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journal homepage: www.elsevier.com/locate/jembePhysiological acclimation of floating *Macrocystis pyrifera* to temperature and irradiance ensures long-term persistence at the sea surface at mid-latitudesEva Rothäusler^{a,b}, Iván Gómez^c, Ulf Karsten^b, Fadia Tala^{a,d}, Martin Thiel^{a,e,*}^a Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile^b Institute of Biological Sciences, Applied Ecology, University of Rostock, Albert-Einstein-Strasse 3, D-18051 Rostock, Germany^c Instituto de Biología Marina, Universidad Austral de Chile, Casilla 567, Valdivia, Chile^d Centro de Investigación y Desarrollo Tecnológico en Algas (CIDTA), Coquimbo, Chile^e Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Coquimbo, Chile

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ABSTRACT

Large numbers of giant kelp rafts are floating along temperate coasts of the southern hemisphere, carrying a wide diversity of associated organisms with them. During voyages, floating kelps are exposed to strong variations in environmental conditions such as UV-radiation (UVR) and temperature that affect algal physiology, growth, and reproductive output. Consequently, it was predicted that the interactive effects of high temperature and UVR suppress algal persistence and reproductive output at the sea surface. This hypothesis was tested by exposing *Macrocystis pyrifera* (Linnaeus) C. Agardh sporophytes to two irradiance (PAR, PAR + UV) and three temperature (cool, ambient, warm) conditions. An outdoor-tank experiment with two consecutive runs (1st and 2nd) was conducted in northern-central Chile (30°S) to assess growth and physiological responses (pigment contents and photosynthesis) of floating *M. pyrifera*. Results showed that after being afloat for 15 days, algae physiologically acclimated efficiently to changing abiotic conditions by a decrease in pigment contents and dynamic photoinhibition. However, in kelps exposed to 20 °C these acclimation processes operated at the expense of growth, resulting in reduced biomass gains, lower blade elongation rates, and diminished reproduction. Overall, floating *M. pyrifera* responded with high physiological plasticity to the tested UV regimes (UVB 30–100 kJm⁻²; UVA 300–2000 kJm⁻²), but under stressful temperature conditions (~20 °C) photoacclimation processes are costly and an important fraction of the energy gained via photosynthesis becomes unavailable for algal growth. We suggest that at mid latitudes (25°S–40°S) detached sporophytes of *M. pyrifera* have the capacity to float for long time periods and over large distances at water temperatures <20 °C.

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1. Introduction

Benthic algae from the genera *Macrocystis*, *Sargassum*, *Cystophora*, *Carpophyllum*, *Ascophyllum*, *Durvillaea*, and *Fucus* possess gas-filled spaces or vesicles that maintain them vertically in the water column (Hurka, 1971; Norton and Mathieson, 1983). Upon detachment from their benthic substratum, these brown algae float to the sea surface where they are dispersed by ocean currents thereby contributing to population connectivity (Fraser et al., 2009; Hinojosa et al., 2010; Martinez et al., 2006). However, at the sea surface the floating algae experience substantially higher levels of UVR and temperature than their benthic counterparts. These abrupt changes in UVR and temperature can compromise algal growth and persistence at the sea surface, as had been previously shown for *M. pyrifera* (Hobday, 2000; Rothäusler et al., 2009). In contrast, holopelagic species such as

Sargassum natans and *S. fluitans* that are found floating in the warm waters of the Sargasso Sea have probably evolved efficient protection mechanisms to endure surface levels of high temperature and UVR (Hanisak and Samuel, 1987; Schofield et al., 1998).

Subtidal macroalgae that are transferred into shallow waters respond to the high UVR near the sea surface with severe inhibition of photosynthetic processes, caused by degradation of pigments, loss in enzyme activity, reduced fluorescence of PSII, DNA damage, which finally translates into decreasing growth and reproductive output (Aguilera et al., 1999; Apprill and Lesser, 2003; Brouwer et al., 2000; Karsten et al., 2001). Similar or even more dramatic effects could be expected for benthic algae with positive buoyancy, which float to the sea surface after detachment. However, some brown algal species produce UV screening substances (phlorotannins) (Gómez and Huovinen, 2010; Swanson and Druehl, 2002), possess optically dense thalli which scatter and attenuate light due to shelf shading (Dring et al., 1996) or light-induced chloroplast movement (Hanelt and Nultsch, 1990). Another important strategy to cope with higher irradiance in shallow waters is to optimize regulatory mechanisms

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(e.g. heat dissipation), which allows algae to quickly recover from high light stress via pigment adjustment, dynamic photoinhibition and repair mechanisms (Bischof et al., 1998; Dring et al., 1996; Edwards and Kim, 2010; Franklin and Forster, 1997; Gómez et al., 2004).

When traveling along the sea surface, algae can experience strong variations in sea surface temperatures (Hinojosa et al., 2006; Rothäusler et al., 2009). Recent studies carried out with floating sporophytes of *Ascophyllum nodosum*, *Fucus vesiculosus*, and *M. pyrifera* showed a negative relationship between temperature and algal growth (Hobday, 2000; Rothäusler et al., 2009; Vandendriessche et al., 2007). In addition, suboptimal water temperatures may affect photosynthetic efficiency, pigment concentrations and enzyme activities of floating algae, similar as shown for attached kelps (Davison, 1987; Gerard and Du Bois, 1988). The interactive effect of UVR and temperature on floating algae has never been tested and the consequences for rafting, including many synergistic and/or antagonistic effects on algal physiology, are poorly known. Previous studies have shown that high water temperatures (>24 °C) produced negative effects on the physiology of floating *M. pyrifera* (Rothäusler et al., 2011a), while under the tested UVR conditions, algae were able to photoacclimate (Rothäusler et al., 2011b). Testing both factors in benthic algae, it had been shown that UVR-induced photoinhibition was less pronounced in antarctic and subantarctic *Ulva* species kept at temperatures around 10 °C than in individuals kept at 0 °C (Rautenberger and Bischof, 2006). Similarly, for the temperate red alga *Gelidium pulchellum* exposure to high solar radiation caused a decline in photosynthesis at 15 °C whereas photoinhibition was mitigated at 25 °C (Gómez et al., 2001). In addition, in three red algal species from arctic and temperate isolates, warmer summer temperatures facilitated repair of UVR induced damage and acclimation to UVR (van de Poll et al., 2002). Increasing water temperatures may therefore initially serve to ameliorate the effects of high light. Similar responses to temperature and UVR could be expected for floating macroalgae as long as temperatures at the sea surface do not surpass their upper thermal limit. However, when reaching their thermal maxima, enzymes involved in photoprotective mechanisms can become damaged, and favorable effects of high temperature may not anymore compensate for UVR induced photoinhibition.

