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Interactive effects of grazing and environmental stress on macroalgal biomass in subtropical rocky shores: Modulation of bottom-up inputs by wave action

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ABSTRACT

In contrast to what is observed in most temperate regions, perennial macroalgae are rare at the mid intertidal level of tropical and subtropical shores, and energy transfer through benthic herbivores largely relies on the consumption of periphyton and ephemeral algae. In this study, we evaluated the interactive effects of environmental stress and mesoherbivore grazing in the regulation of ephemeral macroalgal standing stock along subtropical shores moderately exposed and sheltered from waves in southeastern Brazil. Our results show that grazers can prevent ephemeral algal blooms at the most sheltered shores, and that amelioration of environmental stress, through provision of shade, has no consistent effect on overall biomass or temporal persistence of the algal blooms in these shores. At nearby shores exposed to waves, grazers had no measurable effect on algal biomass and shading rock areas from direct solar radiation can have positive effects on some years, but not on others, probably associated to variation in the species comprising the assemblage. Because nitrate concentration in nearshore waters is remarkably low, we suggest that increased water motion may enhance nutrient flux to the midshore and thus algal blooming. At more exposed sites, algae develop faster and reach a canopy size no longer controlled by grazers. Higher biomass of herbivores at exposed rocky shores is thus best explained as a bottom-up effect of increased plant productivity, without a coupled top-down effect on algae. Thus, besides the well documented effect of waves on temperature and desiccation stresses, wave modulation of nutrient supply may be a very important factor controlling abundance of midshore intertidal macroalgae, and deserves more attention in typically nutrient-depleted tropical and subtropical shores.
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1. Introduction

Thinly filamentous and single-layer foliose algae, characterized by high mass-specific productivity (Littler and Littler, 1980; Nielsen and Sand-Jensen, 1990; Steneck and Dethier, 1994) and the ability to rapidly colonize bare spaces at mid to upper intertidal levels (Littler and Littler, 1980; Lubchenco and Gaines, 1981), are a seasonal to semi-permanent component of rocky shore communities along most of the temperate regions of the world (Hawkins and Hartnoll, 1983a; Hawkins et al., 1992; Jenkins et al., 2008; Poore et al., 2012; Wieters et al., 2009). These algal groups are collectively known as 'ephemerals' because they build up dense patches that develop rapidly, and frequently collapse within a few months. In subtropical and tropical shores, algal assemblages can be highly diversified at the low intertidal level, with several species capable of forming dense canopies and complex mosaics of filamentous forms (e.g. Kennish et al., 1996; Menge and Lubchenco, 1981; Sauer Machado et al., 1996). In contrast, ephemeral macroalgae, together with biofilm coatings on otherwise bare rock, are often the only primary producers over extensive sections of both the upper and mid rocky shore levels (Christofoletti et al., 2011a,b). Therefore, unraveling the mechanisms which determine the abundance and temporal persistence of ephemeral algae is a critical step towards a sound understanding of the processes that regulate rocky shore communities, as well as the pathways of ecosystem functioning in tropical regions.

Most species of ephemeral algae lack structural and chemical defenses against consumers, hold high calorific value and are thus often preferred and readily consumed by different types of intertidal and subtidal herbivores, including invertebrates and fish (Aguilera and Navarrete, 2007, 2012; Hawkins and Hartnoll, 1983b; Hawkins et al., 1992; Kennish et al., 1996; Lubchenco, 1978). This high susceptibility to herbivory has been usually associated with the lower biomass of ephemeral macroalgae observed on many temperate shores (Coleman et al., 2006; Hawkins, 1981; Nielsen and Navarrete, 2004; Poore et al., 2012; Steneck and Dethier, 1994) and on a few tropical intertidal shores

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as well (Kennish et al., 1996; Menge et al., 1985; Vinueza et al., 2006). However, the extent to which grazers control algal biomass may vary substantially at different spatial scales, even within the same shoreline, independently of the general climatic region (e.g. Coleman et al., 2006; Jenkins et al., 2005; Nielsen and Navarrete, 2004; Sauer Machado et al., 1996). Although several studies indicated that consumption pressure may increase towards the tropics (Vermeij, 1978; Brosnan, 1992; Schemske et al., 2009; Freestone et al., 2011), a recent review of more than 600 studies does not support such a latitudinal trend (Poore et al., 2012). Indeed, the uneven number of experimental studies in temperate versus tropical intertidal shores (e.g. Poore et al., 2012) makes latitudinal comparisons rather premature.

Besides grazing, competition with late successional species (e.g. Aguilera and Navarrete, 2012; Hawkins, 1981; Nielsen and Navarrete, 2004; Sousa, 1979) and environmental stress, particularly high temperature (Moore, 1972; Williams, 1993), have also been demonstrated to play roles in the seasonal decline of ephemeral algal biomass. Higher temperatures in tropical areas may impose more severe restrictions to intertidal macroalgal assemblages (Moore, 1972; Williams, 1993) and, therefore, environmental factors capable of mitigating heat and desiccation stress, such as orientation to sunlight and exposure to wave splash, may be crucial. While experiments in tropical Panama suggest that consumers are the overriding factor maintaining low algal and invertebrate cover year round throughout the intertidal zone, with little or no seasonality in their effects (Lubchenco et al., 1984), ephemeral algae at mid shore levels on the coast of Hong Kong are more abundant in winter and decline sharply toward summer (Kennish et al., 1996; Williams, 1993, 1994). Algal blooms at the lower intertidal zone on Hong Kong shores extend longer into the summer, probably because of reduced heat stress at this level (Williams, 1993). In many cases, however, the effect of seasonal intensification of heat stress can be confounded with variation in nutrient supply, especially in nutrient-poor waters (Vinueza et al., 2006). Ormond and Banaimoon (1994) showed that macroalgal abundance peaked during late summer and autumn at intertidal rocky shores along the Hadramout Coast, southern Yemen, coinciding to the seasonal upwelling of nutrient-rich waters and not with air temperature minima. Their results suggest that nutrient limitation may be an additional, or alternative, process to physical stress in the regulation of macroalgal blooming in the tropics.

