



Spatial variation in photosynthetic recovery of intertidal turf algae from acute UVB and temperature stress associated with low tides along the central coast of Chile

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ARTICLE INFO

Article history:

Received 11 February 2013

Received in revised form 18 July 2013

Accepted 11 October 2013

Available online 7 November 2013

Keywords:

Gelidium chilense

Intertidal

Photosynthesis

Temperature

Ultraviolet radiation

Upwelling

ABSTRACT

Ecological consequences of punctuated, extreme climate events depend largely upon species' physiological capacity to tolerate and recover from such stressful events. However, physiological responses of intertidal organisms to repetitive exposure to severe conditions using natural patterns are rarely explored, and we know little about how physiological sensitivity within a species varies over local scales or among natural populations, making it difficult to extrapolate results to the naturally variable environmental conditions encountered in the field. Here, we simulate realistic scenarios of the exposure of the turf-forming alga (*Gelidium chilense*) to atmospheric stressors (UVB and temperature) associated with natural mild or harsh weather conditions that occur when summertime midday low tides coincide with unusually calm seas and particularly warm, sunny days along the central Chilean coast. We show that sudden, short-term exposure to artificial UVB radiation during daytime low tides represents a strong stress factor for *Gelidium* turf algae as measured by the changes in maximal photosynthetic quantum yield (F_v/F_m), and repetitive exposure over a period of 5 d, as it occurs naturally during spring–summer days, can critically compromise the ability of the fronds to recover once the stressor is removed. In contrast, while increased aerial temperature had important effects on the photosynthetic system, this source of stress had no lasting effects on the fronds' capacity to recover, nor did it modify the UVB effects on photosynthesis (i.e. no synergistic effects between these common stressors). The ability of *Gelidium* turf to recover from UVB-induced damage to the photosynthetic apparatus differed between tidal heights and among populations from different sites along the central coast. These results suggest that for many shore communities, abrupt, unpredictable short-term stress events will have greater consequences lower on the shore. We found no evidence that greater upwelling intensity and associated nutrient enrichment of coastal waters could consistently ameliorate recovery from the negative effects of UVB. The complex spatial variation in the turf's ability to recover rapidly from a stress event may alter predictions regarding the effects of extreme climate events and/or climate change on species interactions and species' geographic distribution.

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1. Introduction

One of the potentially most devastating features of our rapidly changing climate for natural ecosystems is the predicted increase in the frequency, duration and severity of extreme events (e.g. Easterling et al., 2000; Meehl et al., 2000; Parry et al., 2007). Consequences of such abrupt events for ecological communities depend, to a large part, upon species' physiological capacity to tolerate and recover from such events, and on how lethal and particularly sublethal effects play-out to modify community dynamics (e.g. species interactions, dispersal, etc.). Thus,

there has recently been heightened emphasis on the importance of incorporating mechanistic approaches to understand the physiological basis of stress responses and performance at the organismal scale (Monaco and Helmuth, 2011; Somero, 2010).

Both organismal physiological traits and environmental stressors are often characterized by strong spatial variation across a species' distribution, such that geographic distribution of physiological stress and its effects often exhibit complex “mosaic” patterns (Finke et al., 2007; Helmuth et al., 2002, 2006; Holtmeier and Broll, 2005; Place et al., 2008; Sagarin and Somero, 2006). Where and with what magnitude acute environmental events affect physiological performance may thus not be easily predicted from the modification of external climate conditions and how they are perceived/experienced locally. Changes in sensitivity/vulnerability of the organism, as results of the previous exposure to this or other stressors (‘physiological memory’) and the

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energetic condition of the individuals, modulate the response to their physical environment. Within a species, different responses of distinct populations to the same environmental conditions have been documented and attributed to the local adaptation and/or phenotypic plasticity, which can fine-tune population responses to local conditions (Davis and Shaw, 2001; Kuo and Sanford, 2009). Beyond studies examining differences along latitudinal gradients or at the species' range edges, little is known about how physiological sensitivity varies among natural populations (Sagarin and Somero, 2006). Such information may provide insight into which populations are at greater risk under regimes of increasing climate extremes and help to identify traits and local effects that buffer the species' ability to withstand stress without the loss of function and therefore recover rapidly from an event.

Macroalgae inhabiting wave-swept intertidal habitats are regularly exposed to multiple, dynamic climate/weather stressors (light and associated UV radiation, temperature, desiccation, etc.) during periods of low tides. When the timing of midday low tides coincides with the periods of unusually calm seas and particularly warm, sunny days (high UV radiation), severe climate-induced physiological stress can be anomalously intense and unusually long in duration (Finke et al., 2007; Harley and Paine, 2009; e.g. Helmuth et al., 2002). Such extreme departures from 'typical' conditions often occur over periods of several consecutive days, due to the dominance of synoptic-scale variability in weather conditions along most of the world, such that macroalgae are repetitively exposed to intense, though short-term climate stressors, depending on hours of air exposure. When these conditions, which occur at comparatively low frequency in comparison to typical lifespans of intertidal macroalgae, exceed a threshold, they lead to a 'bleaching' event, in which algal thalli lose photosynthetic pigments and algal tissues are usually irreparably damaged. Such bleaching events can result in severe disturbance that can be the main factor controlling macroalgal intertidal distributional limits (Harley and Paine, 2009). Thus, in light of the current and predicted human-induced climate changes, and the great ecological importance of many macroalgae as source of food and habitat to a myriad of other organisms (e.g. Paine, 1992; Wieters, 2005), it is critical to improve our understanding of the specific factors that cause acute physiological stress and bleaching in intertidal macroalgae, and separate the potentially interactive effects of UV radiation and atmospheric air temperature. Independent effects of temperature and UV on physiological performance, including photosynthetic efficiency and photoinhibition, for marine primary producers are well documented, but we still know little of their interactive effects under realistic scenarios of exposure to stressors. When acting in concert, deleterious effects may be exacerbated, and indeed synergies among stressors are thought to be quite common (Crain et al., 2008; Williams et al., 2011). For example, low temperature enhances negative effects of UV in intertidal fucoid algae (Altamirano et al., 2003).