The giant kelp *M. pyrifera* is one of the largest seaweeds on temperate coasts in both hemispheres (Dayton, 1985; Graham et al., 2007). Its distributional limits at high latitudes appear to be set by increasing wave action and decreasing insolation, whereas low latitudinal limits appear to be caused mainly by warmer waters associated with low nutrient concentrations (Graham et al., 2007 and references therein). Along the Chilean Pacific coast, this positively buoyant kelp forms extensive populations ranging from intertidal to subtidal habitats (Dayton, 1985; Hoffmann and Santelices, 1997). Floating individuals can be found very frequently in coastal waters (e.g. Macaya et al., 2005), probably contributing to the dispersal of associated organisms (Thiel and Gutow, 2005). In addition, floating fertile individuals of *M. pyrifera* can act as spore carriers, thereby facilitating their own dispersal (Hernández-Carmona et al., 2006; Macaya et al., 2005).

Freely floating *M. pyrifera* from Chile and California are estimated to stay afloat at least 14 days (Macaya et al., 2005; Hernández-Carmona et al., 2006, respectively), and Hobday (2000) even estimated persistence times of kelp rafts that might exceed 100 days. Kelp rafts of *M. pyrifera* are calculated to travel about 7 km per day, allowing them to cover considerable distances (Hernández-Carmona et al., 2006). While the macroscopic sporophytes can thus be important for dispersal of *M. pyrifera* and other kelps, microscopic life stages (zoospores, gametes, and germlings) are extremely susceptible to high solar radiation and elevated temperatures (Cie and Edwards, 2008; Fredersdorf et al., 2009; Graham, 1996; Steinhoff et al., 2007; Tala et al., 2007; Véliz et al., 2006). High sea surface UVR together with varying temperatures might negatively affect reproductive tissues and spore production, hence limiting the dispersal potential of kelps.

Based on the above considerations, the objective of this study was to investigate how different water temperatures together with UVR affect physiological performance and thus the persistence of floating kelps at the sea surface. In an outdoor laboratory experiment, consisting of two consecutive identical experimental runs, individuals of *M. pyrifera* were exposed to three different temperatures and two different UVR regimes. Along the northern Chilean coast, kelp rafts may be transported into warmer oceanic regions with high UVR (low latitudes), which negatively affects acclimation mechanisms and we thus predicted low persistence time and rapid raft disintegration. In contrast, at optimal water temperatures (e.g. during winter and spring conditions) algal UVR acclimation can work efficiently, thereby enhancing kelp persistence at the sea surface. Finally, at very low water temperatures (high latitudes), physiological processes work slowly and here high UVR may also compromise algal floating potential. In addition, it is predicted that elevated water temperatures and UVR negatively affect the reproductive output of floating kelp. Herein, we tested these hypotheses in controlled outdoor experiments by measuring physiological responses, which are descriptors of different physiological processes: (i) primary photosynthetic reactions (e.g. F_v/F_m) determined from chlorophyll a fluorescence kinetics, which allows to examine the energy dissipation processes; (ii) pigment contents, to monitor the light harvesting capacity of algae; and (iii) the presence of reproductive structures to determine if detachment affects the reproductive output of floating kelps. All these physiological variables were finally complemented with measurements of thallus elongation (growth), which is regarded as an integrative variable.

2. Materials and methods

2.1. Algal material and sampling site

Entire *M. pyrifera* sporophytes, including their holdfasts, were collected from a shallow subtidal kelp forest (1–2 m depth) at Caleta San Pedro in Los Vilos (31°54'S, 71°31'W, northern-central Chile) and immediately transported to the seawater laboratory at University Católica del Norte in Coquimbo (29°57'S, 71°20'W) where they were stored over night in a large flow-through seawater tank (~2000 L). At sampling, we extracted 24 experimental sporophytes together with 8 additional sporophytes that served to estimate the initial physiological status of the kelps in their benthic habitat. Since sporophytes were collected within the same population, measurements of initial sporophytes are representative for all experimental sporophytes. Initial sporophytes had a length of approximately 116.1 ± 27.7 cm.

Algae for the experiments were collected in November 2008, i.e. late austral spring. During that time period, in a dense kelp bed, PAR can decrease up to 56%, UVA up to 62% and UVB up to 75% within 1.5 m from the sea surface (I. Gómez et al., unpubl. data from a kelp bed, Isla Damas, 29°14'S 71°31'W, Chile), indicating that sporophytes might experience UVR stress when floating to the sea surface.

2.2. Experimental culture conditions

We examined the effects of different irradiance and temperature conditions on sporophytes of *M. pyrifera* in an outdoor-tank experiment. Due to logistic constraints (large space requirements of experimental tanks, large volumes of water to be cooled down or warmed up), the replicates were distributed over two consecutive runs (hereafter termed 1st and 2nd runs) conducted one after the other during late spring, i.e. under similar environmental conditions (see also below). Each experimental run lasted 15 days. The first run started on 5th and ended on the 20th November. The second run lasted from 22nd November until 7th December. The 1st and 2nd runs were considered separately in a randomized block design.

During each run 24 sporophytes, which were similar in biomass (1st run: 173.4 ± 24.3 g, 2nd run: 163.5 ± 21.9 ; t -test $df = 46$, $p = 0.145$), were individually placed in 90 L transparent flow-through plastic containers, receiving unfiltered natural seawater. Sporophytes were maintained at three different temperatures (Table 1): ambient (incoming ambient seawater temperature), warm (\sim ambient temperature + 3 °C), and cool (\sim ambient temperature – 3 °C). Each temperature treatment had 8 containers, which were subdivided in two groups of solar radiation, (i) photosynthetic active radiation (PAR) and (ii) the complete radiation spectrum (PAR + UV) (see below for details). Thus, for each treatment combination there were 4 replicates in each experimental run.

