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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A B S T R A C T

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

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.
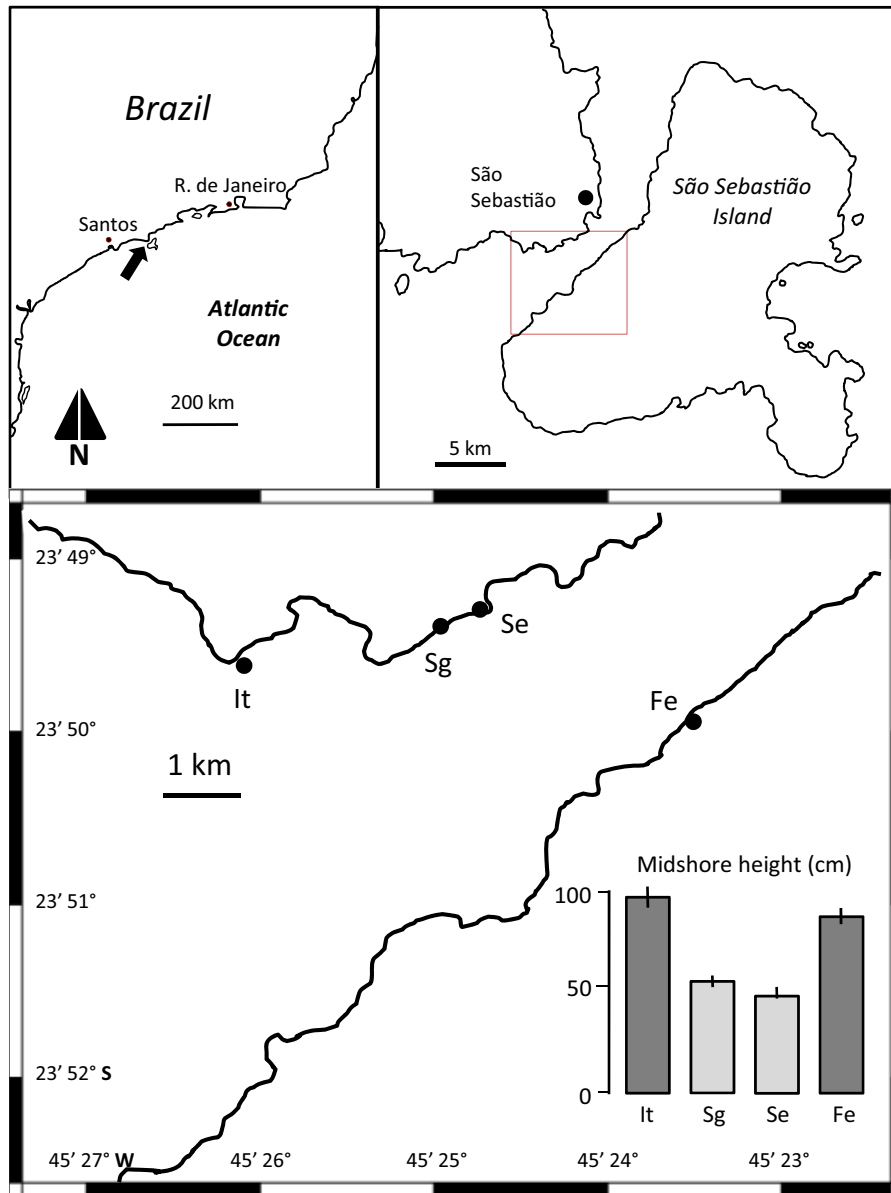
Fig. 1. Map of the study area showing the location of the sampled shores. The bar graph embedded indicates the vertical spread of the midshore zone (mean $\pm$ 1SE), from the upper limit of the coralline algal turf to the upper limit of the chthamalid zone, as an indirect measure of wave exposure (see 'Materials and Methods'). Dark and light grey bars correspond to exposed and sheltered shores, respectively ($p < 0.05$). It: Itassucê, Sg: Saco Grande; Se: Segredo; Fe: Feiticeira.

