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ORIGINAL PAPER

UV-radiation versus grazing pressure: long-term floating of kelp rafts (*Macrocystis pyrifera*) is facilitated by efficient photoacclimation but undermined by grazing losses

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Abstract Large quantities of floating macroalgae are traveling in coastal waters of the SE Pacific and in other temperate climate zones. While afloat, these algae are potentially exposed to full solar radiation, including UVA and UVB, which can have profound effects on their physiological and growth performance. Latitudinal variations in UV-radiation (UVR) are hypothesized to affect floating algae differently with higher impacts at low latitudes than at high latitudes. In addition, UVR together with grazing might accelerate the demise of floating kelps. This hypothesis was tested with outdoor laboratory experiments in which sporophytes of the giant kelp *Macrocystis pyrifera* (L.) C. Agardh were exposed to a combination of different UVR regimes (PAR only, PAR + UV) and grazing at three sites along the Chilean coast (20°S, 30°S, and 40°S). A latitudinal trend in irradiance was detected with increasing values from 40°S to 20°S. Surprisingly, floating *M. pyrifera* responded with a high acclimation potential within this latitudinal UVR gradient. At 20°S, floating kelps were slightly sensitive to UVR, which was reflected in reduced blade growth. At 30°S, physiological responses were hardly affected by the prevailing irradiance but sporophyte growth and thus persistence mainly depended on the presence or absence of amphipod grazers. At high latitudes, grazing had only minor impacts on algal biomass and blade growth, and kelps thrived well under all tested environmental conditions. Overall, our results reveal that floating *M. pyrifera* was only slightly affected by UVR and that sporophytes can efficiently acclimate over a latitudinal UVR gradient that spans from 20°S to 40°S. Given this high acclimation potential, we suggest that these (and possibly other) positively buoyant algae are important dispersal agents over a wide range of temperate latitude conditions.

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Introduction

Benthic algae inhabiting the intertidal and upper subtidal zone are exposed to considerable diurnal and seasonal changes in solar irradiance. The magnitude of solar irradiance exposure depends on cloud cover, tidal rhythm, water turbidity, and sun angle. Solar irradiance is essential for algae in providing energy for photosynthesis and growth, but prolonged exposure to PAR (400–700 nm) and UV-radiation (UVR = UVB + UVA, 280–400 nm) can be harmful (e.g. Aguirre-von-Wobeser et al. 2000;

Yakovleva and Titlyanov 2001; Michler et al. 2002; Bischof et al. 2006).

UVR constitutes only about 5% of the total global solar radiation, but UVA and UVB are biologically important because they can cause photodamage in macroalgae (e.g. Michler et al. 2002; Hoyer et al. 2002). High UVR stress impairs physiological processes such as reproduction, photosynthesis, and finally growth (e.g. Bischof et al. 2002; Roleda et al. 2007; Navarro et al. 2008). However, most intertidal and shallow-water species have developed mechanisms to cope with extreme changes in incident solar radiation by avoidance, physiological acclimation, and production of photoprotective sunscreens such as mycosporine-like amino acids (MAAs, red and green algae) and phlorotannins (brown algae). For example, exposure to UVR induces phlorotannin production in blades of attached *Macrocystis integrifolia* Bory de Saint-Vincent (Swanson and Druehl 2002). Similarly, solar tolerances of *Laminaria digitata* (Hudson) J.V. Lamouroux and *Laminaria hyperborea* (Gunnerus) Foslie increase after cultivation at high irradiance (Franklin and Forster 1997 and references therein).

Since short wavelengths are attenuated faster in the water column (Lobban and Harrison 1994), algae that live in subtidal habitats are sheltered from very high incident UVR and are usually sensitive to high radiation if transplanted close to the sea surface (Dring et al. 1996; Bischof et al. 1998; Karsten et al. 2001; Van de Poll et al. 2001). While the water column mitigates the impact of excessive PAR and UVR, detached benthic macroalgae with positive buoyancy such as e.g. *Ascophyllum nodosum* (Linnaeus) Le Jolis, *Fucus vesiculosus* Linnaeus, *Sargassum* spp., *Durvillaea antarctica* (Chamisso) Hariot and the giant kelp *Macrocystis pyrifera* lose this natural protection once they float on the sea surface. So far little is known about the effects of UVR on the survival potential of floating algae despite their importance as dispersal vehicles for associated organisms in many regions of the world (Thiel and Gutow 2005a).

The giant kelp *Macrocystis pyrifera* can reach sizes up to 40 m, and the basal parts (e.g. reproductive tissues, old vegetative blades) are shaded by the bulk of surface canopies, while the meristematic region is exposed to surface levels of full UVR and PAR. Therefore, *M. pyrifera* can experience strong irradiance gradients ranging from 2,000 μmol photons m^{-2} s^{-1} at the sea surface to 20 μmol photons m^{-2} s^{-1} at the bottom (13 m) (Dean 1985). Once detached as a result of wave action or grazing, the entire sporophyte becomes suddenly exposed to surface levels of UVR. Similar as in benthic (i.e. attached) kelps, elevated levels of UVR may impair photosynthesis (e.g. via loss of pigments), reproductive structures and finally growth (Cabello-Pasini et al. 2000; Véliz et al. 2006; Tala et al. 2007; Wiencke et al. 2007), all of which can negatively affect algal dispersal along the sea surface. Sporophytes of the giant kelp *M. pyrifera* can stay afloat for >100 days (Hobday 2000), and a study by Hernández-Carmona et al. (2006) demonstrated that floating individuals travel at a velocity of ~7 km d^{-1}. Given these estimates, floating kelps can be exposed over long periods of time to high solar irradiance at the sea surface, and one of the main questions regarding the survival of floating kelp is whether and how they can acclimate to these conditions.

Floating algae are not only affected by changing UVR but also by associated herbivores that actively consume their algal rafts (Gutow 2003; Thiel and Gutow 2005b; Vandendriessche et al. 2007a; Rothäusler et al. 2009). For instance, consumption of algal blades results in the loss of photosynthetic tissue, which reduces the ability to fix carbon, thereby affecting the overall growth (e.g. Honkanen and Jormalainen 2002) and thus floating potential of macroalgae. Floating algae attacked by herbivores must allocate resources to wound healing and to the production of chemical or morphological defenses; these resources are not anymore available for growth. Negative effects are thus expected to be more pronounced in floating algae stressed by UVR or by other abiotic factors.

Previous studies had shown that latitudinal differences in irradiance and grazing pressure can affect photosynthesis and growth of benthic algal populations (e.g. Broitman et al. 2001; Bischof et al. 2006; Wiencke et al. 2006). Incident solar radiation as well as grazing pressure by herbivores generally tend to increase with decreasing latitude (e.g. Gaines and Lubchenco 1982; Whitehead et al. 2000). On the other hand, the proportional changes in solar radiation that are caused by stratospheric ozone depletion are more pronounced at high latitudes (Madronich et al. 1998), possibly making these algae even more sensitive to UVR than algae from lower latitudes that receive high irradiance most of the year and might be acclimated to high UVR.

The Chilean coastline extends from 18°S to 55°S, with strong latitudinal variations in abiotic (e.g. UVR or temperature) and biotic factors (e.g. herbivory or competition) (Broitman et al. 2001; Hinojosa et al. 2006; Rothäusler et al. 2009). Thus, we hypothesized that *Macrocystis pyrifera* floating in northern Chile have different survival times (equivalent of potential dispersal distances) than those from the south. Since two previous studies had suggested that kelps floating in northern Chile (at low latitudes) lose their reproductive potential and have high degradation rates after detachment (Macaya et al. 2005; Rothäusler et al. 2009), we predicted that they will be more strongly affected by the high PAR/UVR at the sea surface than their counterparts in southern Chile. In particular, we hypothesized that pigment contents and photosynthesis are suppressed by UVR, which can negatively affect overall

physiological performance and thus growth of floating kelps. Furthermore, the combined effects of associated grazers and near-surface UVR might accelerate the demise of floating kelps. Consequently, we predicted that floating kelps stressed by UVR will be more susceptible to grazing pressure than sporophytes not exposed to UVR.