2.2.1. Seawater treatment

In order to obtain the three different water temperatures (cool, ambient, warm), ambient seawater from the adjacent bay was directly pumped into three large head tanks (\sim 2000 L). One tank was equipped with a heater to warm waters up (+3 °C) while a second one was equipped with a chiller to cool waters down (–3 °C). The water entering the third head tank was maintained at the incoming ambient water temperature. We used the same general set-up as in Rothäusler et al., (2009).

The flow rate for each container was approximately 3 L min^{-1} , which together with additional aeration of the tanks allowed sporophytes to sway freely in the water, so that all algal parts became exposed to prevailing conditions. Water temperatures in the experimental tanks were monitored daily at 9:00, 12:00, 15:00 and 18:00 h (local time) in order to ensure that all tanks remained in the desired temperature ranges (Table 1). All temperatures (cool, ambient, warm) were different from each other ($F_{(2,66)} = 10909.1$, $p > 0.001$) but a significant block effect between the two experimental runs was detected ($F_{(1,66)} = 62.5$, $p = 0.016$) due to a slight temperature increase of the incoming ambient water during the 2nd run (Table 1).

2.2.2. Irradiance treatment

For each run, the eight containers from each temperature treatment (cool, ambient, warm) were subdivided in two radiation treatments: (1) exposure to PAR alone by using Ultraphan cut off foils (URUV farblos 0.12 mm, Digefra, Munich, Germany), which blocked wavelengths < 395 nm, and (2) exposure to complete radiation (PAR + UV) by using Ultraphan foils (295 nm Ultraphan 0.3 mm transparent foil, Digefra, Munich, Germany) that blocked wavelengths < 295 nm. Herein

we did not test for filter artifacts because a previous study by Rothäusler et al., (2011b), using the same tank and filter system, had shown that filter artifacts were negligible. For each experimental run, new filter foils were used. Filter foils were clamped to a frame fabricated with PVC tubes, such as described in Rothäusler et al., (2011b). Filters were swiped every other day with a soft sponge to remove bird droppings and dust, and containers were cleaned occasionally from diatoms.

Throughout the course of each experiment, we continuously monitored the incident UVB (280–320 nm) and UVA (320–400 nm) radiation, 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 any buildings in close vicinity to the experimental tanks (\sim 100 m away). UVR and PAR irradiance was measured every 30 s throughout the day from 9:00 to 18:00 h (local time) and are thus representative of the radiation received by the experimental sporophytes in the tanks. These data were used to calculate daily doses of UVR and PAR by integrating instantaneous data (Table 1). Average noon irradiances of PAR, UVA and UVB showed similar values and did not differ between experimental runs $F_{1,16} = 2.144$, $p = 0.162$; $F_{1,16} = 1.188$, $p = 0.292$; $F_{1,16} = 1.607$, $p = 0.223$, respectively.

2.3. Determination of kelp responsive variables

Physiological responses such as maximal quantum yield (for photosynthetic efficiency), pigment content (indicator for light acclimation) and N-content (indicator for tissue nitrogen status) of upper vegetative blades of *M. pyrifera* were measured at day 15 from the 24 treated sporophytes. Additionally, at the beginning (day 0) of each run all physiological variables were measured from the 8 initial sporophytes.

Sporophyte sampling in the laboratory started at 8:00 h (local time), when one vegetative blade from the upper sporophyte region of each treatment combination was cut off at a distance of approximately 3 cm from the pneumatocyst/lamina transition region. Vegetative blades from the upper sporophyte region were chosen for measurements because they significantly contribute to photosynthetic production of the whole sporophyte (Colombo-Pallotta et al., 2006). These vegetative blade samples were weighed, cleaned from epibionts and stored individually in containers (0.5 L) with seawater. From each carefully cleaned blade sample, 3 small pieces (1–2 cm

Table 1

Average water temperatures in the experimental containers and levels of solar radiation measured during austral spring 2009 in Coquimbo, Chile.

Water temperature (°C)	Experimental period	Irradiance at noon			Daily dose			
		UVB (W m^{-2})	UVA (W m^{-2})	PAR ($\mu\text{mol photon m}^{-2}\text{s}^{-1}$)	UVB (kJ m^{-2})	UVA (kJ m^{-2})	PAR (kJ m^{-2})	
1st run	06 Nov ^a	2.4	10.7	960.5 ± 9.5	75.4	305.4	6051.5	
	07 Nov ^a	2.4	9.0	813.5 ± 2.1	107.6	389.9	8126.3	
	09 Nov	1.2	No data	2009.3 ± 17.2	32.2	No data	11847.9	
Cool 12.4 ± 0.4	10 Nov	1.6	52.2	1393.3 ± 529.8	47.7	1514.1	9147.1	
	Ambient 17.1 ± 0.3	11 Nov	1.0	29.8	824.2 ± 6.9	32.8	992.3	6103.4
	Warm 19.7 ± 0.7	12 Nov	1.3	40.6	1065.9 ± 26.3	28.8	860.7	4979.9
		18 Nov	1.3	36.7	930.4 ± 16.1	40.0	1191.7	6788.2
		20 Nov	1.1	29.8	777.7 ± 10.6	34.2	968.8	5544.8
		21 Nov	2.5	80.0	2049.0 ± 3.3	63.1	1996.6	11474.1
2nd run	24 Nov	2.5	80.2	2055.0 ± 5.7	65.4	2031.1	11555.0	
	25 Nov	1.0	27.3	701.6 ± 8.3	44.6	1316.9	7448.2	
	28 Nov	2.5	80.5	2053.6 ± 3.3	66.2	2038.2	11938.4	
	Cool 12.8 ± 1.1	29 Nov	2.5	80.5	2064.1 ± 2.9	66.4	2126.8	11846.8
		Ambient 17.7 ± 1.5	01 Dec	1.8	51.2	1291.2 ± 20.5	46.2	1365.4
	Warm 20.1 ± 0.6	02 Dec	1.5	38.4	963.1 ± 3.2	38.2	1047.0	5908.7
		03 Dec	1.4	37.7	968.2 ± 6.3	45.5	1329.7	7749.3
		04 Dec	2.6	79.9	2079.1 ± 4.4	68.0	2099.7	12470.5
		05 Dec	2.6	80.9	2048.8 ± 2.0	63.9	1944.9	10873.8

^a Days that were partially cloudy.

long) were cut off and stored immediately in liquid nitrogen ($\sim 80^\circ\text{C}$) or in an oven (60°C) for dry preservation and the later determination of pigments and N-content, respectively. The rest of the blade sample was returned to the containers to be used for the determination of maximal quantum yield. Growth responses such as biomass change and blade elongation rate were measured at day 15 of the experiment. In addition, the reproductive output of floating sporophytes was determined from the 8 initial sporophytes (day 0) as well as from sporophytes that were kept for 15 days under different UVR and temperature regimes.