2.2.2. Nitrate concentration

Since nitrate concentration ($[NO_3]$) varies predictably as a function of temperature (T) for a given area (e.g. Switzer et al., 2003), we obtained estimates of nutrient regimes using the empirical relationship between these two variables within the SSC. To this end, we used the data obtained by Gianesella et al. (2008) during the summer and spring of 1994 and 1997, and by Peres (2013), who conducted discrete weekly nutrient samples in a cross-shore transect, during 3 months in summer and 3 months in winter of 2012. Measurements of nitrate concentrations followed the method proposed by Aminot and Chaussepied (1983). At the same depths, temperature was recorded with a YSI probe and a Seabird 19 CTD profiler. A piecewise non-linear regression (Ryan and Porth, 2007) was fit to these data to take into account the typical two-stage relationship between temperature and nutrient concentration (see Results). The piecewise model implies that, at a given temperature threshold, c, there is a sharp shift in the relationship between nutrient and temperature. Initial estimates for the shifting

threshold, the slopes and intercept of the two linear sections were obtained through Lowess (Locally Weighted Scatterpplot Smoothing) and linear regressions, respectively. Non-linear regression was then used in SAS (Statistical Analysis System) to fit the entire model until convergence was achieved.

2.2.3. Wave exposure

Deployment of chalk blocks (see e.g. Muus, 1968; Kasten and Flores, 2013) to quantify short-term flows during the course of the experiment were unsuccessful due to long periods of calm seas. Therefore, in order to confirm the initial classification of shores, we measured the vertical extension from the upper level of the red algal turf, which marks the beginning of the low shore, to the upper level of the *Chthamalus* zone, where cover exceeds 50%. This corresponds to the 'midlittoral' (Stephenson and Stephenson, 1972) or 'eulittoral' zone (Lewis, 1964), and its height seems to be a reasonable proxy of long-term wave exposure (Lewis, 1964), especially in areas subjected to a microtidal

regime (Pannacciulli and Relini, 2000) such as the coastline of Southeastern Brazil. In this study we referred to this vertical distance as 'midshore height'. Replicate measurements (n = 10) were obtained at regular distances along each of the shores using the bottle and tube method (Hawkins and Jones, 1992), but replacing the bottle by a second ruler. Midshore height data were analyzed using a nested analysis of variance, in which 'shore' was a random factor nested within the two pre-defined levels of wave 'exposure'.

2.3. Grazer biomass

Because among-shore variation of biomass was very large (see Results), wet weight records of blotted individuals, although less precise than dry weight estimates, sufficed for this analysis. The target species were the limpet *Collisella subrugosa* (d'Orbigny) and the periwinkle *Nodilittorina lineolata* (d'Orbigny). Other grazers, *Siphonaria hispida* Hubendick and *Fissurella clenchi* Farfante, which are also small (<2.0 maximum shell length), comprised less than 3% of all observed individuals. Notably, we could not estimate density or biomass of fast-moving consumers (crabs *Pachygrapsus transversus* and fish) and their effects in explaining among-shore differences cannot be ruled out (see Discussion). However, selective exclusion experiments have shown that their effects are restricted to the lower shore (Christofoletti et al., 2010). Thirty quadrats (0.50 X 0.50 m for limpets and 0.05 X 0.05 m for snails) were sufficient to get reliable density estimates of grazers. All shores were surveyed in July 2010 and again in March 2011. All snails in the quadrats were brought to the laboratory and weighted. Limpets were not removed to avoid impacting their populations. In this case, quadrats were first photographed, images were analyzed to obtain the size of all limpets, and individual weight estimates were derived from size vs. weight log-linearized relationships. For all shores, estimated relationships were highly significant (p <0.0001), and regression coefficients were high ($0.83 < r^2 < 0.97$). We used shore-specific size-weight relationships to account for differences in slopes, as indicated through covariance analysis.