The rocky, wave-exposed shores of central Chile, with a tidal range of about 1.8 m and semidiurnal regime, are characterized by exceptionally long and frequent amounts of time the intertidal zone is exposed to low tides that occur during summer middays, when aerial climate conditions are potentially most stressful (Finke et al., 2007). In this system, waves play a major role in the amelioration of heat and desiccation stress. Therefore, when summer days of high solar radiation are coupled with calm seas, it is common to observe bleaching of macroalgae, including encrusting forms such as *Codium dimorphum* (Santelices et al., 1981), kelps, foliose corticated species and, particularly, turf-forming species (predominantly *Gelidium* spp.). Bleaching of the latter is particularly notorious because they often dominate extensive areas in the low intertidal zone (Broitman et al., 2001; Santelices, 1991b; Wieters, 2005). The occurrence and intensity of these events appear to vary among years and sites along the central coast and laboratory studies suggest that *Gelidium* species' sensitivity to and protection from high irradiance can be modulated by nutrients,

particularly nitrates (Correa et al., 1985; Santelices, 1991a). Indeed, nutrient enrichment is known to increase the production of protective substances/pigments and/or accelerate the biochemical recovery of damaged structures (e.g. Geider et al., 1993; Korb et al., 2010), reducing the inhibitory effects of short-term exposure to stress in other macroalgae (e.g. Figueroa et al., 2009).

Nutrient supply in nearshore habitats along the coast of central Chile is largely driven by wind driven upwelling (Narváez et al., 2004; Nielsen and Navarrete, 2004; Poulin et al., 2002a, 2002b; Strub et al., 1998; Wieters et al., 2003). Alongshore variation in upwelling intensity, sea surface temperature and consequently onshore nutrient availability, occurring over scales of 10s–100s of kilometers, characterizes this and other upwelling ecosystems (Figueroa and Moffat, 2000; Jury, 1985; Kelly, 1985; Tapia et al., 2009). Indeed, across central Chile, Wieters (2005; see also Wieters et al., 2009a) demonstrated that meso-scale variation in upwelling explains among-site differences in growth rates of *Gelidium chilense* (Montagne) Santelices & Montalva, generating predictable landscape patterns in turf height and morphology.

In this study, we simulate realistic climate extreme events associated with low tide exposure and ask (1) whether recovery (photosynthetic efficiency) of the dominant turf-forming algae *G. chilense* is compromised by simultaneous (synergistic) effects of UVB radiation and warming (air temperature), (2) whether turfs from upper versus lower edges of the vertical tidal height distribution differ in sensitivity to these stressors, and (3) whether geographic variation in sensitivity/recovery can be related to local differences in upwelling intensity and, therefore, exposure to different nutrient regimes.

2. Methods

2.1. Algal collection

We collected samples of turf algae *G. chilense* from 4 wave-exposed, rocky intertidal sites with contrasting proximity to the major upwelling centers; 2 sites (Pichilemu, Curaumilla) at the known upwelling centers of Punta Roncura-Toro and Punta Curaumilla (Bello, 2001; Fonseca and Farías, 1987; Johnson et al., 1980; Paolini and Barría, 1999; Tapia et al., 2009; Wieters et al., 2003) and 2 sites (ECIM, Montemar) at 'downstream' locations not directly affected by upwelling (Narváez et al., 2004, 2006; Poulin et al., 2002a, 2002b; Wieters et al., 2003).

At each site, 'divet' samples of *G. chilense* were taken from the lower edge of the turfs' vertical distribution in shores with similar slope (20–30°) and orientation during austral summer (January–February) 2012. Collecting from the lower edge attempted to minimize and at the same time homogenize exposure to aerial conditions across sites. At Las Cruces, we also collected turf samples from the upper limit of the vertical distribution (approx. 50 cm vertical) of the same rocky platforms to determine whether turfs originating from the same site, but different tidal heights, respond differently to similarly-controlled climate stressors. At each site, 20 samples of 1 cm² of *Gelidium* turf were randomly collected across 2 rocky benches 10s–100s of meters apart. Divets were taken from areas with 100% *Gelidium* cover and where all turfs were attached directly to the rock surface (i.e. not atop mussels or barnacles). All turfs were carefully removed, including holdfasts, and immediately transported inside a dark cooler to the laboratory, where they were cleaned and transferred to individual aquaria under aerated, running seawater and low light in a constant temperature chamber. Aquaria were filled and evacuated every 6 h to simulate the natural changing tidal regime. Samples were maintained in these tanks for 24 h before stress trials.