2.3.1. Determination of N- and pigment-content

Kelp tissue used for the determination of sporophyte nutrient status was dried to a constant mass at 60°C for 24 h, and afterwards ground to a fine powder by using a mortar. We determined the N-content using an Elementar Vario EL III (Germany) elemental analyzer, calibrated against acetanilide as standard.

Pigments (chlorophyll *a*, *c* and total carotenoids) were determined from blade samples that were stored in liquid nitrogen. Three disks (each with a wet weight, WW, of ~ 12 mg) 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 based on an extraction with N,N-dimethylformamide (DMF) for 24 h at 4°C in darkness. The extinctions of the extract and the determination of Chl *a*, Chl *c* and total carotenoids (mg g^{-1} wet weight) were measured with a spectrophotometer (SCINCO, Korea) as described in Rothäusler et al., (2011b).

2.3.2. Determination of chlorophyll fluorescence

In vivo chlorophyll fluorescence of PSII was measured with a computer-aided portable pulse modulation fluorometer (PAM 2000, Walz, Germany). The vegetative blade samples (1–2 cm long) from day 15 of the experiment were incubated randomly for 20 min in darkness and measured 6 times for maximal quantum yield of fluorescence (F_v/F_m) which is an indicator of quantum efficiency. Variable fluorescence (F_v) represents the difference between the maximal (F_m) and initial (F_o) fluorescence emission. Mean values of the 6 measurements represented the average response for each sporophyte.

2.3.3. Determination of sporophyte growth

Net sporophyte growth responses such as biomass change (percent d^{-1}) and blade elongation rate (cm d^{-1}) were calculated based on measurements from day 0 and day 15 of the experiment. Net percent biomass change per day (NBC) was calculated using the equation $NBC = (FW - IW)/T * (100/IW)$, where *FW* and *IW* are the final and initial wet weight of the sporophytes, respectively, and *T* is the duration of the experiment in days. Net blade elongation rate (NBER) of apical blades of *M. pyrifera* was determined by using the punch-hole method (Parke, 1948). In the first 3 blades below the apical meristem, a 3 mm diameter hole was punched at a distance of 9 cm from the pneumatocyst/lamina transition region. The hole was in the center of these actively growing blades and the displacement rate of these holes was measured. NBER was calculated using the equation $NBER = (H_f - H_i)/T$, where H_f is the final (day 15) and H_i the initial hole position (day 0) and *T* the duration of the experiment in days.

2.3.4. Determination of reproductive status

In order to determine the effect of UVR and temperature on algal reproductive status, all sporophytes were checked for the presence of sporophylls at the end of the experiment, i.e. after 15 days of floating. In addition, the eight sporophytes from the start of each experimental run (initial) were also sampled for the presence of sporophylls to determine the reproductive status of algae in the field. Sporophylls were inspected for the presence of reproductive areas (sori) by holding them against a light source. When more than three reproductive sporophylls were detected, they were selected randomly

and brought to the laboratory, where photos were taken for the subsequent determination of percent reproductive area allocation. However, in most of the treatments algae had only three (or fewer) reproductive sporophylls, which is in accordance to previous studies (Rothäusler et al., 2009; 2011b), where these sporophylls adequately represented the reproductive output of floating kelp.

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 that spores were motile and viable.

2.4. Kinetics of photoinhibition and recovery

In order to examine the recovery of upper vegetative blades of *M. pyrifera* after natural irradiance exposure and at ambient water temperature, a short-term bioassay was conducted with upper vegetative blades from sporophytes that were collected at the same site. Blades with their pneumatocysts were maintained individually in 2 L flow-through plastic containers with aeration, and either exposed to full solar radiation (= PAR + UV) or kept without UVR (= PAR) on 28th November 2008. We conducted four replicates for each filter treatment. Before each measurement of maximal quantum yield (F_v/F_m), from each blade six small disks (6 mm diameter) were punched out randomly along the blade with a cork borer. Afterwards these sample disks were incubated in the dark for 20 min and each measured one time for maximal quantum yield of chlorophyll fluorescence (F_v/F_m).

After 1 h of exposure time to natural solar radiation (from 9:00 to 10:00 h), initial measurements of F_v/F_m were conducted. Thereafter, upper blades under their corresponding filter foils (PAR and PAR + UV) were exposed for 4 h (from 10:00 to 14:00 h) to natural solar radiation and F_v/F_m was measured again. To induce recovery of photosynthesis, starting at 14:00 h the plastic containers were shaded with a mesh to reduce the incoming solar radiation (reduction of UVB and UVA up to 60% and PAR up to 50%). Chlorophyll fluorescence was then measured 2 h (at 16:00 h) and 5 h (at 19:00 h) after the start of the recovery phase.

2.5. Statistics

In order to evaluate whether abiotic factors such as temperature, PAR, UVA and UVB varied between the experimental runs a one-factorial ANOVA with the random factor block (1st and 2nd runs) was applied. Physiological and growth responses of floating *M. pyrifera* were analyzed by a 3-factorial ANOVA, with the fixed factors temperature (cool, ambient, warm) and irradiance (PAR, PAR + UV), and the random factor block. Prior to analyses, percent net biomass data were arcsine transformed and all data were tested for homogeneity of variances, using Levene's test. When assumptions required for ANOVA were not met, data were ln, log or square root transformed. If these transformations did not remove heteroscedasticity, we proceeded with the parametric analysis, but lowered the α -level from 0.05 to 0.01 (Underwood, 1997). When the ANOVA revealed significant differences, a post-hoc Tukey HSD was applied. Kinetics of photoinhibition and recovery of blades of *M. pyrifera* were analyzed with repeated measures ANOVA.