Statistical comparisons for the overall biomass of grazers followed the same procedure as explained above for the midshore height data. In this case, however, data were log-transformed prior to analysis to meet homoscedasticity.

2.4. Grazing and shading effects at two shores (2008-2009)

Early observations showed that cleared spaces at upper shore levels are often colonized by ephemeral foliose (*Ulva lactuca* L., *Porphyra* sp C. A. Agardh) and filamentous algae (*Ectocarpus* Lyngbye, *Bangia* Lyngbye) (see also Sauer Machado et al., 1996). In order to assess the role of herbivory and shading on ephemeral algal biomass, we conducted an experiment in the *Chthamalus*-dominated zone at Itassucê and Segredo between May 2008 and April 2009. These two shores were selected to represent different levels of wave exposure, moderately exposed and sheltered, respectively, within the SSC. Fifteen 10 X 10 cm plots, spaced a few meters apart, were cleared at each shore using paint scrappers and metal brushes to remove all propagules and leave only bare rock as the starting condition. Note that compared to some studies, these are rather small sampling units designed to allow us more available bedrock space, which was limited in our sampling shores, and were deemed sufficiently large to fit macroalgal mats. Also, benthic consumers are generally smaller than those found in most other regions (see below in 'Results') and their effects would be detected in these small plots. Five replicates of three different treatments were randomly allocated to the cleared plots: a) Exclusion of all grazers, which was conducted by attaching a 9 X 9 X 5 cm square PVC frames, screened with a 1.4-mm microfiber mesh, which worked as a cage. In order to minimize accidental entrance of limpets and periwinkles, the bottom rim of the cage was fitted with a 0.5-cm thick ethylene vinyl acetate (EVA) rubber layer. b) A 'shade' that reduced direct solar radiation and heat stress during daytime low tides,

but allowed grazing inside the plots. In this case we used the same frame as for exclusions, but opened 5-cm wide entrances at two opposed sides that allowed access to all benthic consumers (molluscs and crabs). C) Control plots, which were marked with screws at two opposing corners but otherwise left untouched. In this treatment, all grazers were allowed to entry and environmental conditions were unaltered.

The abundance of all sessile organisms was followed at approximate monthly intervals throughout the 12 month long experiment. During field visits, digital images were taken of all plots, cages were repaired or replaced when needed, and grazers that have accidentally entered the exclusion plots were removed. In the laboratory, the percentage cover of sessile species was recorded using intersection points in a 100 point grid placed at the core of each plot, leaving aside a 1-cm margin where edge effects might occur. Throughout the experiment, the only organisms accounting for more than 2% cover were foliose and thin filamentous ephemeral algae. In order to convert algal cover into biomass per unit area, 5 replicate 5 X 5 cm samples were collected by scrapping all algal material off the rock in areas with 100% cover of either foliose or filamentous algae. Algal samples were weighted after removing excess water. The average weight for foliose and filamentous algae was used to estimate biomass (wet weight, g) from cover data per plot. Biomass per unit area was much higher for foliose (7.12 g. plot^{-1}, corresponding to 879 g.m^{-2}) than filamentous algae (1.76 g.plot^{-1}, i.e. 217 g.m^{-2}).

A clear unimodal seasonal pattern of ephemeral biomass was observed on both shores and for all treatments (see 'Results'). To facilitate analysis and evaluate treatment effects on the total algal biomass observed throughout the season, we integrated algal biomass across all sampling periods in each plot, and then divided by the total duration of the season (s, in days) to provide mean estimates. Assuming linear changes of biomass between successive sampling intervals, we provide estimates of integrated biomass by summing from the first ($i = 1$) to the last sampling date ($i = N$) in the season, and by weighting by the time elapsed between observations, according to:

$$\overline{B_w} = \frac{1}{s} \sum_{i=1}^{N} \frac{\left(B_{t_i} + B_{t(i-1)} \right)}{2} \times \left(t_i - t_{(i-1)} \right)$$