2.2. Low tide stress trials

To test whether temperature and UVB conditions typically experienced during extended spring–summer daytime low tide periods interactively affect turf photosynthetic activity and recovery from photo-inhibition, we conducted a laboratory experiment during austral

summer (Jan–Feb) of 2012. Unlike most studies that use single pulse or press application of stressors, we mimicked multi-day events in the intertidal zone such that turfs were exposed to controlled abiotic conditions over consecutive daytime low tides and allowed to recover under moderate, ambient conditions in between. To this end, treatments were applied during 6 h each day, corresponding to daytime low tides, allowing algae to recuperate outdoors under simulated semi-diurnal tidal cycle and natural ambient temperature and light conditions during 18 h between daytime low tide treatment applications. The experiment was run for 5 consecutive days to emulate the synoptic timescale variability in weather conditions typical of central Chile (Kaplan et al., 2003; Tapia et al., 2009). During daytime low tides, individual turf divet samples were brought into an indoor climate chamber and placed in petri dishes above which uniform, artificial light was provided and local air temperature was controlled. Treatments included: a) relatively cool ($15 \pm 0.5^\circ\text{C}$) and b) warm ($27.5 \pm 1^\circ\text{C}$) levels of air temperature, which were controlled with electric heaters (Kendal, Chile) and monitored with temperature loggers (iButtons, USA.), combined with c) the presence of augmented artificial UVB radiation and d) white light conditions alone. Uniform PAR irradiance of $20 \mu\text{mol photons/m}^2 \cdot \text{s}$ was provided by 2 fluorescent tubes (TLT40W/54RS Day Light, Philips, Brasil), while artificial UVB radiation was augmented with 2 UV-B (280–320 nm) tubes (UVB-313EL, Q-Lab Corporation, Cleveland, USA) placed to emit 0.27 mW/cm^2 on turf samples, coincident with maxima natural summertime UVB irradiance measured at Las Cruces (unpublished data, ECIM weather station, Las Cruces). The spectral composition of experimental light regimes during midday low tide exposures is presented in Fig. 1. PAR was kept low, and thus natural PAR:UVB ratios were not used, to assure that UVB effects on photosynthesis were not masked by high PAR induced effects. Irradiance was measured with a light meter connected to a portable PAM fluorometer, the Diving-PAM (Walz, Germany; see below), and a UV radiometer (Solar Light, USA). It must be noted that temperatures selected represented typical mean (cool) and average maxima (warm) for low zone air temperatures observed during spring low tides and not the maxima that can occur in this system ($>30^\circ\text{C}$, Aguilera and Navarrete, 2012; Finke et al., 2009). Moreover, air temperature is not necessarily a good indicator of thallus temperature (Bell, 1995), which peaked at 14 and 23.5°C in our cool and warm experimental treatments, respectively. In the field, maximum thallus temperatures can reach 27.5°C and are often associated with bleaching events (Wieters, unpublished data). Therefore our temperature treatments can be considered moderate. Thallus temperatures were measured with portable infrared thermometers (model IRT0401, Kintrex, USA). To avoid potential artifacts

associated with desiccation, we moistened frond surfaces of all turf samples with seawater every hour with an eye dropper and maintained relative humidity nearly at 100%. Localized relative humidity was measured with iButton (USA) loggers. For each site, five replicates of each treatment were assigned at random.

Between daytime low tide treatment applications, algae were held outdoors in aquaria with running seawater and continuous aeration. Aquaria continued to be filled and emptied every 6 h to simulate the natural tidal cycle (Finke et al., 2007) and were positioned randomly on outdoor tables under an opaque roof (20–25% of full sunlight), providing moderate ambient light conditions that were well within the range of that required for photosynthesis (e.g. would not limit potential repair mechanisms) but below photoinhibitory levels that could mask recovery from daytime low tides. Average temperature during recovery was $16.7 \pm 1.6^\circ\text{C}$, while the daily course of solar radiation at our incubation site during outdoor recovery is indicated in Fig. 2.

To evaluate the down regulation of the photosynthetic apparatus and its subsequent recovery, in vivo chlorophyll fluorescence of PSII was measured with a portable pulse-amplitude modulation fluorometer (Diving PAM, Waltz, Effeltrich, Germany) (Schreiber et al., 1986). As an indicator of the physiological condition/status of turf blades, maximal quantum yields of PSII (F_v/F_m) were measured immediately before and after exposure to daytime low tide treatments. At time of measurement, individual turf samples were removed from the petri dish and inserted into a custom-made dark chamber, where they were incubated for 10 min so as to assure virtually all PSII reaction centers were “open” prior to estimation of minimum fluorescence (F_o), corresponding to fluorescence yield at the instant a dim beam was introduced. Afterward, a saturating pulse of light (pulse duration = 0.6 s) was applied and maximum fluorescence (F_m) was determined. For all measurements, the end of the fiber optic probe of the PAM-fluorometer was mounted to the algal samples at a distance of 5 mm. Variable fluorescence (F_v) was calculated as the difference between the fluorescence when PSII reaction centers were fully reduced (F_m) and the minimum fluorescence in the dark (F_o). Recuperation of photosynthetic activity was estimated as the difference between F_v/F_m after 0 h exposure and the daily 18 h recuperative period following daytime low tide. Changes in photosynthetic capacity under emersion (in air) during daytime low tide treatment applications were estimated as the difference between F_v/F_m immediately before and after daytime low tide exposure. For simplicity, photoinhibition as used here refers to the decrease in photosynthetic quantum yield (as evidenced by lower values of variable fluorescence normalized to F_m), regardless of photochemical mechanism (Falkowski and Raven, 2007; Krause, 1988).

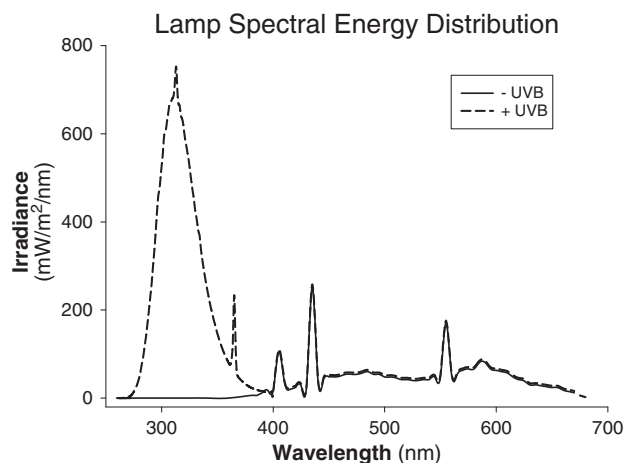


Fig. 1. Spectral composition of the experimental light regime exposed to macroalgal turfs during daytime low tide stress treatments. PAR + UVB, dotted line; PAR alone (-UVB), solid line.