Estimating the persistence of floating kelps at the sea surface along different PAR and UVR regimes is an important step to gain insights into the dispersal capacity of *Macrocystis pyrifera* and its associated organisms. Herein we tested the responses of kelps along a latitudinal UVR gradient. Within this natural gradient, we experimentally examined the physiology and growth of floating *M. pyrifera* under different UVR and grazing treatments. Growth integrates all acclimation mechanisms and damaging effects and is therefore probably the best indicator for overall UVR sensitivity (Karsten 2008). Kelp responses were studied through changes in growth rates, pigment content, and photosynthesis.

Materials and methods

Sampling sites of sporophytes and associated amphipods

During austral summer 2008, identical outdoor experiments were carried out consecutively at three locations (Iquique, 20°14′S, 70°08′W, starting date: Feb 24th 2008; Coquimbo, 29°58′S, 71°21′W, starting date: Jan 3rd 2008; Calfuco, 39°45′S, 73°23′W, starting date: Jan 30th 2008) along the Chilean Pacific coast (Fig. S1), where algae were exposed to the prevailing natural solar radiation. Experiments were first conducted at the central and southern site and afterward at the northern site, in order to make environmental conditions (e.g. water temperature, nutrient availability) comparable among sites. At each site, 32 complete sporophytes including their holdfasts were detached via snorkeling at low tide from shallow subtidal kelp beds (1–3 m depth). Within a kelp bed, at 1.5 m depth, PAR irradiance can decrease up to 56%, UVA up to 62% and UVB up to 75% compared to levels at the sea surface (Gómez et al., unpubl. data from a *Macrocystis pyrifera* kelp bed, Isla Damas, 29°14′S 71°31′W, Chile), suggesting that detached sporophytes can experience UVR stress when afloat.

Along the Chilean coast, two species of giant kelp, namely *Macrocystis integrifolia* and *Macrocystis pyrifera*, are readily identified based on morphological characteristics. However, two recent studies showed independently from each other and by using different approaches (growth morphology and barcoding) that there is only one species, namely *M. pyrifera* (Demes et al. 2009; Macaya and Zuccarello 2010).

At all experimental sites, the amphipod *Peramphithoe femorata* Krøyer was used as grazer because it lives in very close association with attached and floating sporophytes (Cerda et al. 2009). Amphipods were collected in the same kelp beds where algae were extracted except for Calfuco, where they were collected on the island of Chiloe (41°52′S, 73°50′W). Based on presently accepted morphological characters, the amphipods used in the experiments were identified as *P. femorata*. After collection, sporophytes and amphipods were transported in coolers at ambient water temperatures to the laboratory, stored in tanks with running seawater, and processed within 24 h after collection.

Experimental design and exposure conditions

Field-collected sporophytes were cultivated for 15 days in 90-L transparent flow-through plastic containers (dimensions: 42 × 40 × 64 cm) at ambient seawater temperatures. These containers attenuate UVB by 11%, UVA by 13%, and PAR by 0%. Measurements were conducted about 1 cm below the water surface of an experimental tank and values correspond to diffusive light attenuations. Field values measured at 10 cm depth showed similar results, confirming that conditions in our experiments are representative for algae floating in the pelagic environment. We tested for UVR effects on sporophyte performance by manipulating the radiation regimes during the experiments. Thus, a combination of two radiation treatments was set up: (1) for photosynthetic active radiation (PAR) alone by using Ultraphan cut off foils (URUV farblos 0.12 mm, Digefra, Munich, Germany), which blocked wavelengths <395 nm and (2) for exposure to complete radiation (PAR + UV) by using Ultraphan foils (295 nm Ultraphan 0.3 mm transparent foil, Digefra, Munich, Germany) that only blocked wavelengths <295 nm (spectra of these filter foils are published in Figueroa et al. 1997). In addition, sporophytes were kept without filter foils under natural solar radiation (NATSR), allowing to test for potential filter artifacts in comparison with the PAR + UV treatment. No filter artifacts were detected for all comparisons of the presented dependent variables, and therefore we concentrated only on the main effects and all analyses were done for the data from PAR and PAR + UV treatments; wherever appropriate the data from the NATSR treatment are presented for comparative purposes.

Each radiation treatment consisted of 8 experimental containers that were subdivided into two groups: four containers that received amphipods and four containers that were kept grazer-free. Twenty-four sporophytes with their holdfast (cleaned from grazers and epiphytes under flowing seawater) were distributed individually over the experimental tanks, and thus each tank received one sporophyte. In order to ensure that no fauna was accidentally

introduced into the experimental tanks via the holdfasts, these were checked visually and eventual remaining organisms removed with forceps. For each experimental site, we choose individual sporophytes of similar mass (Iquique 181.6 ± 32.9 g, Coquimbo 170.8 ± 24.3 g, and Calfuco 151.2 ± 27.3 g) and length (Iquique 137.9 ± 24.6 cm, Coquimbo 90.5 ± 22.9 cm and Calfuco 121.0 ± 48.3 cm) in order to diminish size/age effects on sporophyte responses. Amphipods were added at a proportion of 1 amphipod per 4 g algal wet weight, which roughly corresponds to abundances found on natural kelp rafts (Hinojosa et al. 2007). Previous feeding experiments had shown that one amphipod consumed on average ~37 mg kelp tissue d^{-1} (Rothäusler et al. 2009).

Unfiltered seawater flowed individually (3 L min^{-1}) into experimental containers. Sporophytes in the containers were maintained with aeration to guarantee that algae can freely sway in the water such that all algal parts become equally exposed to radiation treatments. Filter foils were clamped to a frame fabricated with PVC tubes and fixed approximately 25 cm above the containers to ensure air circulation. Filters were cleaned every day with a soft sponge and containers were occasionally cleaned from diatoms.

Throughout the course of the experiment, continuous monitoring of incident UVB (280–320 nm) and UVA (320–400 nm) radiation was conducted, using 2π UV-B-071 and UV-A-071 sensors (Walz, Effeltrich, Germany) connected to a Li-Cor-1400 data logger (Li-Cor Bioscience USA). In parallel, photosynthetically active radiation (PAR) data were gathered with a Li-190SA quantum sensor. Radiometers were placed free of interference from surrounding buildings and UVR and PAR irradiance was measured every 15 s throughout the day from 9:00 to 18:00 h (local time). These data were used to calculate daily doses of UVR and PAR by integrating instantaneous data. Average irradiance of UVB and UVA were higher at the northernmost experimental site (Iquique: UVB 1.9 ± 0.1, UVA 67.1 ± 2.0 Wm^{-2}, respectively) than in central (Coquimbo: 1.3 ± 0.6, 46.9 ± 19.3 Wm^{-2}) and southern Chile (Calfuco: 1.4 ± 0.3, 47.0 ± 12.5 Wm^{-2}) (Table S1). Highest average PAR was also registered in Iquique (1983.5 ± 39.6 μmol m^{-2} s^{-1}), followed by Coquimbo (1729.4 ± 576.4 μmol m^{-2} s^{-1}), and lowest PAR prevailed in Calfuco (1468.6 ± 464.9 μmol m^{-2} s^{-1}). The same pattern was detected for the daily doses of irradiance, calculated for the same periods as average irradiance values (Table S1). In addition to the irradiance measurements, we monitored the water temperature in the experimental tanks at 9:00, 12:00, 15:00, and 18:00 h (local time). Ambient water temperature was slightly higher in Coquimbo (18.2 ± 1.0°C) than in Iquique (16.8 ± 0.9°C) and Calfuco (15.4 ± 1.3°C) (Table S1).