In one plot at Segredo, the cage was proven repeatedly ineffective in excluding herbivores, probably because of substrate irregularities, and was therefore removed from the analysis. Treatment effects on integrated biomass of ephemeral algae (foliose and filamentous combined) were tested using a two-way analysis of variance, in which 'shore' (Segredo and Itassucê) and 'treatment' (control, half-cages and cages) were the main factors and considered fixed effects (shores selected to be representative of wave regimes). Data were log-transformed to meet homoscedasticity. In case of significant treatment effects, orthogonal planned contrasts (see Kuehl, 1994; Quinn and Keough, 2002) were used to test: a) the effect of 'shading' by contrasting control vs. half-cage plots, and b) 'grazing', by contrasting exclusion cages vs. half-cages.

2.5. Variation in grazing and environmental stress across wave exposures (2010)

Since the effects of shading and grazing on ephemeral algal biomass reversed in importance between Itassucê and Segredo (see Section 3.1. of Results), we conducted a second experiment on four shores over the next season. Under a constant herbivory rate, increased splash (waves) may favor the development of ephemeral algae by ameliorating environmental conditions in the intertidal zone in different ways, for instance, by reducing desiccation and heat stresses and by increasing nutrient delivery. In less favorable conditions, reduced growth would make developing algae more susceptible to herbivory preventing seasonal algal blooms. Alternatively, the 'shading effect' observed

in previous experiments could be due to direct effects of physical stress on macroalgae, or to the indirect effect through modifying grazers consumption rates under the shades. In order to test these hypotheses, we modified the treatment design and repeated the experiment on the two original shores and two additional ones, Saco Grande (sheltered) and Feiticeira (moderately exposed). This provided replication within exposure levels and allowed us to test whether the relative importance of grazing and environmental stress varies predictably according to wave exposure. Repeating the experiment on Segredo and Itassucê also allowed us to examine between-year variation in processes controlling algal blooms.

Clearings of experimental plots and caging procedures were conducted in the same way as explained above. In addition to a) exclusions provided by a full cage, b) 'shading' of algae and grazers provided by half cages and c) 'controls' under natural grazing and environmental conditions, we added: d) square fences (9 X 9 X 3 cm), assembled with a 5-mm stainless steel mesh, with upper 2-cm flap bent outwards. This treatment excluded grazers but still maintained natural heat and desiccation stress within the plots (see Aguilera and Navarrete, 2012), and e) half-fences, in which the two opposite corners of the fence were cut off removing 3 cm in each side, thus allowing benthic grazers and providing a procedural control for the fence. In cages, fences and respective procedural controls, EVA rubber was used in the bottom rim for a better adherence to the rock surface. All treatments were replicated 5 times at each shore allowing at least 1 m between plots.

This experiment started on June 2010, and all shores were visited in 4 occasions (July, August, October and November 2010). Cover and average biomass estimates of foliose and filamentous ephemeral algae were obtained as indicated above. We decided not to run a single analysis considering 'shores' a nested factor within 'exposure', both orthogonal to 'treatment', because a much higher algal cover at all exposed shores and factor combinations rendered variances highly heterogeneous and obscured the effects of other terms of the model (see Section 3.2.2. of 'Results'). To simplify the analyses and facilitate interpretation, we ran instead two separate two-way analyses of variance for sheltered and exposed shores, in which 'shore' was consid-ered a random factor with two levels, and 'treatment' a fixed factor with five levels (control, fence, half-fence, cage and half-cage). Data from sheltered shores were also heteroscedastic, but in this case due to exceedingly high variation in a single factor combination (fenced plots at Segredo). Log transformation did not solve the issue, but we decided to proceed because replication was comparatively high and data balanced, allowing a safe interpretation of results (Underwood, 1997). In case of significant 'treatment' effects, planned comparisons tested for a) direct shade effects on algal assemblage (cage vs. fence), b) total effect of shading on algae through direct effects and through potential alteration of grazers' feeding, together (control vs. half-cage), c) fence artifacts (control vs. half-fence), d) effects of grazers under natural environmental conditions (control vs. fence) and e) effects of grazers under shades, where environmental stress is reduced (cage vs. half-cage). These *a priori* contrasts were not orthogonal; but since they tested a different set of hypotheses correction for the degrees of freedom was not considered necessary (see discussion in Quinn and Keough, 2002).