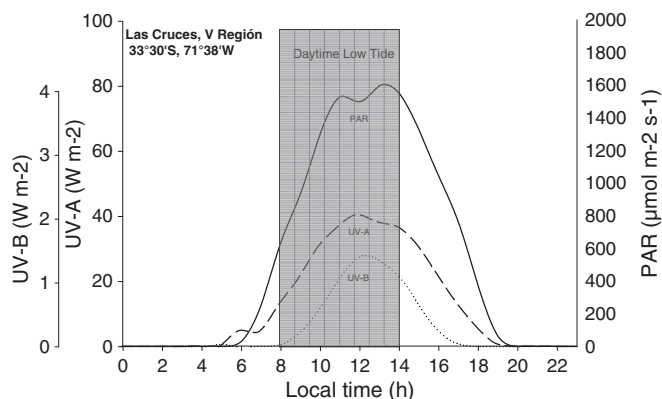


Fig. 2. Daily course of solar radiation measured at outdoor incubation site at Las Cruces during experimental trials. The shaded area represents the period when turf algae were brought indoors and exposed to controlled, artificial light conditions.

2.3. Data analysis

To determine whether turfs originating from different tidal heights within a single site, Las Cruces, respond differently to similarly-controlled climate stressors, we compared Fv/Fm after 18 h recuperation, using a three-way repeated measures ANOVA with the 5 observations on successive days as repeated measures and considering tidal height (low, high), temperature (cool, warm), and UVB (+/–) as fixed factors. We used Mauchly's sphericity test applied to the orthonormalized form of the variance-covariance matrix to test whether the data met the assumption of sphericity. Normality and homogeneity of variance were tested by visual inspection of normal probability plots and residual plots. Untransformed data satisfied these assumptions reasonably well. Therefore, the results of univariate repeated measures analysis are presented and no correction was necessary.

To determine whether low zone turfs originating from sites of different upwelling condition respond differently to similarly-controlled climate stressors, we compared log-linearized rates of recuperation (calculated up to 72 h) using a split-plot design, in which upwelling (center, downstream) and site nested within upwelling (random factor) formed the “main plot” factors; UVB radiation (+/–), temperature (cool, warm) and the interaction terms among them and with the main plot factors formed the “sub-plot” sources of variance. The appropriate error terms for hypothesis testing were obtained following Kuehl (1994). Normality and homogeneity of variance were tested by visual inspection of normal probability plots and residual plots. All analyses were performed in SAS® 9.0 (SAS Institute Inc., Cary, NC, USA).

To further explore whether turfs differentially endure emersion under contrasting climate conditions, we compared the differences in Fv/Fm immediately before and after daytime low tide exposures (i.e. in air) using a two-way repeated measures ANOVA with 2 observations (first and last days) as repeated measures and considering temperature (cool, warm) and UVB (+/–) as fixed factors. Separate analyses were conducted for low zone turf from each site. We restricted analyses to 2 time periods because the data for the 5 consecutive days did not meet the assumption of sphericity. Normality and homogeneity of

variance were tested by visual inspection of normal probability plots and residual plots.

3. Results

3.1. Comparisons between zones: Las Cruces

Under the same controlled environmental conditions, maximum quantum yield of photosystem II (Fv/Fm) following recovery from daily low-tide stress events was overall greater for turf originating from the upper limits of distribution than for turf lower on the shore (Fig. 3, Table 1, significant effect of zone). However, the magnitude of the effect of zone origin depended upon the presence of UVB and time (Table 1, significant 3-way interaction). Differences in photosynthetic efficiency between zones largely disappeared after 3–4 days of exposure to augmented UVB, when photoinhibition was significantly and similarly strong with values of Fv/Fm near 0.1 thereafter for all algal turfs.

Temperature stress alone had no clear effect on algal turf recovery (Fig. 3, Table 1). The photoinhibition consistently observed immediately after stressful high-temperature events during low tides (Fv/Fm reduced by 7% for high zone and 21% for low zone) was only temporary. Within 18 h after each event each day, turf fully recovered to its original pre-stressed condition. We also found no evidence of significant interactive effects of combined temperature and UVB radiation.

By far, the most damaging effect to *Gelidium* turf was caused by augmented UVB radiation, which significantly and negatively affected PS II recovery (Fig. 3, Table 1; significant main effect of UV). Moreover, the effect was dynamic, accumulating over time (significant UV × time interaction). Fv/Fm values quickly and continuously decreased over the first 3 days of exposure until reaching values near 0.1. After 3 days, photosynthetic apparatus was sufficiently damaged, with no significant recovery, so that no further inhibition was observed and photosynthetic activity remained constantly low during the following days. After this time, turf algae began to bleach, disintegrate, and die.