Measurements of sporophyte responses

Physiological and growth responses of *Macrocystis pyrifera* were measured at days 5, 10, and 15 of the experiment. In order to assess the physiological performance of the kelp sporophytes, chlorophyll fluorescence of PSII (F_v/F_m) (an indicator of primary photochemical reactions of photosynthesis) was measured at each of the three sampling days. Electron transport rate (ETR, indicator for the relative PSII electron rate) as well as pigment content (indicator for light adaptation and overall physiological performance) and N-content (indicator for tissue nutrient status) was measured only at day 15 of the experiment. Each sampling day started at 8:00 h (local time), when one vegetative blade from the upper sporophyte region from each treatment combination was cut off with scissors at a distance of approximately 3 cm from the pneumatocyst/lamina transition region. Afterward, vegetative blade samples were weighed, cleaned from epibionts and stored individually in containers (0.5 L) with seawater. From each previously cleaned blade sample, 4 small pieces (Sects. 1–2 cm long) were cut off and immediately used for physiological measurements. In addition, at the start of the experiment (day 0), each variable was measured from vegetative blades of 8 initial algae in order to estimate the physiological performance of attached *M. pyrifera* in the field.

Growth responses such as biomass change (percent d^{-1}), blade elongation rate (cm d^{-1}), and loss of distal blade tissue rate (cm d^{-1}) were measured at each sampling day, while the within-sporophyte biomass distribution (percent) was determined at the end of the experiment.

Pigment- and N-determination

Blade samples for pigment content were frozen in liquid nitrogen and stored at −80°C for later analysis. To determine the nutrient status of floating kelp, the N-content was measured from fresh blade sections, which were dried for 24 h at 60°C.

Pigments (chlorophyll *a*, *c* and total carotenoids) were determined from blade samples taken at the start (day 0) and the end of the experiment (day 15). From each blade Sect. 3, disks were cut off with a cork borer and used individually for pigment determination. Measured pigment contents of these 3 sample disks represented the mean value for one sporophyte. The determination of pigments was based on an extraction with N,N-dimethylformamide (DMF) for 24 h at 4°C in darkness. The extinctions of the extract were measured in a scanning SUV-2120 spectrophotometer (SCINCO, Korea). The Chl *a* contents were calculated using the dichromatic equations described by Inskeep and Bloom (1985). For Chl *c* contents and crude

estimations of total carotenoids of the extract, the methodology of Henley and Dunton (1995) was followed. Pigment content was expressed as mg g^{-1} wet weight.

To determine the nutrient status of sporophytes at the start and the end of the experiment, dried material was ground using a mortar, samples of 1–3 mg were burned (900°C) and total concentrations of N were measured automatically in an elemental analyzer (Elementar Vario EL III, Germany) using acetanilide as standard.

Chlorophyll fluorescence measurements

In vivo chlorophyll fluorescence of PSII was determined with a portable pulse modulation fluorometer (PAM 2000, Walz, Effeltrich, Germany). To determine the maximal quantum yield of fluorescence (F_v/F_m), at each sampling day, one blade section of each treatment combination was incubated for 20 min in the dark and measured six times. Mean values of the six measurements represented the average response for each sporophyte. Electron transport rates (ETR) were estimated from the effective quantum yield of fluorescence versus light curves ($\Delta F/F'm-E$). At days 0 and 15, three small disks were cut off with a cork borer from one blade section of each treatment combination. Each sample disk was put in a stainless-steel chamber and irradiated individually with increasing intensities of PAR (up to 500 µmol photon m^{-2} s^{-1}) provided by a LED lamp of the PAM device (Schreiber et al. 1994). Measurements were conducted at the start (day 0) and end of the experiment (day 15). The ETR was estimated by relating the effective quantum yield of fluorescence ($\Delta F/F'm$) and the intensity of the radiation as follows:

$$\mathrm{ETR} = \Delta F/F'm \times E_{\mathrm{PAR}} \times A \times F_{\mathrm{II}}$$

where E is the irradiance of PAR, A is the absorptance of the sample disk, and F_{II} is the fraction of absorbed quanta directed to PSII, which has been estimated to be close to 0.8 for brown algae (Grzymski et al. 1997). The absorptance was measured in sample disks according to the technique described by Mercado et al. (1996), using a fixed light source. To estimate ETR parameters, a modified non-linear function from Jassby and Platt (1976) was fitted to each data set:

$$\mathrm{ETR} = \mathrm{ETR}_{\max} \times \tanh \times (\alpha_{\mathrm{ETR}} \times I/\mathrm{ETR}_{\max})$$

where $\mathrm{ETR}_{\max}$ is the maximal ETR (µmol e^- m^{-2} s^{-1}), tanh is the hyperbolic tangent function, α_{ETR} ([µmol e^- m^{-2} s^{-1} (µmol photons m^{-2} s^{-1})]) is the initial slope of the photosynthesis vs. irradiance relationship and defines the electron transport efficiency at low irradiance, and I is the irradiance (for further details see Gómez et al. 2004). The saturation irradiance for electron transport (E_k: µmol photons m^{-2} s^{-1}) was also calculated as the intercept between α_{ETR} and the $\mathrm{ETR}_{\max}$ values. Additionally, we calculated the non-photochemical quenching (NPQ) capacity of floating kelps using the non-photochemical (qN) and photochemical quenching (qP) coefficients of chlorophyll fluorescence, which were registered during the electron transport rate measurements. The following equation was used: $\mathrm{NPQ} = qN/qP$.

Within-sporophyte biomass distribution

At the start (day 0) and day 15 of the experiment, we conducted destructive sampling in order to determine the wet biomass distribution of the different sporophyte components within a single individual. Each sporophyte was separated into holdfast, stipe, vegetative blades, pneumatocysts (gas-filled bladders), reproductive blades, and sporophylls using a scalpel. Algal parts were weighed (g) separately and the wet weights of algal samples that had been taken for physiological analyses were added to the vegetative blade biomass. Afterward percent within-sporophyte biomass distribution for each sporophyte component was calculated on the basis of the total wet weight.

Sporophyte growth responses in time

Growth of floating sporophytes was measured as (a) total biomass change, (b) blade elongation rate, and (c) loss of distal blade tissue rate. In order to determine biomass change, sporophytes were weighed at each sampling date and the wet weights of samples taken for physiological analysis were added. Percent biomass change per day (BC) was calculated using the equation $\mathrm{BC} = (\mathrm{FW}-\mathrm{IW})/\mathrm{IW}*(100/T)$, where FW and IW are the final and initial wet weight of the sporophytes at the respective sampling dates and T the time period in days between subsequent sampling dates.

Macrocystis pyrifera grows with an apical meristem that is located at the top of each stipe. As the meristem grows to the surface, it splits off new apical blades that show high growth activity. Blade growth was estimated by punching a 3-mm-diameter hole in the central part of these apical blades at a distance of 9 cm from the pneumatocyst/lamina transition region, using a cork borer. We marked the first three apical blades at day 0 of the experiment. The exact distance from the pneumatocyst/lamina transition region to the holes was then measured at days 5, 10, and 15. Mean values of the measured distances from the three blades were calculated (representing growth of one individual) and expressed as daily elongation rate (cm d^{-1}). If holes become displaced toward the most distal blade part, a new hole was made on the same blades at 9 cm from the pneumatocyst/lamina transition. When blades were lost due to grazing or disintegration, new apical blades directly above the old ones were perforated.

The total length of the marked apical blades (L_f) was measured at days 0, 5, 10, and 15 of the experiment in order to estimate the distal loss of blade tissue. We first calculated the expected length (L_e) according to Tala and Edding (2005) by adding the hole displacement (=growth) to the initial length of apical blades. The loss of distal blade tissue rate (LBR, expressed as cm d^{-1}) was then calculated using the equation LBR = $(L_e - L_f)/T$, where L_e and L_f are the expected and the final length of apical blades at the respective sampling dates and T the time period in days between subsequent sampling dates.

Reproductive status of floating sporophytes

To test for the effects of UVR and herbivory on the reproductive status of algae, three sporophylls (if present) were extracted from the 24 experimental algae after 15 days of floating. The eight initial sporophytes from the start of the experiment were also sampled for sporophylls in order to determine the reproductive status of algae in the field. Total sporophyll area and percentage of fertile area (sorus) from the total sporophyll area were measured using Image-Pro, version 4.0 (Media Cybernetics, Inc., Bethesda, MD, USA). Sporulation assays confirmed for all three sites that zoospores were motile and hence viable.