3. Results

3.1. Environmental data

3.1.1. Temperature and nitrate concentration

Fig. 2 shows daily time series of air and sea-surface temperature at Segredo, from July 1st to November 30th, for both seasons, to facilitate comparisons. Mean air temperatures were very similar between seasons (on average only 0.1 °C warmer in 2010), although more variable during 2010 than 2008. Minimum daily temperatures (ca. >17-19 °C) between July and September were slightly lower in 2010 compared to
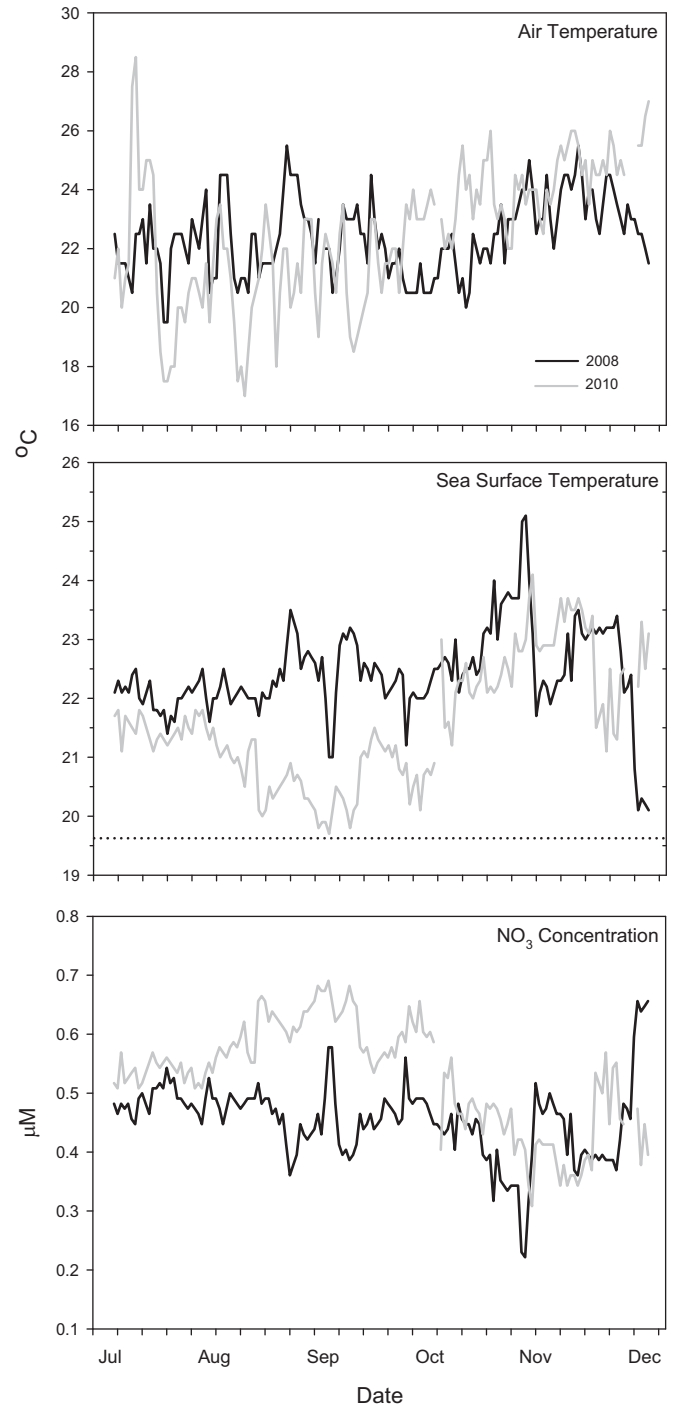
Fig. 2. Daily time series of sea surface temperature, air temperature and nitrate concentration at surface from July 1st to November 30th, during 2008 and 2010, encompassing the shared calendar of fieldwork for the two experiments conducted in this study. Sea surface data consist of manual records taken each day at 0800 ($\pm$0.1 °C), and air data are average values calculated from daily maxima and minima ($\pm$1 °C). Nitrate concentration estimates were calculated from nitrate vs. temperature relationships fit to data retrieved from other sources (Gianesella et al., 2008; Peres, 2013). In the middle plot, the dotted line indicates a critical surface sea temperature (*c*, see 'materials and methods'), separating two conditions in which responses of nitrate concentration to temperature are very different. Above this threshold, as observed over both sampling periods, nitrate is already near depletion and decaying rate with increasing temperature much lower.

