most of species of the former genus *Enteromorpha* including *E. intestinalis* (now *Ulva intestinalis*) have high photosynthetic capacities. In our study, the lower photosynthetic capacity (Table 3) measured in *A. utricularis* and *D. ligulata*, which exhibit saccate or leathery morphology, respectively, are associated to less chlorophyll *a*, a lower surface-to-volume ratio and a great proportion of structural tissues (Weykam et al. 1996). The brown alga *D. confervoides* takes an intermediate position probably because of its terete and branched thallus morphology.

The light saturation point of photosynthesis (I_k) is regarded as an indicator of the photoadaptive status of macroalgae with respect to their position in the littoral zone. For macroalgae from polar and Chilean cold-temperate waters, I_k -values are higher in species occurring in the eulittoral and the upper sublittoral than those determined in seaweeds growing below 10 m water depth (reviewed by Wiencke et al. 2007, Gómez et al. 2004). Thus, macroalgae from the midlittoral are better adapted to strong irradiances than species from the sublittoral. Such a clear general pattern could not be confirmed in this study. One reason might be the small number of species used in this study or alternatively, that all examined macroalgae inhabited shallow sites. Apparently, the studied algae are exposed to high irradiance conditions in summer and may be regarded as moderate sun-adapted organisms, irrespective of their position on the shore. For example, the eulittoral *U. intestinalis* and the upper sublittoral *D. confervoides* exhibited ranges of I_k comparable. Depending

on the biogeographic region, I_k values 50 and 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ indicate firstly sun-adapted characteristics and secondly that species are capable to cope with strong solar irradiance conditions by dynamic photoinhibition (Poole & Raven 1997, Gómez et al. 2004, Hanelt et al. 1994). In contrast, only species occurring in deeper waters are characterized as shade-adapted (reviewed by Wiencke et al. 2007).

Acclimation to UV-radiation

Photosynthetic efficiencies were directly affected by incident UV radiation in all examined macroalgae collected in the tidal zone of the Strait of Magellan. The ratio of F_v/F_m is an important and sensitive parameter to assess the physiological state of algae and plants exposed to environmental stress (Krause & Weis 1991). UV-B-radiation leads to a stronger inhibition of PSII because of the higher energy content of UV-B waveband in comparison to UV-A waveband. In contrast to changes of F_v/F_m during UV-exposure, there was only a small impact of incident UV-radiation on photosynthetic capacities, hence, F_v/F_m is revealed as a more sensitive parameter for evaluation of UV-susceptibility of macroalgae than fluorescence-based P-I curves determined. This is in line with other studies performed on UV-mediated stress on brown and red macroalgae (Dring et al. 1996, Bischof et al. 1999). This suggests that the capture of light energy by the light harvesting complexes and energy transfer efficiency from the light harvesting complexes (LHC) to PSII of macroalgae might be more affected (Clendennen et al. 1996) than the photosynthetic reaction centers of PSII which may still remain active (Hanelt et al. 1997, Bischof et al. 1999).

Many studies have been undertaken to reveal correlations between susceptibility or tolerance of macroalgae to UV-radiation and their vertical distribution (reviewed by Bischof et al. 2006). Gómez et al. (2004) demonstrated that UV-tolerance of 18 intertidal macroalgae from Chile is rather related to metabolic adjustments than to morpho-functional groups or to vertical distribution. In our study, neither the morphology of macroalgal thalli nor the tidal distribution of examined species could be correlated to the extent of photoinhibition

during UV-exposure or rate of recovery (m_{rec}) in dim PAR. The ability of recovery in dim PAR is regarded as an important parameter for evaluation of UV-susceptibility (Hanelt et al. 1997, Bischof et al. 1999). Despite PAR is important for repair, the results show that the macroalgae recovered after UVR exposures, meaning that low PAR intensities used in this study, despite unrealistic, did not impair repair significantly. The rate of recovery was found to be independent on the extent of UV-induced photoinhibition and suggests that adverse effects of UV radiation on PSII were absent. Hence, this is a hint that acclimation of surveyed Patagonian macroalgae to UV-radiation is based on species-specific adjustments of metabolism and photoprotective strategies. Furthermore, they exhibited a high acclimation potential to UV radiation regardless to their position on the shore.

Porphyra columbina

Porphyra columbina seems to be a very well acclimated species to enhanced UV radiation indicated by the low increase of inhibition of PSII, its complete recovery already after 4 h and unaffected P-I curves.

Porphyra umbilicalis from the upper eulittoral (0 m) of the Island of Helgoland (Germany) revealed no reduction of Fv/Fm even after 96 h of UV-exposure (Dring et al. 1996). The high UV tolerance determined in several species of *Porphyra* is certainly due to the high content of UV-absorbing mycosporine-like amino acids (Karsten et al. 1998, Hoyer et al. 2003, Huovinen et al. 2004).