Statistics

A three way mixed model ANOVA was used to evaluate the effects of latitudinal differences (Site: Iquique, Coquimbo, Calfuco; random factor), Grazing (presence/absence of herbivores; fixed factor), and UVR (PAR, PAR + UV; fixed factor) on the pigment and N-contents, on the P–I curve variables (ETR_{max}, α, and E_k), and on NPQ at the end of the experiment. When ANOVA revealed significant differences, a post hoc Tukey HSD was applied. Maximal quantum yield (F_v/F_m) and growth responses (percent biomass change, blade elongation rate, rate of distal blade tissue loss) were analyzed with repeated-measures ANOVA, with the within-subject factors Site (Iquique, Coquimbo, Calfuco) and Time (days 5, 10, and 15), and the between-subject factors Grazing (with and without grazers) and Filter radiation treatment (PAR, PAR + UV). If the assumption of sphericity (Mauchly-Test), required for repeated-measures ANOVA, was not met, the univariate approach with Greenhouse-Geisser adjusted degrees of freedom of the *F*-test was considered (Von Ende 1993). For BER and LBR from each sporophyte ($n = 4$), three blades were used for measurements and the grand mean of these measurements represented the final value of BER and LBR. However, during the experiment, in Calfuco one sporophyte lost all 3 blades and in Iquique one sporophyte at day 10 and also at day 15 had lost the three marked blades, which could thus not anymore be used for the determination of BER and LBR. Given the relatively limited number of lost replicates, no substitutes were created, and consequently analyses were run unbalanced with a repeated-measures ANOVA model (Type III) for both variables. Prior to analyses, percent biomass change data as well as maximal quantum yield data were arcsine transformed and all data were tested for homogeneity of variances, using Levene's test. Heterogeneous data were ln, log, or square root transformed. Since data transformation in some cases did not remove heteroscedasticity, data were analyzed using a more conservative $a = 0.01$ (Underwood 1997).

To test for the effects of Site (Iquique, Coquimbo, Calfuco; random factor), Grazing (presence/absence of herbivores; fixed factor), and UVR (PAR, PAR + UV; fixed factor) on within-sporophyte biomass distribution, a permutational multivariate analysis of variance (PERMANOVA) on the basis of Euclidean distance was carried out (McArdle and Anderson 2001; Anderson 2001, 2005). The p-value was calculated by using 9999 permutations (Anderson 2005). If the PERMANOVA showed significant differences, pair-wise a-posteriori comparisons were conducted.

Results

N-content

The nitrogen content between algae kept without filter foils (NATSR) and algae kept with PAR + UV foils did not differ, and thus no filter artifact was detected ($F_{(1,35)} = 0.564$, $P = 0.531$). The N-content was site dependent ($F_{(2,36)} = 16.013$, $P = 0.044$) with highest values in Calfuco compared to Iquique and Coquimbo ($P < 0.001$ for both comparisons). However, results showed that all sporophytes had N concentrations above 1.2% after the 15 days of experimental floating. Tissue nitrogen lower than 1% indicate nitrogen starvation (Gerard 1982), and thus our values suggested that *Macrocystis pyrifera* had sufficient N available throughout the duration of the experiments.

Pigment content

Testing for filter artifacts, algae kept under NATSR did not differ from algae kept at PAR + UV (Chl *a* $F_{(1,34)} = 1.020$, $P = 0.419$; Chl *c* $F_{(1,34)} = 0.199$, $P = 0.699$; carotenoids $F_{(1,34)} = 0.431$, $P = 0.579$). Concentrations of chlorophyll *a* (Chl *a*), chlorophyll *c* (Chl *c*), and total carotenoids of experimental kelps did not differ among treatments after being afloat for 15 days. No significant effect of UVR,

grazing, and experimental site was detected (Table 1, Table S2).

Photosynthetic characteristics

No filter artifacts were observed for the electron transport rate variables (ETR_{max} $F_{(1,36)} = 0.383$, $P = 0.599$; alpha $F_{(1,36)} = 0.502$, $P = 0.552$; E_k $F_{(1,36)} = 7.890$, $P = 0.107$). At our southernmost location (Calfuco), floating sporophytes maintained highest ETR_{max} values after 15 days afloat (Table 2), causing a significant site effect ($F_{(2,36)} = 45.156$, $P < 0.001$) (Table S3). The ETR_{max} values from Calfuco were significantly higher than ETR_{max} values from Iquique ($P < 0.001$) and Coquimbo ($P < 0.001$), but there were no differences in ETR_{max} values between Iquique and Coquimbo ($P = 0.059$). No significant differences were detected for E_k and the initial slope α (Table S3) at the end of the experiment.

No filter artifact was evident for non-photochemical quenching values (NPQ) ($F_{(1,35)} = 2.495$, $P = 0.254$). NPQ values of kelps did not significantly differ among treatments after being afloat for 15 days (Table 2, Table S3). However, there was a tendency that algae from Coquimbo showed higher NPQ values than algae from Iquique and Calfuco.

The maximal quantum yield of PSII (F_v/F_m) were not different between NATSR and PAR + UV-treated algae ($F_{(1,12)} = 0.341$, $P = 0.570$). F_v/F_m values differed between sites ($F_{(2,24)} = 12.809$, $P > 0.001$; Fig. 1, Table 3), and highest fluorescence values were detected at the northernmost experimental site (Iquique), which were significantly different from Coquimbo (mid latitude, $P = 0.004$) and Calfuco (high latitude, $P = 0.001$), where lower fluorescence values were detected. The maximal quantum yield was similarly low in Coquimbo and Calfuco, with no differences between these two sites ($P = 1.000$). Furthermore, there was a significant interaction effect for site × time on maximum quantum yield ($F_{(4,28)} = 6.844$, $P < 0.001$). At all three sites, F_v/F_m changed differently over time. While at the northernmost site, F_v/F_m remained high during the course of the experiment, in Coquimbo and Calfuco highest photosynthetic efficiencies were measured at day 5 (for both irradiance treatments), but then declined until the end of the experiment.

Within-sporophyte biomass distribution and reproductive status

No filter artifact was evident for within-sporophyte biomass distribution (P[perm]-value = 0.2873). At all three locations, the initial biomass distribution changed after sporophytes had floated for 15 days under different irradiance and grazing conditions (Fig. 2, Table 4). Within-sporophyte biomass distribution of experimental algae was different between sites (P[perm]-value = 0.0001). The northernmost site (Iquique) significantly differed from Coquimbo (mid latitude, P[perm]-value = 0.0011) and Calfuco (high latitude, P[perm]-value = 0.0004). Furthermore, biomass distribution from Coquimbo was significantly different from Calfuco (P[perm]-value = 0.0024). Also there was a significant interaction effect for

Table 1 Pigment content (mg pigments g^{-1} wet weight; grand means ± SD) of Chl *a*, Chl *c*, and carotenoids from *Macrocystis pyrifera* sporophytes at the start (Initial) and at the end (at day 15) under the three radiation treatments (PAR, PAR + UV, NATSR) and in absence (C = CONTROL) and presence (G = GRAZING) of amphipod grazers, for each experimental site (Iquique, Coquimbo, Calfuco)

	Initial	PAR		PAR + UV		NATSR	
		Control	Grazing	Control	Grazing	Control	Grazing
Iquique							
Chl *a**	0.73 ± 0.07	0.29 ± 0.05	0.23 ± 0.03	0.27 ± 0.05	0.21 ± 0.02	0.34 ± 0.07	0.15 ± 0.13
Chl *c**	0.09 ± 0.01	0.07 ± 0.01	0.05 ± 0.01	0.05 ± 0.02	0.03 ± 0.00	0.05 ± 0.01	0.03 ± 0.02
Carotenoids	0.34 ± 0.03	0.15 ± 0.02	0.13 ± 0.01	0.16 ± 0.01	0.12 ± 0.01	0.18 ± 0.03	0.10 ± 0.07
Coquimbo							
Chl *a**	0.60 ± 0.06	0.26 ± 0.05	0.24 ± 0.02	0.33 ± 0.01	0.27 ± 0.02	0.32 ± 0.03	0.25 ± 0.07
Chl *c**	0.08 ± 0.03	0.05 ± 0.02	0.04 ± 0.01	0.12 ± 0.05	0.04 ± 0.03	0.05 ± 0.01	0.04 ± 0.01
Carotenoids	0.29 ± 0.03	0.14 ± 0.04	0.15 ± 0.01	0.19 ± 0.01	0.18 ± 0.01	0.18 ± 0.02	0.14 ± 0.03
Calfuco							
Chl *a**	0.46 ± 0.02	0.81 ± 0.03	0.72 ± 0.04	0.48 ± 0.04	0.65 ± 0.12	0.77 ± 0.15	0.82 ± 0.08
Chl *c**	0.18 ± 0.05	0.14 ± 0.06	0.11 ± 0.02	0.06 ± 0.02	0.09 ± 0.06	0.10 ± 0.02	0.09 ± 0.01
Carotenoids	0.20 ± 0.06	0.31 ± 0.01	0.28 ± 0.04	0.18 ± 0.03	0.28 ± 0.02	0.29 ± 0.06	0.37 ± 0.05