3. Results

3.1. Algal responses to UVR and variable temperatures

3.1.1. Nitrogen content

The N-contents of initial sporophytes were commonly above 2.0%, which was slightly higher than the N-content of experimental algae from both runs. However, the results showed that all sporophytes used in the experiments had N concentrations $> 1.4\%$. Similar N values

were detected for *M. pyrifera* from other areas and indicate that sporophytes are not N limited (Gerard, 1982; van Tussenbroek, 1989).

3.1.2. Pigment content

Sporophyte contents of Chl *a*, Chl *c* and total carotenoids were highest in initial algae for both experimental runs (Fig. 1). After algae were afloat for 15 days under different irradiance and temperature conditions, pigment contents declined with respect to initial values. Overall, sporophytes responded similarly to the new irradiance and temperature conditions in the experimental containers, regardless of the treatment combination. However, PAR + UV treated sporophytes from the 1st run had significantly higher carotenoid contents than sporophytes from the 2nd run ($F_{(1,36)} = 147.000$, $p = 0.007$). In addition, cool treated sporophytes from the 1st run showed highest carotenoid contents, independent of irradiances ($F_{(1,36)} = 82.333$, $p = 0.012$). No significant differences were detected between runs for the contents of Chl *a* and Chl *c* (Table 2).

3.1.3. Photosynthetic measurements

Photosynthetic efficiency (F_v/F_m) of initial sporophytes was higher than that of experimental sporophytes (Fig. 2). However, all experimental sporophytes maintained maximum quantum yields above 0.5 (Fig. 2). Generally, sporophytes from the 2nd run showed a slightly stronger photoinhibition than sporophytes from the 1st run. Consequently, highest photoinhibition due to a decrease in F_v/F_m by

18% was measured for the PAR + UV cool treatment compared to initial sporophytes. Also there is a general tendency for both runs that F_v/F_m of PAR + UV algae was lower than that of PAR algae but this was not significant (Table 3).

3.1.4. Biomass change and blade elongation rate

Net biomass changes of sporophytes exposed to different UVR and temperature conditions for 15 days showed no significant differences between treatment combinations and experimental runs (Fig. 3A, Table 4A). However, there was a tendency for both runs that algae grown in warm waters gained less biomass compared to those maintained at cool and ambient temperatures. Also in the ambient temperature treatment, PAR exposed algae from the 1st run showed a slightly higher net biomass gain than algae exposed to full irradiance. The same tendency could be observed for the 2nd run, where PAR exposed algae showed insignificantly higher net biomass gain. Overall, sporophytes from the 1st run gained more biomass than sporophytes from the 2nd run (Fig. 3A).

For both runs, net blade elongation rates (NBER) were similar (Fig. 3B, Table 4B), with values ranging between 0.3 and 3.0 cm per day. NBER was highest in the cool and ambient treatment of both experimental runs while lowest NBER were detected in the warm temperature, which was independent from irradiance treatments.

3.1.5. Reproductive output

Initial sporophytes showed low reproductive output (1st run) or even no presence of sporophylls (2nd run) but it was observed that many of these initial sporophytes had sporophylls that were starting to mature (Fig. 3C). After 15 days afloat, algae maintained at ambient and cool water temperatures showed presence of sporophylls and high reproductive output, regardless of irradiance treatments. For both runs, the lowest reproductive output was detected in the warm treatments.

3.2. Kinetics of photoinhibition and recovery

On 28th November, when the kinetics of maximal quantum yield was measured, average noon irradiance of UVB and UVA was 2.5 W m^{-2} and 80.5 W m^{-2} , respectively, and PAR was $2060 \mu\text{mol photon m}^{-2} \text{ s}^{-1}$ indicating very strong natural insolation (Table 1, Fig. 4). The short-term exposure of upper vegetative blades of *M. pyrifera* to 4 h of midday solar radiation indicated highest photoinhibition in the PAR + UV treated algae with respect to values from the start of the experiment (initial algae = 100%) (Fig. 5). The fluorescence of PAR treated blades decreased by 28% whereas in PAR + UV treated blades photoinhibition of photosynthesis was 67% ($F_{(1,6)} = 23.265$, $p = 0.003$). However, the recovery from photoinhibition was similar for both irradiance treatments and after 5 h of shaded conditions blades from both

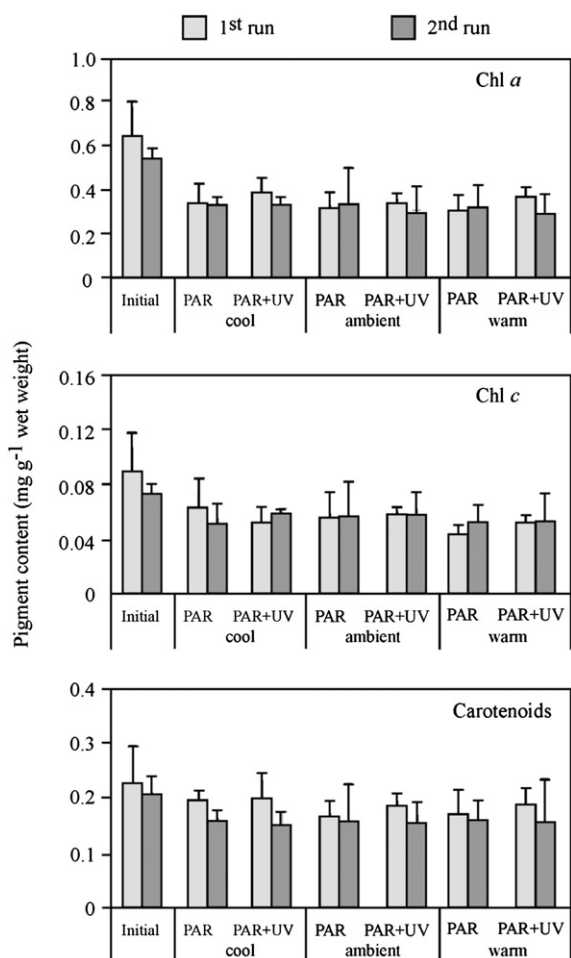


Fig. 1. Pigment content (mg pigments g^{-1} wet weight) of Chl *a*, Chl *c* and carotenoids from *M. pyrifera* sporophytes at the start (initial) and at the end (day 15) of both runs (light gray = 1st run, dark gray bars = 2nd run) under the two radiation treatments (PAR, PAR + UV) and the three temperature treatments (cool, ambient, warm); figure shows grand means \pm S.D.