2008 (ca. 19-20), remaining very similar later in the year. Maximum temperatures were similar between years, around 24-25 °C, exceeding 28 °C only on one date (July 7th) in 2010.

In the case of SST, however, there were consistent differences between years. On average, water temperature was 1.3 °C lower in 2010. Between late July to mid October, this difference reached 3 °C. Throughout the season and on both years, daily surface temperatures were above the critical temperature threshold at which a switch in the temperature-nitrate relationship is observed ($c = 19.7$ °C; Table S1, Fig. S1), indicating that nutrients were nearly depleted throughout the course of the experimental studies (Fig. 2). Estimates of nitrate concentration based on SST were exceedingly low, compared to nearshore conditions in other regions (i.e. Bustamante et al., 1995; Menge et al., 1997; Nielsen and Navarrete, 2004; Shirodkar et al., 2009), varying from 0.2 to 0.7 μM, and were much lower in 2008 than 2010 for a large part of the year (Fig. 2).

3.1.2. Wave exposure

The vertical extension of the midshore assemblages, a proxy of wave exposure, did not differ between shores within each exposure level ($F_{sh(exp)} = 2.88$, $p > 0.05$), but, as expected, the midshore extension was significantly larger at shores initially classified as 'exposed' than those classified as 'sheltered' ($F_{exp} = 45.98$, $p < 0.05$). In fact, the vertical spread of sessile midshore assemblages at Saco Grande and Segredo is about 0.50 m, while this same measure is near the double at Itassucê and Feiticeira (Fig. 1 insert).

3.2. Grazer biomass

The overall biomass of limpets and periwinkles, and hence grazing potential, also differed significantly according to levels of wave exposure ($F_{exp} = 49.17$, $p < 0.05$, Fig. 3). Mollusc grazer biomass was 3 to 15 times greater in exposed than in sheltered shores, while differences between shores of similar condition were not significant ($F_{sh(exp)} = 1.58$, $p > 0.05$). Periwinkles made up most of the biomass (80%). Across all shores, average shell length of snails *Nodilittorina lineolata* and limpets *Collisella subrugosa* were 2.3 ± 1.1 and 9.6 ± 2.3 mm, respectively.

3.3. Grazing and shading effects at two shores (2008-2009)

The occurrence of ephemeral algae on these shores was clearly seasonal (Fig. 4). Algae colonized plots at the upper-shore level at Itassucê and Segredo from late winter to early spring. Regardless of the grazer treatment, and whether shaded or not, algal blooms disappeared by early to mid-summer. Treatment effects were different between the two shores, as indicated by the interaction term in
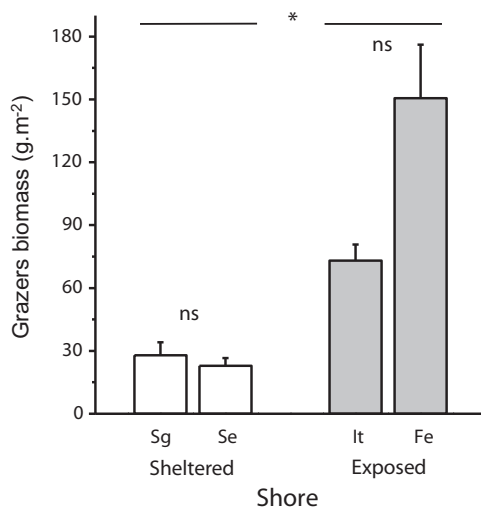

Fig. 3. Total herbivore biomass at rocky shores along the São Sebastião Channel exposed to different conditions of wave exposure. Shore abbreviations as in Fig. 1. ns: non-significant differences; * $p < 0.05$.