* Significant differences at level 0.01; for statistical results, see Table S2 in the supplementary material

Table 2 Electron transport rates variables (ETR_{max}, Alpha and E_k; grand means ± SD) and non-photochemical quenching values (NPQ) from *Macrocystis pyrifera* sporophytes at the start (Initial) and at the end (at day 15) under the three radiation treatments (PAR, PAR + UV, NATSR) and in absence (C = Control) and presence (G = Grazing) of amphipod grazers, for each experimental site (Iquique, Coquimbo, Calfuco)

	INITIAL	PAR		PAR + UV		NATSR	
		Control	Grazing	Control	Grazing	Control	Grazing
Iquique							
ETR_{max}*	37.98 ± 13.16	25.30 ± 6.24	34.58±9.58	29.78 ± 13.40	22.28 ± 10.11	27.75 ± 8.49	22.28 ± 15.01
Alpha	0.46 ± 0.05	0.25 ± 0.11	0.30 ± 0.15	0.37 ± 0.13	0.30 ± 0.13	0.38 ± 0.05	0.27 ± 0.12
E_k	86.44 ± 37.84	133.79 ± 95.91	144.17 ± 68.39	82.91 ± 30.39	82.58 ± 52.29	76.83 ± 32.09	98.83 ± 58.90
NPQ	3.00 ± 0.49	2.08 ± 0.29	1.63 ± 0.14	3.15 ± 1.84	3.77 ± 1.78	2.64 ± 0.66	2.83 ± 0.72
Coquimbo							
ETR_{max}*	40.47 ± 4.96	14.6 ± 5.28	21.46 ± 1.49	24.21 ± 9.88	18.55 ± 5.61	25.08 ± 8.66	20.27 ± 6.53
Alpha	0.47 ± 0.04	0.40 ± 0.06	0.40 ± 0.04	0.40 ± 0.05	0.40 ± 0.08	0.41 ± 0.09	0.41 ± 0.05
E_k	87.92 ± 17.16	38.05 ± 14.86	54.04 ± 5.47	60.83 ± 22.38	46.43 ± 8.91	61.37 ± 12.94	49.51 ± 12.21
NPQ	2.46 ± 0.42	7.05 ± 2.44	4.78 ± 0.80	4.43 ± 0.80	6.17 ± 0.78	3.83 ± 0.67	6.68 ± 1.84
Calfuco							
ETR_{max}*	44.41 ± 10.58	55.21 ± 10.02	50.17 ± 8.44	48.61 ± 10.88	49.25 ± 15.54	50.75 ± 2.84	48.53 ± 8.65
Alpha	0.44 ± 0.03	0.42 ± 0.03	0.38 ± 0.02	0.43 ± 0.08	0.38 ± 0.04	0.38 ± 0.02	0.38 ± 0.04
E_k	102.76 ± 27.56	131.89 ± 21.04	130.29 ± 14.60	116.59 ± 23.58	127.75 ± 29.74	135.92 ± 20.55	129.00 ± 30.61
NPQ	2.63 ± 0.27	1.38 ± 0.25	1.58 ± 0.16	2.19 ± 0.20	1.84 ± 0.99	1.77 ± 0.07	1.84 ± 0.14

* Significant site effects were detected for this variable; for statistical results see Table S3 in the supplementary material

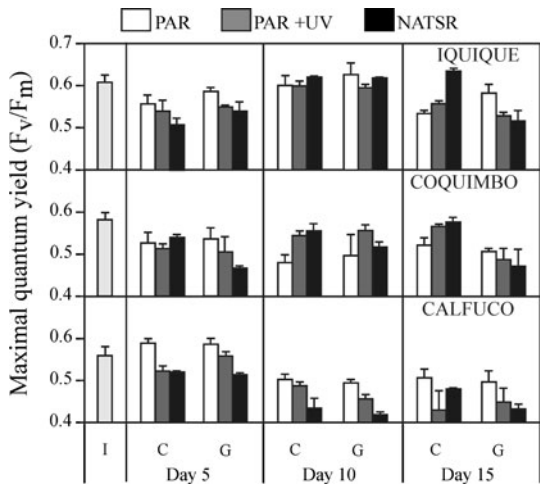

Fig. 1 Maximal quantum yield (F_v/F_m) from *Macrocystis pyrifera* sporophytes at the start (I = Initial) and at the end (at day 15) of the experiments, under the three radiation treatments (PAR, PAR + UV, NATSR) and in absence (C = Control) and presence (G = Grazing) of amphipod grazers, for each experimental site (Iquique, Coquimbo, Calfuco); figure shows grand means ± SD

site × grazing (P[perm]-value = 0.0056). At the northernmost site, no grazing effect on biomass distribution was detected. However, at mid latitudes, a significant grazing effect was observed (P[perm]-value = 0.0186), probably due to the decreasing percentage of vegetative blades from grazed sporophytes. Similarly, at the southernmost site, a grazing effect on biomass distribution was detected, where grazed sporophytes had less sporophylls after 15 days of floating than control sporophytes (P[perm]-value = 0.0003).

Initial (benthic attached) sporophytes from Calfuco (high latitude) and Iquique (low latitude) showed highest reproductive status (Fig. 3). After 15 days of floating, some sporophytes from these sites could maintain their sporophylls and high reproductive status in all treatment combinations. However, at high latitudes, grazed sporophytes lost most of their sporophylls. Similar results were found for Coquimbo (mid latitude), where only ungrazed sporophytes had sporophylls at the end of the experiment.

Biomass change

Testing for filter artifacts, algae kept under NATSR did not differ from algae maintained with PAR + UV ($F_{(1,12)} = 0.176$, $P = 0.682$). Changes in sporophyte biomass were markedly different between the three locations ($F_{(2,24)} = 15.846$, $P < 0.001$; Fig. 4, Table 5a). In Calfuco, the highest biomass increase was detected, which was significantly different from Iquique ($P = 0.001$) and Coquimbo ($P = 0.002$), where sporophytes gained less biomass during the experiment. Biomass change did not differ between Iquique and Coquimbo ($P = 1.000$).