Ulva intestinalis

The green macroalga *U. intestinalis* exhibited a reduction of Fv/Fm followed by a fast recovery completed within 24 h. This indicates a transient and rapidly reversible down-regulation of photosynthetic activity. Down-regulation of the photosynthetic apparatus was interpreted by Russell et al. (1995) as a photoprotective strategy primarily developed to dissipate excess PAR energy, which might be also active as a response to ultraviolet radiation. A small distinct increase of PSII inhibition and a fast subsequent recovery were also reported of the same species from the Northern and Southern hemisphere

exposed to artificial and solar radiation (Cordi et al. 1997, Gómez et al. 2004, Huovinen et al. 2006). Furthermore, a decrease of ETRmax after four hours of UV-A-exposure and its subsequent complete recovery after four hours (not shown) suggests that UV-A-radiation did not cause serious detrimental effects on the photosynthetic and enzymatic apparatus of the Calvin-Benson cycle.

UV-stress experiments conducted by Gómez et al. (2004) and Huovinen et al. (2006) using specimens of *U. intestinalis* occurring in the upper midlittoral near Valdivia (Chile) showed a less pronounced photoinhibition of approximately 10 % and lower. The authors concluded that this species seems to be less susceptible to UV-radiation because of possibly highly efficient physiological acclimation to prevailing UV-conditions. This is in line with earlier studies by Cordi et al. (1997) who deduced a development of protection mechanism against UV-B-radiation.

Furthermore, in tide pools at the Strait of Magellan (R. Rautenberger, personal observation), *U. intestinalis* is protected against desiccation and its impairments on photosynthesis. Additionally, rising temperatures of the water of tide pools caused by heating of incident solar radiation might protect photosynthesis of *U. intestinalis* against UV-radiation, e.g., by more efficiently operating photoprotective mechanisms. This was shown for two *Ulva* species from southernmost Chile and the Antarctic region (Rautenberger & Bischof 2006). Furthermore, low fluctuations of seasonal photoinhibitory response to ultraviolet radiation reflect a good adaptation to ambient irradiance conditions (Huovinen et al. 2006), which may be operating in Patagonian assemblages of *U. intestinalis*.

Adenocystis utricularis

Results of the brown alga *A. utricularis* suggest that this species was also well acclimated to UV-radiation possibly by regulatory mechanisms. Inhibition of PSII after four hours of UV-exposure was one of the highest compared to the other species. Subsequent (fast) recovery of photosynthetic activity and unaffected photosynthetic capacities after four hours of UV-exposure seems to indicate that photosynthesis was rather down regulated than

damaged. Rautenberger & Bischof (2008) also reported such a fast reversible photoinhibition in Antarctic members of this species. Hanelt et al. (1994) concluded from their field-experiments of diurnal changing solar irradiance in the Antarctic that *A. utricularis* is able to cope with strong radiation stress (including UV-radiation) in virtue of its ability for dynamic photoinhibition, which acts as a photoprotection mechanism (reviewed by Wiencke et al. 2007). Although these findings refer to Antarctic individuals, photosynthesis of Patagonian individuals of *A. utricularis* might also be protected by a rapidly reversible photoinhibition without further damage of the photosynthetic apparatus. During low tide, *A. utricularis* is exposed to arising ultraviolet radiation, which is accompanied by desiccation of algae. Apparently, photosynthesis could be additionally protected by the special thallus morphology of *A. utricularis*. Internal water reservoir inside the saccate thallus keeps it moistened and, thus, it avoids its desiccation (Hanelt et al. 1994).

Desmarestia confervoides and *D. ligulata*

Apparently, photosynthesis of *D. confervoides* and *D. ligulata* collected from the upper sublittoral was also transiently down regulated as shown for the midlittoral species. Nevertheless, the acclimation potential of both species from the same genus and the same tidal position was different and supports the idea of a species-specific phenomenon. Besides metabolic adjustments, UV-sunscreen substances may contribute to protect against UV-radiation. For example, Fairhead et al. (2005) have found phlorotannins, a type of phenolic compounds, in two Antarctic endemic species of *Desmarestia* (*D. anceps* and *D. menziesii*) but they could not provide evidence for their role in UV-protection (Fairhead et al. 2006). Overall, the laboratory experiment was designed to simulate weighted daily UV-B doses according to Caldwell (1971) occurring under ozone depletion in austral springtime and summer irradiance conditions over the southernmost South America in 2004 and 2005, respectively (database from National Science Foundation UV Monitory Network).

In conclusion, our results suggest that adult sporophytes of macroalgal species growing in

the intertidal zone of the Strait of Magellan, in virtue of their ability for photoacclimation, are capable of coping with these UV-B doses. Here, a rapid and transient down regulation of photosynthesis seems to be the main mechanism under suddenly increasing UV levels. However, other adverse effects of enhanced UV-radiation, e.g., on small developmental stages of macroalgal species like spores and gametophytes may not be ruled out (Mansilla et al. 2006, Wiencke et al. 2007) and, therefore, further studies are needed.

ACKNOWLEDGEMENTS

The authors thank the Alfred Wegener Institute for Polar and Marine Research (Bremerhaven, Germany) for financial support to work in Punta Arenas. Further funding was provided by the Deutsche Forschungsgemeinschaft (BI 772/2-1,2) and the Helmholtz-Gemeinschaft deutscher Forschungszentren (VH-NG-059). The collaboration of Nelson Navarro and Mauricio Palacios (both Universidad de Magallanes in Punta Arenas) during collecting algal material and laboratory work is gratefully acknowledged.

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Associate Editor: Vivian Montecino

Received January 1, 2008; accepted September 25, 2008