In temperate regions, nutrient concentration in surface waters is usually strongly and negatively correlated to temperature (Kamykowski and Zentara, 1986; Strickland et al., 1970), explaining severe nutrient limitation owing to prolonged stratification of the water column during exceptional hot summers (e.g. Peeters and Peperzak, 1990; Strom and Fredrickson, 2008). In tropical and subtropical regions, the trophic state of coastal waters is generally low during most of the year (Longhurst, 1998). Episodic nutrient inputs in these systems may benefit opportunistic species, capable of rapid nutrient uptake and fast growth, driving substantial changes in benthic assemblages. While experimental assays have shown that different macroalgae can respond positively to pulsed nutrient additions, especially to phosphate and ammonium (e.g. Lapointe, 1985, 1987; Schaffelke and Klumpp, 1998a,b), little is known on the general effects of nutrient inputs along most shores of the world (but see Thompson et al., 2004 for processes controlling biofilms), despite their likely importance to fuel up biological interactions along intertidal coastlines.

In addition to reducing desiccation stress through water splash (Kaehler and Williams, 1998), wave exposure can enhance benthic primary productivity because it facilitates nutrient uptake by increasing effective submersion times, especially in microtidal regions, and by decreasing the thickness of the boundary layer on the surface of algal tissues (Barr et al., 2008; Hepburn et al., 2007; Wheeler, 1980). In this study, we characterized the extent of seasonal blooming of mid shore ephemeral algae, and experimentally measured the effects of herbivory and amelioration of environmental stress (shading) on algal biomass under varying wave exposures. Based on nutrient measurements and temperature records, we also estimated the nutrient regime at our study shores for a better interpretation of experimental results. We also estimated the biomass of limpets and periwinkles at the sampled shores to evaluate whether variability of grazing potential was spatially correlated with algal productivity.

2. Methods

2.1. Study area

This study was undertaken along a 6-km stretch of the São Sebastião Channel (SSC), which is located on the subtropical southeastern coast of Brazil, in São Paulo State. Average sea surface temperature (SST) within the channel varies from 21 °C in winter to 24 °C in summer (Silva et al., 2005), and the tidal regime is predominantly semidiurnal, with maximum range around 1.3 m. Air temperature over 35 °C is not rare during summer and temperature at the intertidal surface of rocks may exceed 40 °C (Kasten and Flores, 2013). Available data on nutrient concentration in coastal waters are limited, but there are strong evidences that overall nutrient availability is very low (usually below 1 μm/l; Gianesella et al., 1999). High-frequency nutrient inputs are expected during summer months due to the intrusion of South-Atlantic Central Waters (SACW; Castro-Filho et al., 1987; Sumida et al., 2005), but a seasonal trend for chlorophyll concentration in shelf waters, with maxima during winter months (Castro-Filho et al., 1987; Ciotti et al., 2010; Sumida et al., 2005), indicates that other nutrient sources than those delivered by SACW may be more relevant.

Experiments were conducted on four different rocky shores: two of them facing occasional swell from the southeast during the passage of low atmospheric pressure fronts (Feiticeira and Itassucê), and the other facing the São Sebastião Island, and therefore expected to be less exposed to wave action (Segredo and Saco Grande, Fig. 1). All shores are within a distance of a few km from the Center for Marine Biology (CEBIMar), and were chosen with no other concerns than accessibility to sites of different exposure to wave action, within the generally protected channel. A clear vertical zonation pattern was observed at all shores. The midshore zone, following the midlittoral term by Stephenson and Stephenson (1972), comprises an upper band, characterized by the barnacle *Chthamalus bisinatus* Pilsbry and patches of ephemeral macroalgae, and a lower band, dominated by the barnacle *Tetraclita stalactifera* (Lamarck) and epilithic algae, interspersed with small mussel beds of *Brachidontes solisianus* d'Orbigny. Barnacles and macroalgal cover at this level rarely exceed 50-70% of the substrate, and rock surfaces are either completely bare, or coated by biofilms of different species (Christofoletti et al., 2011a). The low shore is characterized by an algal mosaic composed mostly of perennial species and by colonial invertebrates. Experiments were conducted at the upper midshore, where the barnacle *Chthamalus bisinuatus* takes most of the available space and forms a distinct horizontal band. At this tidal level, limpets and littorines are especially abundant and probably the main benthic animals consuming macroalgae (see below).

2.2. Environmental data

2.2.1. Temperature

In order to better interpret results of experimental manipulations, we obtained daily time series of environmental variables for the two sampling periods considered in this study. Air temperatures were obtained from a Campbell weather station installed within the CEBIMar area, 18 m above sea level. Sea surface temperature (0.5 m deep) was recorded manually at the same location on a fixed daily schedule.

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