Table 3 Results from the statistical analysis of maximal quantum yield (F_v/F_m), using repeated-measures ANOVA, with the within-subject factor Time and Site (Iquique, Coquimbo, Calfuco), and the between-subject factors Filter (PAR, PAR + UV) and Control (C) and Grazing (G)

Fv/Fm	*df*	*F*-ratio	*P*-value
Within subjects			
Site	2	12.809	**<0.001**
Site × Filter	2	1.910	0.170
Site × CG	2	0.300	0.774
Site × Filter × CG	2	0.428	0.657
Error	24		
Time	2	3.220	0.058
Time × Filter	2	0.908	0.417
Time × CG	2	0.370	0.694
Time × Filter × CG	2	0.190	0.828
Error	24		
Site × Time	4	6.844	**<0.001**
Site × Time × CG	4	0.507	0.731
Site × Time × Filter	4	0.644	0.634
Site × Time × Filter × CG	4	0.306	0.873
Error	48		
Between subjects			
Filter	1	1.912	0.192
CG	1	0.021	0.888
Filter × CG	1	0.764	0.399
Error	12		

P-values in bold highlight significant differences at $p < 0.05$

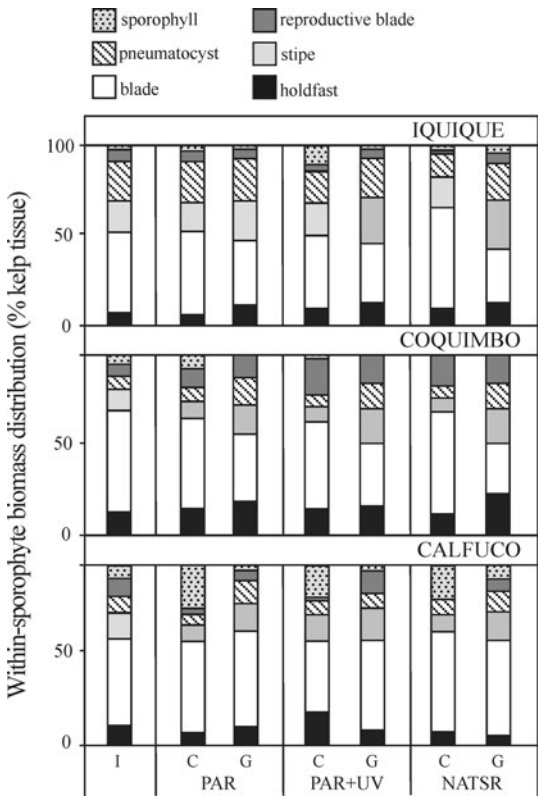

Fig. 2 Within-sporophyte biomass distribution of *Macrocystis pyrifera* sporophytes at the start (I = initial; $n = 8$) and after 15 days of experimental floating ($n = 4$), for each experimental site (Iquique, Coquimbo, Calfuco) and treatment combination (PAR, PAR + UV, NATSR and C = Control, G = Grazing). Data represent mean percent values

Table 4 Results from the statistical analysis of within-sporophyte biomass distribution using PERMANOVA

Within biomass change	*df*	MS	*F*-ratio	*P*-value
Site	2	2300.6233	7.6583	**0.0001**
Filter	1	632.5115	0.0878	0.1151
CG	1	2453.4223	2.6721	0.0976
Site × Filter	2	232.4208	0.7737	0.6137
Site × CG	2	918.1492	3.0563	**0.0056**
Filter × CG	1	196.1881	0.8564	0.5258
Site × Filter × CG	2	229.0750	0.7625	0.6266

Filter = irradiance treatment (PAR, PAR + UV), C = Control and G = Grazing and Site (Iquique, Coquimbo, Calfuco). *P*-values in bold highlight significant differences at $p < 0.05$

Overall, biomass change significantly varied over time ($F_{(2,24)} = 30.339, P < 0.001$), with differences between days 5 and 10 ($P = 0.030$), between days 5 and 15 ($P < 0.001$) and days 10 and 15 ($P = 0.001$) of the experiments. Furthermore, biomass change of floating algae depended significantly on the presence of grazers ($F_{(1,12)} = 14.428$, $P = 0.003$), and there was an interaction effect for time × grazing ($F_{(2,24)} = 16.075$, $P < 0.001$). Initially, at all three sites, grazing did not have a strong effect on sporophyte biomass. No differences between control and grazing were detected at day 5, but at the subsequent sampling days the biomass of grazed sporophytes decreased in comparison with control sporophytes. Even in Calfuco, where algae showed relatively high biomass gains, PAR-treated sporophytes lost biomass in the presence of grazers (Fig. 4).

Blade elongation rate (BER) and loss of distal blade tissue rate (LBR)

For both variables, kelps treated with NATSR did not differ from PAR + UV-treated kelps (BER $F_{(1,7)} = 0.126$, $P = 0.733$; LBR $F_{(1,7)} = 2.108$, $P = 0.190$). Blades of *Macrocystis pyrifera* actively grew in all grazing and irradiance treatments, but a significant site effect was detected ($F_{(2,18)} = 9.364$, $P = 0.002$), with differences between Iquique and Coquimbo ($P = 0.002$) (Fig. 5, Table 5b). Generally, BER slightly decreased over time in Iquique, Coquimbo and Calfuco ($F_{(1.273,11.457)} = 124.441$, $P < 0.001$), while blade losses increased. Grazing

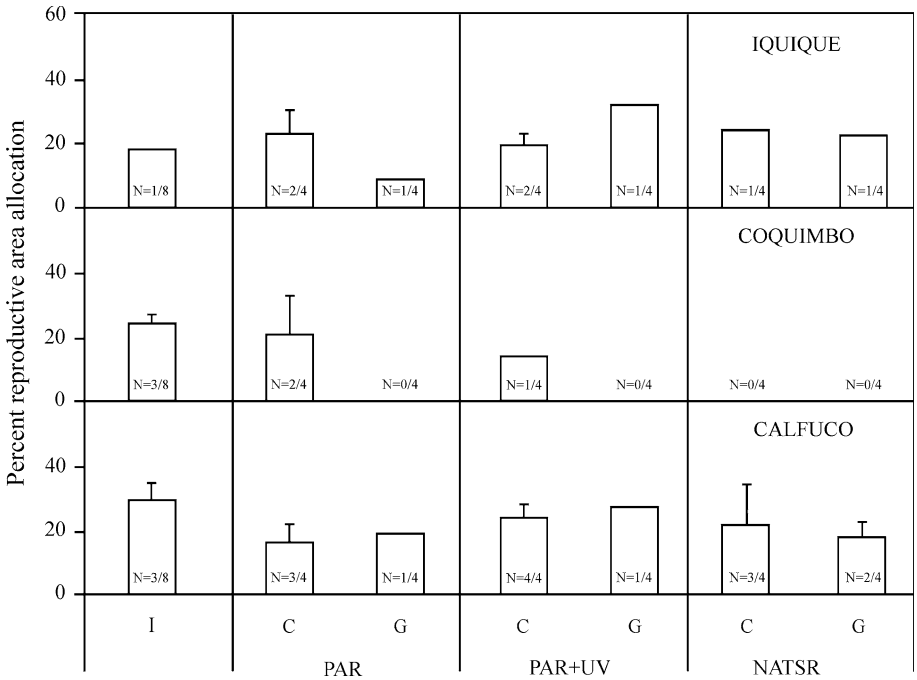

Fig. 3 Reproductive output of *Macrocystis pyrifera* at the start (I = initial) and the end of the experiments, for each location (Iquique, Coquimbo, Calfuco) and treatment combination (PAR, PAR + UV, NATSR, and C = Control, G = Grazing), expressed as percentage reproductive area allocation. N = number of sporophytes with sporophylls/number of replicates; if present from each sporophyte $n = 3$ sporophylls were measured, and if >2 measurements were obtained we calculated the mean for each replicate; figure shows grand means ± SD

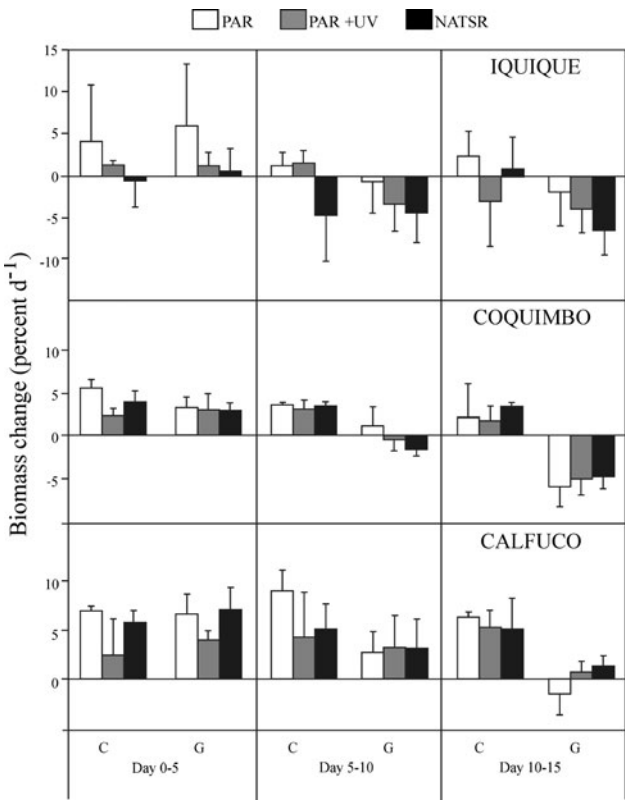

Fig. 4 Percent biomass change d^{-1} of *Macrocystis pyrifera* (mean ± SD., $n = 4$) under the three radiation treatments (PAR, PAR + UV, NATSR) and in absence (C = Control) and presence (G = Grazing) of amphipod grazers, for each experimental site (Iquique, Coquimbo, Calfuco)