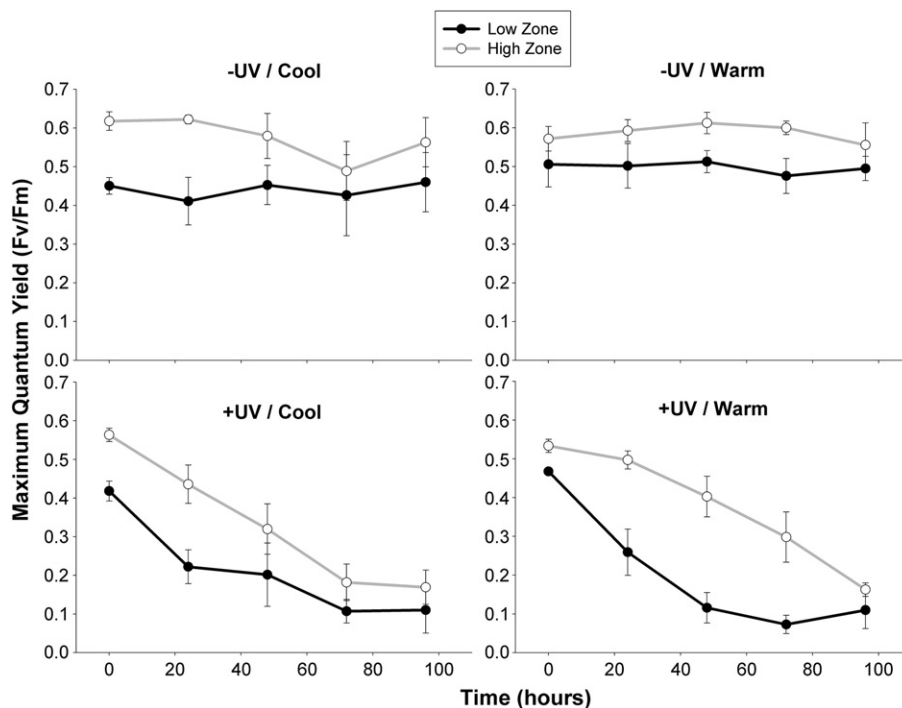


Fig. 3. Las Cruces. Responses of *Gelidium* turf originating from the relatively high (gray line) or low (black line) intertidal zone at Las Cruces. Data are maximum quantum yield of photosynthesis (Fv/Fm) as measured after 18 h of recovery from daily, repetitive low tide exposure to each atmospheric stress treatment.

Table 1

Repeated-measures analysis of variance of the effects of intertidal zone, presence of UVB, and aerial temperature on recovery of maximum quantum yield of photosystem II (Fv/Fm) on 5 consecutive time periods. p-values in bold indicate that factor is significant at $\alpha = 0.05$.

Source	df	F	p
<i>A) Between subjects</i>			
Zone	1	28.57	<0.0001
UV	1	99.98	<0.0001
Temp	1	1.24	0.27
Zone x UV	1	0.58	0.45
Zone x Temp	1	0.004	0.95
UV x Temp	1	0.11	0.74
Temp x UV x Zone	1	1.01	0.32
Error	32		
<i>b) Within subjects</i>			
Time	4	30.84	<0.0001
Time x zone	4	4.1003	0.0094
Time x UV	4	21.23	<0.0001
Time x temp	4	1.32	0.2863
Time x UV x zone	4	1.22	0.0324
Time x temp x zone	4	1.53	0.2199
Time x temp x UV	4	0.17	0.9500
Time x temp x UV x zone	4	0.53	0.7132
Error	128		

3.2. Geographic variability

In general, the temporal patterns described above were similar to that observed for all sites (Fig. 4). However, the magnitude of the deleterious effect of UVB varied depending upon the site of origin (Fig. 4, Table 2, significant interaction UV x site (upwelling)). Contrary to that expected, differences among sites were unrelated to simple categorization of relative upwelling intensity (Table 2, non-significant effect of Upwelling). The decrease in maximum quantum yield Fv/Fm following the recovery from daily low-tide stress events was greatest

for turf originating from Las Cruces. Elsewhere, negative effects of UVB were more moderate.

3.3. Responses of emerged turf

In general, maximum quantum yield (Fv/Fm) of emerged turf in air decreased during daytime low tides (Fig. 5). Although the exposure to higher temperature and/or UVB leads to greater immediate reductions in photosystem II, large variation among individual turf samples rendered differences non-significant at all sites except Las Cruces, where higher temperature had a significant negative effect on photosynthetic efficiency in air (Table 3). The magnitude of the adverse effect of emersion on Fv/Fm decreased over time at all sites (Fig. 5, Table 3, significant effect of time) and was significantly, negatively correlated with Fv/Fm at the beginning of each midday low tide period (Pearson = -0.60 , $p < 0.0001$).

4. Discussion

Along the central coast of Chile, the semidiurnal tidal regime guarantees that intertidal organisms are temporarily exposed to aerial conditions in the middle of the day during summer afternoons and, therefore, to potentially extreme temperatures and light (UV radiation); probably among the most stressful in the world (Finke et al., 2007). However, events of particularly harsh conditions are relatively rare, and thus far largely unpredictable, as the ameliorating role of waves necessitates coincident calm seas. Moreover, such transitory stressful conditions tend to be highly variable over synoptic timescales (3–6 days), following variability in weather and sea conditions (Kaplan et al., 2003; Tapia et al., 2009). Most studies have not examined effects of this naturally varying temporal regimes of different and potentially interacting stressors. Here, we show that sudden, short-term exposure to UVB radiation during daytime low tides represents a strong stress

