



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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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

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