significantly suppressed BER at all experimental sites ($F_{(1,9)} = 25.437$, $P = 0.001$). Furthermore, in presence of amphipods BER decreased over time (time × grazing, $F_{(1.273,11.457)} = 6.691$, $P = 0.020$), but at different rates at the three sites (site × time × grazing, $F_{(4,48)} = 2.663$, $P = 0.048$). While the effect of grazing in Coquimbo and Calfuco was already evident between days 0 and 5, in Iquique the factor grazing only became effective between days 10 and 15. Furthermore, there was a significant interaction between time × irradiance on BER ($F_{(1.273,11.457)} = 6.088$, $P = 0.026$) with the tendency that PAR-treated algae from Iquique showed higher elongation rates between days 5 and 10 of the experiment than UVR-treated algae. There is a strong tendency that LBR was highest in the presence of amphipods at the northern and central sites (Fig. 5, Table 5c). However, no significant effect of grazing, irradiance, and site on LBR was detected.

Discussion

Our results indicate that floating sporophytes of *Macrocystis pyrifera* are physiologically viable under the tested UVR regimes at all three sites. However, at the northernmost site, where highest irradiance prevailed, kelps showed a slight sensitivity to UVR, which was reflected in diminishing growth responses. In central Chile, where similar irradiance levels were detected as in southern Chile, sporophyte growth and thus persistence mainly depended on

Table 5 Results from the statistical analysis of (a) biomass change, (b) blade elongation, and (c) distal blade tissue loss, for each experimental site using repeated-measures ANOVA, with the within-subject factors Time and Site (Iquique, Coquimbo, Calfuco), and the between-subject factors Filter (PAR, PAR + UV) and Control (C) and Grazing (G)

	(a) Biomass change			(b) Elongation rate			(c) Tissue loss		
	df	*F*-ratio	*P*-value*	*df*	*F*-ratio	*P*-value	*df*	*F*-ratio	*P*-value*
Within subjects									
Site	2	15.846	**<0.001**	2	9.364	**0.002**	2	0.318	0.731
Site × Filter	2	1.364	0.275	2	1.778	0.197	2	0.385	0.686
Site × CG	2	1.174	0.326	2	3.238	0.063	2	0.418	0.665
Site × Filter × CG	2	0.858	0.437	2	0.228	0.799	2	0.143	0.868
Error	24			18			18		
Time	2	30.339	**<0.001**	1.273_{GG}	101.044	**<0.001**	1.296_{GG}	3.196	0.093
Time × Filter	2	2.288	0.123	1.273_{GG}	6.113	**0.025**	1.296_{GG}	0.225	0.706
Time × CG	2	16.075	**<0.001**	1.273_{GG}	6.691	**0.020**	1.296_{GG}	1.496	0.254
Time × Filter × CG	2	0.571	0.572	1.273_{GG}	0.174	0.744	1.296_{GG}	0.612	0.491
Error	24			11.457			11.667		
Site × Time	4	2.347	0.068	4	4.464	**0.005**	4	0.149	0.962
Site × Time × Filter	4	1.060	0.387	4	2.432	0.065	4	0.957	0.443
Site × Time × CG	4	0.916	0.462	4	2.663	**0.048**	4	0.523	0.719
Site × Time × Filter × CG	4	0.821	0.518	4	0.350	0.842	4	0.957	0.443
Error	48			36			36		
Between subjects									
Filter	1	6.041	0.030	1	2.137	0.178	1	1.310	0.282
CG	1	14.428	**0.003**	1	25.437	**0.001**	1	6.398	**0.032**
Filter × CG	1	0.826	0.381	1	0.969	0.351	1	0.440	0.524
Error	12			9			9		

df_{GG} denotes that degrees of freedom were adjusted following the Greenhouse-Geisser *F*-test, if sphericity requirement were not met

* Significant differences at level 0.01. *P*-values in bold highlight significant differences at $p < 0.05$

the presence or absence of amphipod grazers. In contrast, at the southernmost site, floating kelp thrived best and grazing seemed to play only a minor role for kelp survival. The results suggest a high capacity and plasticity of photoacclimation in *M. pyrifera*, which permits survival of floating sporophytes for long time and dispersal over long distances at the sea surface.

Effect of latitudinal UVR regimes on floating kelp

Exposure to high PAR and UVR is known to decrease photosynthesis or even damage the photosynthetic apparatus and consequently affect growth performance in a number of marine benthic algae (e.g. Aguilera et al. 1999; Karsten et al. 2001; Michler et al. 2002). When *Macrocystis pyrifera* becomes detached and float on the sea surface, all blades of the entire sporophyte can become exposed to surface levels of UVR as a result of wave action in their pelagic environment. During their floating period, floating kelps can also experience latitudinal differences in UVR, which may induce photoprotective mechanisms. For instance, in northern and central Chile, characterized by high irradiance, there was the tendency that pigment concentrations decreased during the experiment, following the typical pattern of photoacclimation to high-light conditions (Falkowski and LaRoche 1991). Similarly, a decline in pigment content had also been identified as a photoprotective mechanism in northern and central Chile in a previous study (Rothäusler et al., accepted). In contrast, in southern Chile where lower irradiance was recorded, pigment concentrations of floating kelps slightly increased, enhancing the chance of photons being absorbed and ultimately harvesting more light for energy requirements, similar as described in Falkowski and LaRoche (1991).

Light reactions that take place in thylakoids were also variably affected by the prevailing irradiance at different latitudes. For instance, at the southernmost experimental site, photosynthetic performance of experimental algae became saturated at similarly high-light levels as initial algae, suggesting that *Macrocystis pyrifera* can cope with the summer irradiance conditions at this site, even when afloat. However, maximal quantum yield of photosynthesis was strongly inhibited after 10 and 15 days of floating in Calfuco. Apparently, a decrease in F_v/F_m in response to

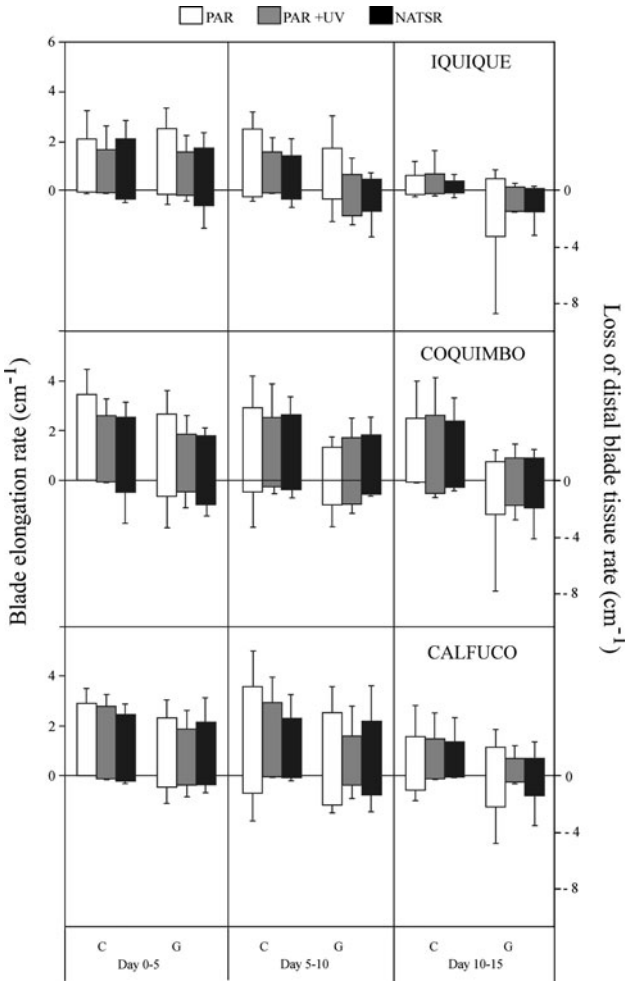

Fig. 5 Elongation rate (cm d^{-1}) and loss of distal blade tissue rate (cm d^{-1}) of apical blades of *Macrocystis pyrifera* under the three radiation treatments (PAR, PAR + UV, NATSR) and in absence (C = Control) and presence (G = Grazing) of amphipod grazers, for each experimental site (Iquique, Coquimbo, Calfuco). Three blades were marked for each treatment combination ($n = 4$) to ensure that at least one marked blade was available at the survey day, and if >2 measurements were available we calculated the mean for each replicate; figure shows grand means ± SD