Table 2

Results from the statistical analysis of kelp pigment contents (Chl *a*, Chl *c* and carotenoids), using a 3-factorial ANOVA, with the fixed factors Light (PAR, PAR + UV) and Temp (= temperature: cool, ambient, warm) and the random factor Block (1st and 2nd runs). P-values in bold highlight significant differences at $p < 0.01$.

	Chl <i>a</i> *			Chl <i>c</i> *			Carotenoids*		
	df	F	p	df	F	p	df	F	p
Light	1	0.142	0.771	1	1.960	0.395	1	0.184	0.742
Temp	2	11.721	0.079	2	1.386	0.419	2	0.984	0.504
Block	1	0.943	0.508	1	0.076	0.784	1	6.553	0.120
Light \times Temp	2	3.752	0.210	2	0.058	0.945	2	9.000	0.100
Light \times Block	1	54.394	0.018	1	0.207	0.694	1	147.000	0.007
Temp \times Block	2	1.349	0.426	2	0.471	0.680	2	82.333	0.012
Light \times Temp \times Block	2	0.031	0.970	2	1.023	0.370	2	0.004	0.996
Error	36			36			36		

*Significance level at 0.01.

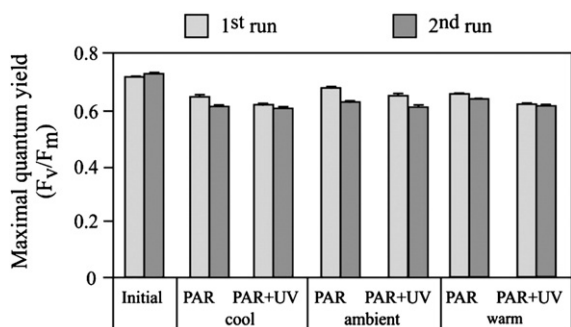


Fig. 2. Maximal quantum yield (F_v/F_m) of *M. pyrifera* sporophytes at the start (initial) and at the end (day 15) of both runs (light gray bars = 1st run, dark gray bars = 2nd run) under the two radiation treatments (PAR, PAR + UV) and the three temperature treatments (cool, ambient, warm); figure shows grand means \pm S.D.

treatments had almost completely recovered (PAR = 5% photo-inhibited; PAR + UV = 4% photoinhibited).

4. Discussion

The results of the present study show that floating sporophytes of *M. pyrifera* can acclimate to temperature (12–20 °C) and natural irradiance levels (PAR, PAR + UV) tested herein. We observed that algae responded with an adjustment of photosynthetic pigments and primary photochemical reactions to the new irradiance and temperature climate while afloat. However, sporophytes maintained in warm waters showed indications of suppressed growth and reproduction (regardless of UVR treatment), confirming that (i) temperature effects are more important than UV-effects, and (ii) that the temperatures in the warm treatments (~20 °C) are approaching the upper thermal limit of *M. pyrifera*.

4.1. Responses to UVR and temperature

Benthic macroalgae have to respond and adjust to daily and seasonally varying levels of temperature and irradiance conditions (Gómez et al., 2009; Karsten et al., 2009; Lobban and Harrison, 1994; Lüning, 1990). When detached, algae experience stronger temperature changes and UVR than their benthic counterparts, which can compromise their acclimation potential and thus persistence at the sea surface (Rothäusler et al., 2009). Interestingly, herein floating individuals of *M. pyrifera* have the potential to acclimate to a temperature range between 12 °C and 20 °C. However, acclimation mechanisms of floating kelps can probably only operate in a narrow temperature range, where benthic *M. pyrifera* normally occur. At 20 °C, acclimation of experimental algae was costly, which was evidenced by a decline in growth and reproduction. In contrast, algae kept at cool (12–13 °C) and ambient (17–18 °C) water temperatures

Table 3

Results from the statistical analysis of maximal quantum yield (F_v/F_m), using a 3-factorial ANOVA with the fixed factors Light (PAR, PAR + UV) and Temp (= temperature: cool, ambient, warm) and the random factor Block (1st and 2nd runs).

	F_v/F_m		
	df	F	p
Light	1	38.440	0.102
Temp	2	1.219	0.451
Block	1	6.545	0.114
Light \times Temp	2	0.143	0.875
Light \times Block	1	2.041	0.289
Temp \times Block	2	15.122	0.062
Light \times Temp \times Block	2	0.089	0.915
Error	36		