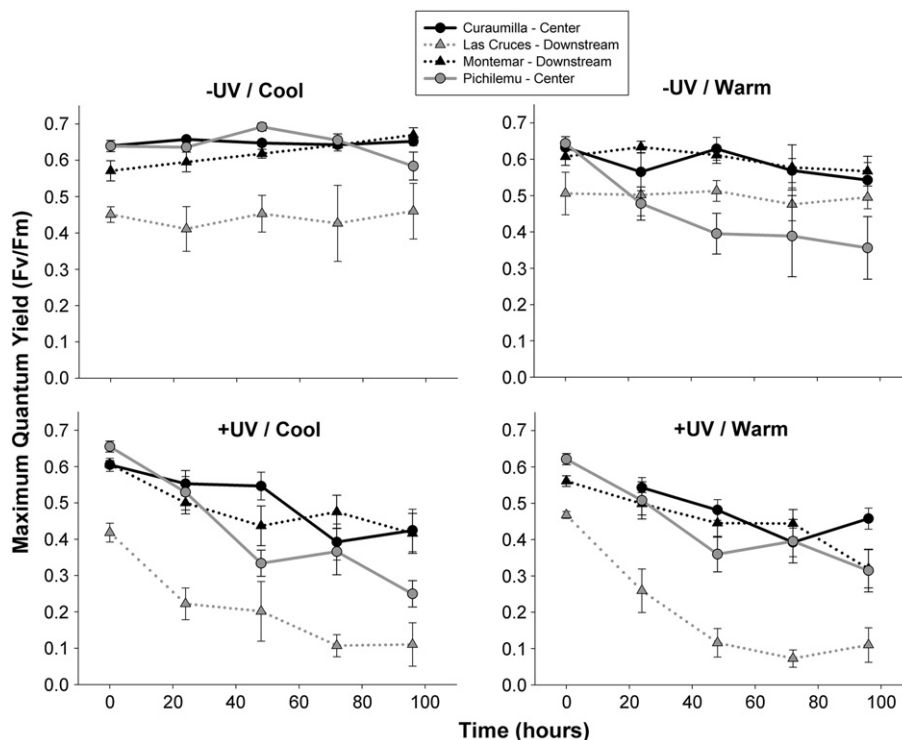


Fig. 4. Geographic variation. Responses of *Gelidium* turf originating from 4 sites of contrasting upwelling condition; centers = solid lines, downstream = dotted lines. Northern sites are in black, whereas southern sites are gray. Data are maximum quantum yield of photosynthesis (Fv/Fm) as measured after 18 h of recovery from daily, repetitive low tide exposure to each atmospheric stress treatment.

Table 2

ANOVA of the physical effects on recovery rates of maximum quantum yield of photosystem II (log-transformed data). Comparisons include all combinations of contrasting light (+/–UVB) and low tide aerial temperature (cool, warm) at sites of contrasting upwelling intensity (center, downstream). The random effects of sites are nested within upwelling. Experimental units for UV and temperature are nested within those for upwelling and site in a split-plot design. p-values in bold indicate that factor is significant at $\alpha = 0.05$.

Source	df	MS	F	p
<i>Main plot</i>				
Upwelling	1	0.00002019	0.13	0.7534
Site (upwelling)	2	0.00015598	13.83	<0.0001
<i>Sub plot</i>				
Temp	1	0.00003201	4.18	0.1776
UV	1	0.00030650	3.28	0.2118
Temp × UV	1	0.00000021	0.03	0.8745
Temp × Upw	1	0.00000074	0.10	0.7858
UV × Upw	1	0.00008890	0.95	0.4322
UV × temp × Upw	1	0.00004460	1.36	0.3641
Temp × site (Upw)	2	0.00000766	0.68	0.5106
UV × site (Upw)	2	0.00009344	8.28	0.0006
UV × temp × site (Upw)	2	0.00003285	2.91	0.0616
Error	64	0.00001128		

factor for *Gelidium* turf algae, and repetitive exposure over a period of 5 d, as it occurs naturally during spring–summer days, can critically compromise the ability of the fronds to recover once the stressor is removed. In contrast, while increased aerial temperature had important effects on the photosynthetic system, this source of stress had no lasting effects on fronds' capacity to recover, nor did it modify the UVB effects on photosynthesis, i.e. no synergistic effects between these common stressors. We also showed that *Gelidium* turf found higher on the shore, close to the upper edge of their tidal height distribution, initially had greater capacity to recover from UVB-induced stress, but this apparently greater photoprotection all but disappeared after 3–4 days of repetitive exposure. Moreover, our results suggest that UVB effects are modulated by algal turf traits that vary over meso-scales of 10s to 100s of kilometers.

Repetitive exposure to UVB during consecutive low tides leads to pronounced and accumulating inhibition of photosynthesis, suggesting that UVB is a strong driver, at least partially, of the extensive turf bleaching observed in the field. Poor recovery of Fv/Fm after UVB exposures points to UV-induced damage of PSII, rather than transient, reversible down-regulation of photosynthetic efficiencies, which can be considered a mechanism of photoprotection (e.g. Bischof et al., 2000). While particular biochemical changes are unknown, damage produced by inhibition often involves oxidation or denaturalization of pigments and proteins and sometimes includes suppression of repair mechanisms that protect reaction centers (Bischof et al., 2000; Takahashi and Badger, 2011). We observed that the effect of an equal dose of UVB changed over time, such that recovery rapidly decreased with repetitive exposure. These results suggest that consecutive irradiation within short time intervals (18 h recovery periods) may increase subsequent sensitivity of fronds to UVB-induced stress. The 18 h recovery period between exposures was chosen to emulate the time low intertidal macroalgae are typically immersed between periods of midday low tides. While intertidal macroalgae often exhibit high acclimation potential to prolonged UV radiation (e.g. Bischof et al., 2006), we still know little about biological responses to repetitive, short-term exposures. From the point of view of the ecology and evolution of stress responses, this type of information is critical indeed.