high irradiance occurred faster than an associated reduction in the electron transport rate, reflecting an efficient down-regulatory mechanism of photoinhibition (Hanelt 1998). Also the minor decreases in ETR_{max} compared to the values of initial algae indicate that the prevailing irradiance was not stressful for the experimental algae. In addition, the electron transport was held at a rate sufficient to maintain efficient C assimilation, which is also evident from the relatively high biomass gains at this site.

At the central and northern experimental site, where highest summer shortwave radiation prevailed, the differences in photochemical responses between floating kelps can be linked to a different potential for non-photochemical quenching, associated with energy dissipation via heat. Blades of *M. pyrifera* are known to have a high potential for this energy dissipation mechanism (García-Mendoza and Colombo-Pallotta 2007). In our study, calculated NPQ values indicated that algae from Iquique exhibited in general low non-photochemical quenching, which was correlated with a relatively low decrease in effective quantum yield and ETR_{max}. In the case of algae from Coquimbo, the low values for ETR_{max} were associated with relatively high energy dissipation via heat. Apparently, these algae were subject to stressful irradiance conditions during the experiments as indicated by the low F_v/F_m values. Overall, our findings reveal that floating sporophytes can efficiently acclimate to the prevailing irradiance at different latitudes via different mechanism of excitation energy dissipation, thereby effectively protecting their photosystems from photodamage (e.g. Hanelt et al. 1997; Hanelt 1998).

Previous studies on the photoprotective mechanisms of *M. pyrifera* had been conducted only with benthic sporophytes (e.g. Clendennen et al. 1996; Gómez et al. 2004; Colombo-Pallotta et al. 2006; Edwards and Kim 2010). Herein we reveal for the first time the high photoacclimation potential of entire floating sporophytes to the PAR/UVR climates at the sea surface. While studies with benthic *M. pyrifera* found that blades near the sea surface are better adapted to high-light conditions and those in deeper water are better adapted to low-light conditions (Colombo-Pallotta et al. 2006; Edwards and Kim 2010), our results suggest that entire sporophytes of floating *M. pyrifera* show plastic responses to the high irradiance levels at the sea surface.

The photoacclimation responses of *Macrocystis pyrifera* in northern Chile appeared to be costly, which is reflected in their diminished growth in the UVR treatments. Similar observations had been reported by Aguilera et al. (1999) and Michler et al. (2002) for several species of brown algae from the Arctic, where growth rates were significantly higher in sporophytes exposed to PAR alone than in sporophytes exposed to a combination of PAR and UVR. Probably, energy-consuming processes, such as diversion of photosynthates or repair of damaged proteins during photoinhibition, could have operated at the expense of growth, similar as reported for juvenile Laminariales sporophytes from the northern hemisphere (Roleda et al. 2007). These processes might be responsible for the observed decline in blade growth of UVR-treated kelps at the northernmost site. Nevertheless, despite the prevailing high irradiance conditions, some sporophytes from northern Chile were able to maintain their reproductive status after 15 days of floating.

Algal responses to herbivores

During their journey at the sea surface, floating algae are not only subject to new light regimes but also to grazing

attacks by associated herbivores. At mid latitudes (Coquimbo), a strong grazing effect on vegetative blades of *Macrocystis pyrifera* was detected. Vegetative blades of the same species are known to be mostly undefended (Rothäusler and Thiel 2006; Pansch et al. 2008) and therefore were probably preferred by *Peramphithoe femorata* over tough stipes and holdfasts. In addition, in central and southern Chile, loss of sporophylls was pronounced in the grazing treatments. Possibly, at these sites, the irradiance conditions at the sea surface were stressful for sporophylls, which provoked a softening of this tissue, making it more susceptible to amphipod grazing (Rothäusler et al. 2009). Also high water temperatures >18°C in central Chile might be responsible for the relative low biomass of sporophylls in benthic and floating *M. pyrifera*, which require low temperatures to reproduce (Buschmann et al. 2004) and to maintain their reproductive structures while afloat (Macaya et al. 2005). Furthermore, the strong grazing effect on vegetative blade tissue is reflected in biomass loss and in a decreased blade growth of kelps from central Chile, suggesting that sporophyte survival strongly depends on associated herbivores. Although these grazing effects were only evident for growth responses, one can assume that algae reacted with an increased demand for energy and carbon and thus showed an overall decline in their photosynthetic responses (decrease in ETR_{max} and F_v/F_m). Carbon-based resources might be needed for wound sealing and the production of defensive compounds, and the increasing demand for energy in defensive mechanisms may have suppressed sporophyte growth. Grazing damage caused by the same grazer had also been identified as an important factor for sporophyte survival of floating *Macrocystis* spp. in central Chile in a previous study (Rothäusler et al. 2009).

It is known that vegetative blades of *Macrocystis integrifolia* are capable to withstand low levels of herbivory by *P. femorata* due to compensatory growth (Cerda et al. 2009), but grazing pressure in the present experiments was comparatively high. Although not tested herein, at our southernmost site (Calfuco), where grazing had only minor impacts on the growth activity of *M. pyrifera* floating kelps may have responded with the production of UV-absorbing phenolic compounds in the treatments with UVR (e.g. Swanson and Druehl 2002 for *M. integrifolia*); these secondary metabolites also serve as grazer repellents (Van Alstyne 1988; Pavia and Toth 2000). The fact that kelps in the PAR treatment were more consumed by grazers further suggests that *M. pyrifera* not exposed to UVR did not induce such compounds, making them more susceptible to grazer attacks. Results presented herein highlight the need for further studies that investigate the production of phlorotannins in floating *Macrocystis pyrifera*.

Global light regimes and its implications for floating algae

Floating *Macrocystis pyrifera* feature successful mechanisms to cope with the incident PAR and UVR levels that prevail along the Chilean Pacific coast. Algae growing in intertidal habitats or at very shallow water depths, such as e.g. *Ascophyllum nodosum, Fucus vesiculosus* and *Sargassum* spp., have developed efficient physiological and biochemical acclimation mechanisms to cope with high UVR (e.g. Pavia et al. 1997; Nygard and Ekelund 2006; Figueroa et al. 2009). Consequently, these species have a better survival potential and hence higher floating persistence (Vandendriessche et al. 2007a, b) when detached from their primary substratum than species that naturally grow at greater water depth.

Non-buoyant algae, such as e.g. *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders, *Laminaria solidungula* J. Agardh and *Phycodrys rubens* (Linnaeus) Batters, were highly UV-sensitive (decline in growth and photosynthetic responses and even photobleaching) when transplanted from deeper to near-surface waters (Aguilera et al. 1999; Karsten et al. 2001). In contrast, buoyant algae that grow throughout the entire water column, such as *Macrocystis pyrifera*, appear to display efficient acclimation mechanisms in response to a broad range of UVR levels. Therefore, we suggest that floating at the sea surface might be an integral component of the life history of *M. pyrifera*, where transport along the sea surface represents an important dispersal strategy, similar to other well-studied buoyant macroalgae (e.g. *Sargassum muticum* (Yendo) Fensholt–Norton 1977; Deysher and Norton 1982). Efficient floating dispersal is supported by the high acclimation potential against various environmental factors.

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