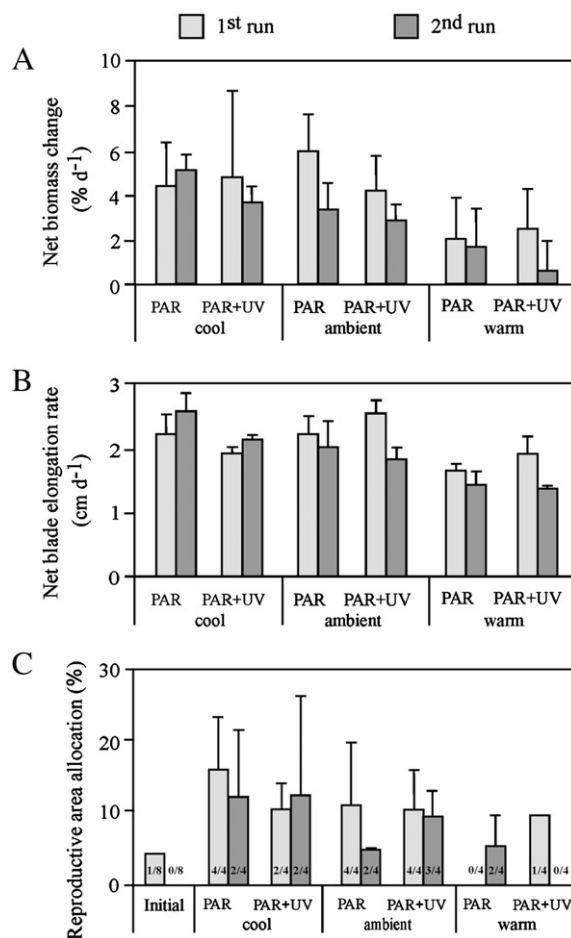


Fig. 3. (A) Net biomass change ($\% d^{-1}$), (B) Net blade elongation rate ($cm d^{-1}$) and (C) Percent reproductive area allocation of *M. pyrifera* at the end (day 15) of both runs (light gray bars = 1st run, dark gray bars = 2nd run) under the two radiation treatments (PAR, PAR + UV) and the three temperature treatments (cool, ambient, warm); figure shows grand means \pm S.D. Note that numbers in the bars represent the number of sporophytes with sporophylls/number of replicates.

were in better metabolic balance and energy demands for acclimation did not exceed the energy necessary for growth. A previous study had shown that at water temperatures >20 °C kelps lost tissue and finally sank (Rothäusler et al., 2009), suggesting that we herein worked close to the upper temperature limit of this species. Accordingly, the tested temperature range was appropriate to examine how *M. pyrifera* can respond to environmental changes when floating at the sea surface.

Table 4

Results from the statistical analysis of (A) Net biomass change and (B) Net blade elongation rate, using a 3-factorial ANOVA, with the fixed factors Light (PAR, PAR + UV) and Temp (= temperature: cool, ambient, warm) and the random factor Block (1st and 2nd runs).

	(A) Net biomass change			(B) Net blade elongation rate*		
	Df	F	p	df	F	p
Light	1	2.136	0.382	1	0.481	0.614
Temp	2	13.408	0.069	2	2.019	0.331
Block	1	6.121	0.489	1	0.899	0.426
Light \times Temp	2	0.077	0.929	2	2.867	0.259
Light \times Block	1	0.813	0.463	1	3.503	0.202
Temp \times Block	2	0.942	0.515	2	8.671	0.103
Light \times Temp \times Block	2	1.074	0.352	2	0.140	0.876
Error	36			36		

*Significance level at 0.01.

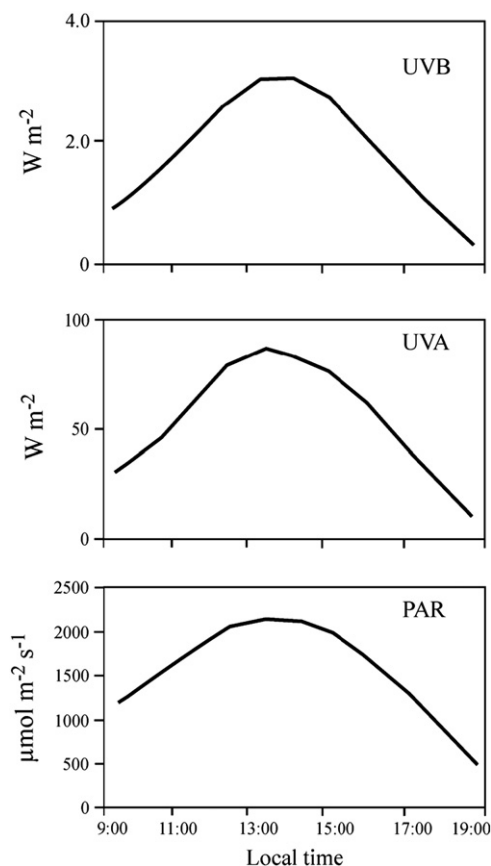


Fig. 4. Daily course of natural solar radiation (UVB = 280–320 nm, UVA = 320–400 nm, PAR = 400–700 nm) measured from 9:00 to 19:00 h local time during the 28th of November, when kinetics of maximal quantum yield were determined.

Detachment of algae and transfer to the sea surface affected the pigment content of experimental algae. In both runs, at the end of the experiment, pigments (Chl *a*, Chl *c* and carotenoids) of floating *M. pyrifera* sporophytes declined compared to initial algae. Two previous studies, carried out with floating *M. pyrifera* under different environmental conditions (Rothhäusler et al., 2011a; b), had already shown that algae followed the well known pattern of photoacclima-

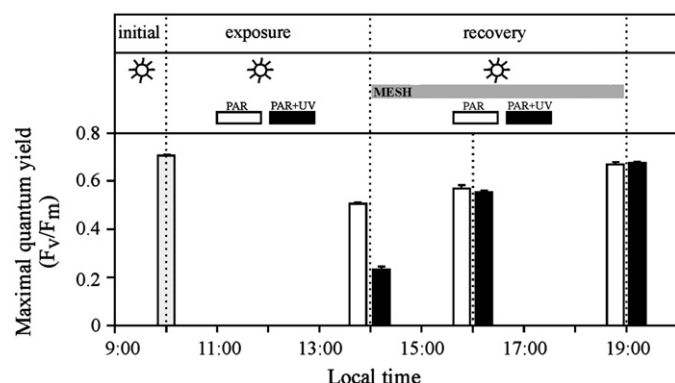


Fig. 5. Kinetics of maximal quantum yield (F_v/F_m) of upper vegetative blades of *M. pyrifera* exposed on the 28th of November to natural solar radiation; from the start (at 9:00 h): fluorescence measurements were conducted at 10:00 h (after 1 h exposure to solar radiation = initial, represented by a light gray bar), at 14:00 h (when algae had been exposed for 4 h to PAR alone, white bars, and to PAR + UV, black bars), and at 16:00 h and 19:00 h (when algae had been kept for their recovery for 2 h and 5 h, respectively, under a screen mesh to reduce radiation). Data are means \pm S.D. of $n = 4$ vegetative blades.