Previous studies have emphasized thermal dependence of UV damage (e.g. Altamirano et al., 2003; Muller et al., 2008; Rautenberger and Bischof, 2006; Roos and Vincent, 1998; Van De Poll et al., 2002), leading to speculation that photorepair processes may have different temperature characteristics (Pakker et al., 2000). Several studies have shown detrimental effects of UV on photosynthesis to be exacerbated at low temperatures (Gómez et al., 2001; Rautenberger and Bischof, 2006), which slow metabolic rates and enzymatic activities (e.g. Rubisco); whereas at higher temperatures photoprotective mechanisms appear to operate more efficiently (stimulated) and may even be able to compensate for UVB damage (Van De Poll et al., 2002). Our results, in contrast, show no dependence of UVB effects on air temperature at which the fronds were exposed. Air temperature is expected to act by

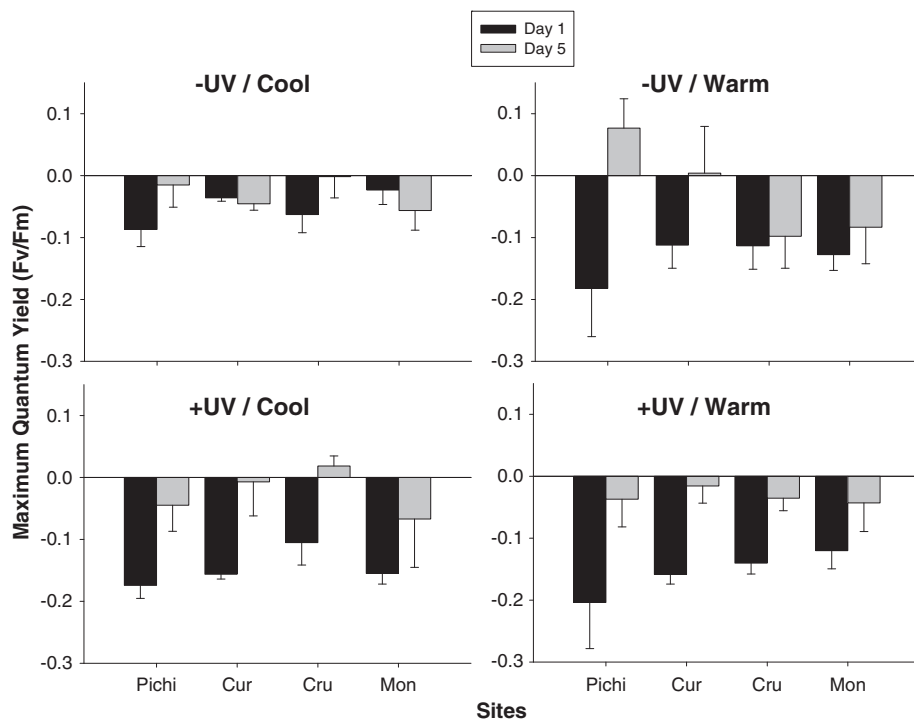


Fig. 5. Responses of emerged *Gelidium* turf originating from 4 sites during daytime low tide. Data are differences in maximum quantum yield of photosynthesis (Fv/Fm) immediately before and after daytime low tide on day 1 and day 5 of daily, repetitive low tide exposure to each atmospheric stress treatment.

Table 3
Repeated-measures analysis of variance of the effects of the presence of UVB and aerial temperature on the differences in maximum quantum yield of photosystem II (Fv/Fm) during daytime low tide emersion on 2 time periods corresponding to days 1 and 5. p-values in bold indicate that factor is significant at $\alpha = 0.05$.

Source	Pichi			Cura			Cruces			Mont		
	df	F	p	df	F	p	df	F	p	df	F	p
<i>A) Between subjects</i>												
UV	1	3.23	0.0913	1	1.35	0.2627	1	0.04	0.8455	1	0.56	0.4662
Temp	1	0.03	0.8609	1	0.09	0.7695	1	11.82	0.0034	1	0.33	0.5747
UV × temp	1	0.02	0.8962	1	0.0158	0.9017	1	0.71	0.4107	1	2.25	0.1528
Error	16			16			16					
<i>b) Within subjects</i>												
Time	1	19.15	0.0005	1	24.72	0.0001	1	7.68	0.0136	1	2.20	0.1574
Time × UV	1	0.06	0.8122	1	5.35	0.0343	1	1.91	0.1864	1	1.69	0.2126
Time × temp	1	2.46	0.1365	1	2.22	0.1554	1	0.35	0.5644	1	0.31	0.5827
Time × UV × temp	1	1.09	0.3113	1	2.71	0.1193	1	0.06	0.8108	1	0.55	0.4685
Error	16			16			16			16		

directly modifying thallus heat balance and indeed air and thallus temperatures were correlated in our experiments. It is possible that the temperature required to inhibit metabolism is lower than that used in our experiment. Likewise, our high temperatures were also conservative in that they were still several degrees below the maximum temperatures that can be registered on extreme days (Finke et al., 2009). Here, temperatures were chosen to reflect mean and average maxima conditions typically observed in the field (low intertidal) during daytime spring–summer low tides, rather than to investigate the biology of the photosynthetic response. Moreover, aerial temperature treatments simulated fluctuations occurring during low tide and thus were not applied during the recuperative periods, which contrasts with most previous laboratory experiments (Altamirano et al., 2003; Henry and Van Alstyne, 2004; Hoffman et al., 2003; Van De Poll et al., 2002), and might help explain lack of interaction with UVB effects. The rate of recovery of photosynthesis upon reimmersion in seawater following a low tide can depend on the temperature experienced by the algal fronds during air exposure, at least when nearing the upper limit of thermal tolerances of the algal species (Bell, 1993; Dring and Brown, 1982; Smith and Berry, 1986). Although our experiments probably did not reproduce extreme temperature conditions nor near thermal tolerance limits, the increased temperature treatment had clear inhibitory effects on the photosynthetic system, yet it did not alter the response to UVB radiation.

Within the same site and rocky platform, we found that the sensitivity of conspecific *Gelidium* turf to UVB, as estimated by their recovery after exposure, depended on the vertical position of the plants on the shore. Individuals originating from higher on the shore, at the upper edge of vertical distribution, showed greater ability to recover from UVB-induced damage associated with daily low-tide stress events. While variation in UVB sensitivity often appears to explain distribution of different species across tidal height with those higher on the shore being less sensitive (Altamirano et al., 2003; Bischof et al., 2006; Gómez et al., 2004), much less is known about within-species local variation and under which conditions plants can physiologically acclimate to abrupt climate-induced stress. The biochemical mechanisms of protection and repair of photosynthetic system in this species are unknown, but may be related to induced accumulation of UV-screen substances (mycosporine-like amino acids and phenols) as shown in other macroalgae (Han and Han, 2005; Karsten et al., 1998). Indeed, relatively high concentrations of such UV-absorbing compounds have been observed for intertidal *Gelidium* further south along the Chilean coast (Huovinen et al., 2004). If this is the case, then repeated, chronic exposure to UVB may allow acclimatization that can protect against extreme events. Indeed, plants acclimated at high light often recover more quickly and completely from short-term extreme events than plants acclimated at low light conditions (e.g. Bischof et al., 1998). In some cases, acclimation of photosynthesis to light occurs rapidly and within several days (Bischof et al., 1999), which suggests that *Gelidium* turfs found in the upper shore could indeed get acclimated to stress conditions by frequent

exposure to 'background' UVB radiation conditions in central Chile. Although acclimation appears to be the most parsimonious explanation for differences between responses of low and upper shore turfs to stress, the existence of genetic differentiation along the intertidal gradient cannot be ruled out at this point without further transplant experiments. In any case, the differences observed in our experiment help explain why we see more intense and more extensive bleaching in the lower edge of *Gelidium* distribution than in the upper shore that is more exposed to aerial conditions (pers. obs.). They also suggest that for many shore communities, abrupt, unpredictable short-term stress events will have greater consequences lower on the shore.

The ability of turf algae to recover from UV-induced damage to photosynthetic apparatus differed significantly among populations from different sites along the central coast. Turf of *Gelidium* originating from Las Cruces showed poorer recovery from UV damage than turf originating from the other sites. This variability again suggests the importance of acclimation to local conditions and the importance of prior (recent) history of exposure to stressors. But, contrary to our expectations, we found no evidence that greater coastal upwelling intensity and associated nutrient enrichment of coastal waters could consistently ameliorate the negative effects of UVB radiation. This result was surprising. Other studies have shown increased growth rates of *Gelidium* turf, as well as other corticated macroalgae species at areas of more intense upwelling and colder temperatures (Nielsen and Navarrete, 2004; Wieters, 2005). Moreover, nutrient enrichment experiments run under laboratory conditions show that high nutrient supply decreases vulnerability of macroalgae to photoinhibition by UVB (Cabello-Pasini et al., 2011; Figueroa et al., 2009, 2010; Korbee et al., 2005), which corresponds well with laboratory studies showing that this *Gelidium* species' sensitivity to and protection from high irradiance can be modulated by nutrients, particularly nitrates (Correa et al., 1985; Santelices, 1991a). Lack of consistent differences between sites of varying upwelling intensity points to the complexity of the algal response and/or the difficulty to extrapolate laboratory results to the naturally variable environmental conditions encountered in the field. Indeed, upwelling conditions vary over seasonal and synoptic timescales (Narváez et al., 2004; Tapia et al., 2009) and while these pulsed nutrient enrichment events accumulate in the form of algal biomass (Wieters, 2005), we do not know how the enrichment would favor the recovery of the fronds to irradiance and UVB. Further experiments evaluating variation in algal responses among sites must consider multiple periods of time and, ideally, close quantification of all relevant environmental conditions at each site.

The consequences of acute, sublethal stress events have the potential to be far-reaching due to turf ecological dominance. *Gelidium* turfs serve as mediators of settlement and facilitate recruitment of intertidal mussels (Navarrete and Castilla, 1990; Navarrete et al., 2005; Wieters, 2005) and represent the habitat (refuge) for many mobile species (Wieters et al., 2009b). These crucial interactions can

potentially be drastically modified when individuals suffer from non-lethal physiological stress. The cost of reduced productivity and/or repair during recovery is likely to limit the energy available for turf growth and reproduction (Menge and Sutherland, 1987). Along our study region, growth rates determine local turf morphology that, in turn, determines their habitat-structure traits, triggering a chain of changes in the direction and/or magnitude of positive interactions (Wieters, 2005; Wieters et al., 2009b).

Our study adds to growing empirical evidence that physiological traits that determine a species' sensitivity to environmental stress vary in a complex manner across its distributional range (e.g. Gilman et al., 2006; O'Neill et al., 2008; Sorte et al., 2011). Populations that are fine-tuned to local abiotic conditions are expected to behave differently under changing environmental conditions and climate, making critical the incorporation of intraspecific variation to accurately predict species risk and distribution. In this case, our data suggest that traits that buffer turf ability to recover rapidly from acute stress events vary over meso-scales of 10s–100s kilometers along the coast, challenging the relevance of predictive methods that view physiological traits as fixed within a species (e.g. species distribution models, 'climate envelope').

Acknowledgments

We are grateful to H. Buck-Weise for the field and laboratory assistance. This research was funded by Fondecyt grants (#1100920 and #1130167) to E. Wieters. We also appreciate further financial support by Proyecto ICM – P10-033F, desarrollado con aportes del Fondo de Innovación para la Competitividad, del Ministerio de Economía, Fomento y Turismo. [RH]

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