tion to high light conditions, with pigment contents decreasing during the 15 days of experimentation. Wheeler (1980) also reported a decrease in pigments for young sporophytes of *M. pyrifera* from southern California when these were transplanted from subtidal habitats to the sea surface. The capability to adjust the pigment pools contributes to the protection of the photosynthetic apparatus against the high light energy (Demmig-Adams and Adams, 1992) experienced at the sea surface. In addition, in our 1st run the carotenoid content was slightly higher in PAR + UV treated sporophytes than in sporophytes kept with PAR alone. This pattern is comparable to the previously reported high carotenoid contents in surface and subcanopy blades of *M. pyrifera* from Baja California, which has been related to photoprotection against high UVR and PAR (Colombo-Pallotta et al., 2006). A similar trend has also been observed for the pelagic *Sargassum natans* that can tolerate high irradiance by increasing the contents of these photoprotective pigments via the xanthophyll cycle (Schofield et al., 1998). Our findings indicate that helps acclimate in response to the daily doses of UVR in the experimental containers (mimicking conditions at the sea surface), because otherwise the high UVR would result in a direct damage of the pigment protein complexes with concomitant loss of photosynthetic capacity (Bischof et al., 2000; Figueroa et al., 1997).

In line with this, no major effect on the maximal quantum yield of PSII (F_v/F_m) was evident, supporting our assumption that sporophytes can temporarily cope with the incident solar radiation at the sea surface. This is most likely achieved by switching on energy dissipating mechanisms as confirmed by the high capacity of experimental algae for dynamic photoinhibition, a protective regulation mechanism for the photosynthetic apparatus triggered by high PAR. Photoinhibition has been shown to be less severe when algae are exposed to moderate solar irradiance (Altamirano et al., 2000; Figueroa et al., 1997) or when they grow in shallow subtidal and intertidal habitats (Apprill and Lesser, 2003; Hanelt, 1998). Possibly our algae, which were collected between 1 m and 2 m depth, were less susceptible to photodamage caused by high PAR and concomitantly high UVR when floating at the sea surface than algae that become detached at deeper depths. *M. pyrifera* growing in a shallow subtidal kelp bed in southern Chile responded to high natural irradiance with dynamic photoinhibition (Gómez et al., 2004), similar as shown herein for our experimental algae. In addition, the tested temperature ranges (12–20 °C) had no effect on the photoinhibitory capacity of experimental *M. pyrifera*, as the measured photochemical parameters are not dependent on enzyme reactions and hence are less affected by water temperatures (Hanelt et al., 2003). A study by Clendenning (1971) showed for surface fronds of *M. pyrifera* that the photosynthetic activity was not impaired when they were kept for 2 days at 24 °C under low irradiance conditions. These findings suggest that herein variations in water temperature (12–20 °C) did not mitigate or amplify effects of UVR on photosynthesis of *M. pyrifera*, thus differing from some red and green macroalgae which typically exhibit enhanced photosynthesis in warmer waters (Gómez et al., 2001; Rautenberger and Bischof, 2006).

Non-buoyant kelp species, such as *Saccharina latissima* and *Laminaria hyperborea*, responded with similar high plasticity to a broad range of temperatures and irradiances (Bolton and Lüning, 1982; Gerard, 1988; Lüning, 1990; Machalek et al., 1996). In the case of *S. latissima* (formerly *Laminaria saccharina*) the acclimation range was related to the degree of irradiance variability in the natural habitat, which decreased with increasing depth of the population sampled (Gerard, 1988). Probably, sporophytes of *M. pyrifera* from deeper waters could have responded differently, e.g. with a decrease in photosynthesis and lower recovery, such as observed for the deep-water Arctic kelp *Laminaria solidungula* when kept at 1 m depth (Karsten et al., 2001) and for *Alaria esculenta* when exposed to high light levels after ice breakup (Bischof et al., 1999). It is known that the recovery of photoinhibition is more rapid in sun-acclimated algae

than in algae growing in deeper waters or in those transferred to the surface from shaded locations (Gómez and Figueroa, 1998; Jiménez et al., 1998).

4.2. Implications for algal dispersal

The physiological plasticity of *M. pyrifera* to different temperatures and UVR irradiance enhances its possibility to persist for long time periods at the sea surface and thus disperse over large distances. Even though this suggests a high potential for passive dispersal of associated organisms via floating kelps, there exists evidence that the dispersal of algal spores was limited at temperatures around 20 °C, where experimental kelps showed lowest presence of sporophylls. Similarly, Buschmann et al. (2004) had shown that benthic *M. pyrifera* from mid latitudes require comparatively low water temperatures (<15 °C) for germination and zoospore release.

It is known that the floating thalli of various macroalgae can act as a primary long-distance dispersal vector by carrying viable spores over hundreds of kilometers (Hernández-Carmona et al., 2006; Macaya et al., 2005; Martínez et al., 2006), thereby connecting and forming new populations (Buchanan and Zuccarello, in press; Fraser et al., 2009). However, previous studies carried out with floating *M. pyrifera* suggested that high surface temperatures at low latitudes together with elevated irradiance were probably responsible for the loss of sporophylls (Macaya et al., 2005; Rothäusler et al., 2009), thereby limiting the potential of floating sporophytes to serve as propagule vector. Kelps that were found in warm waters off the coast of northern Chile had no sporophylls (Macaya et al., 2005), suggesting that they were physiologically stressed and not able to invest energy in reproduction while maintaining their floatability. Consequently, physiological measurements can help to better understand the floating persistence of algal rafts. Possibly, sporophylls from deeper growing sporophytes, which are acclimated to lower temperatures and light conditions (Graham et al., 2007) may suffer even higher stress at the sea surface than those of the algae used herein.

Overall, *M. pyrifera* seemed to be well equipped for long distance dispersal given the observed phenotypic acclimation to temperature and light conditions tested herein. Especially at mid-latitudes, where our study was conducted, rafting dispersal via floating *M. pyrifera* appears to be highly likely at temperatures ranging between 12 °C and 20 °C, conditions that permit freely floating kelps to stay afloat for at least two weeks (Macaya et al., 2005). Future studies should investigate whether sporophytes inhabiting shallow waters are better acclimated for the rafting lifestyle than their deeper growing counterparts.

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