Table 1. The most important factor controlling the development of ephemeral blooms at Itassucê was environmental stress, since algal cover was much higher in shaded half-cage plots compared to controls (Fig. 4, Table 1, planned comparison a), while similar cover was recorded in cage and half-cage plots, exposed to benthic grazers (Fig. 4, Table 1, planned comparison b). In contrast, grazing was the single most important factor controlling algal blooms at Segredo, since ephemerals remained nearly absent in both half-cage and controls, but thrived in caged plots (Fig. 4, Table 1, paired comparisons a, b). It is noteworthy that during this 2008/9 season, ephemeral blooms were almost absent in undisturbed (control) plots at both sites.

3.4. Variation in grazing and environmental stress across wave exposures (2010)

When providing proper replication of shores within levels of wave exposure, results indicate a much higher biomass of ephemeral algae under more exposed conditions across all treatments (Fig. 5). At Itassucê and Feiticeira the overall weighed average, combining all treatments, was 0.84 g.plot^{-1}, that is, almost four times than estimated at Segredo and Saco Grande (0.22 g.plot^{-1}). Biomass of ephemerals between shores of similar wave exposure was not significantly different (Table 2).

As expected, grazing effects were different between levels of wave exposure. At sheltered shores and under ambient environmental conditions (no shading), grazers exerted a strong negative effect, preventing development of ephemeral mats (Fig. 5, Table 2 planned contrast e). As observed in the previous season at Segredo, grazers also had a significantly negative effect on ephemeral algal biomass when feeding under the artificial shades (Fig. 5 and Table 2, planned contrast d). Also, as in 2008/9, there was almost no development of ephemeral algal blooms in controls, and amelioration of environmental stress through provision of shade had no significant effects on algal biomass in the presence of grazers (Table 2, planed contrast b), or in their absence (Fig. 5, Table 2, planned contrast a). No artifacts of fences were detected (Table 2, planned contrast c).

At exposed shores, and as observed at Itassucê the previous season, no significant grazing effects were observed (Table 2), and algal biomass in controls was similar to that observed in cages and fences from which grazers were excluded with and without provision of shade, respectively (Fig. 5). But in contrast to the 2008/9 experiment at Itassucê, there was no significant effect of shading on algal biomass (Fig. 5, compare control and half cage). Lack of shading effects was largely due to the much higher algal biomass observed in control (undisturbed) plots during the 2010 season, reaching an average value around 1.25 g.plot^{-1}, while in 2008/9 it did not surpass 0.1 g.plot^{-1}.

Differences in the identity of the dominant species composing the ephemeral algal blooms were observed between seasons, especially at Itassucê. In 2008/9, *Ulva* comprised the bulk of the total cover of ephemeral algae, but it was totally absent during 2010, when *Porphyra* was the sole foliose ephemeral species observed (Fig. 6). The relative share of filamentous algae at Segredo increased from 2008/9 to 2010 (Fig. 6), which explains the reduction of total algal biomass at this shore during this latter season (Figs. 4, 5).

4. Discussion

As in many other tropical or subtropical intertidal shores around the world, the macroalgal cover at the midshore level of southeastern Brazil, and especially along the SSC, is mostly restricted to ephemeral species, with no succession to perennial forms. Together with biofilms, ephemeral macroalgae are the major sources of primary production in this habitat, and thus mechanisms controlling their development can have profound consequences in benthic rocky shore assemblages and the coastal ecosystem. Our results show that grazers can prevent ephemeral algal blooms at the most wave-protected shores, and that amelioration
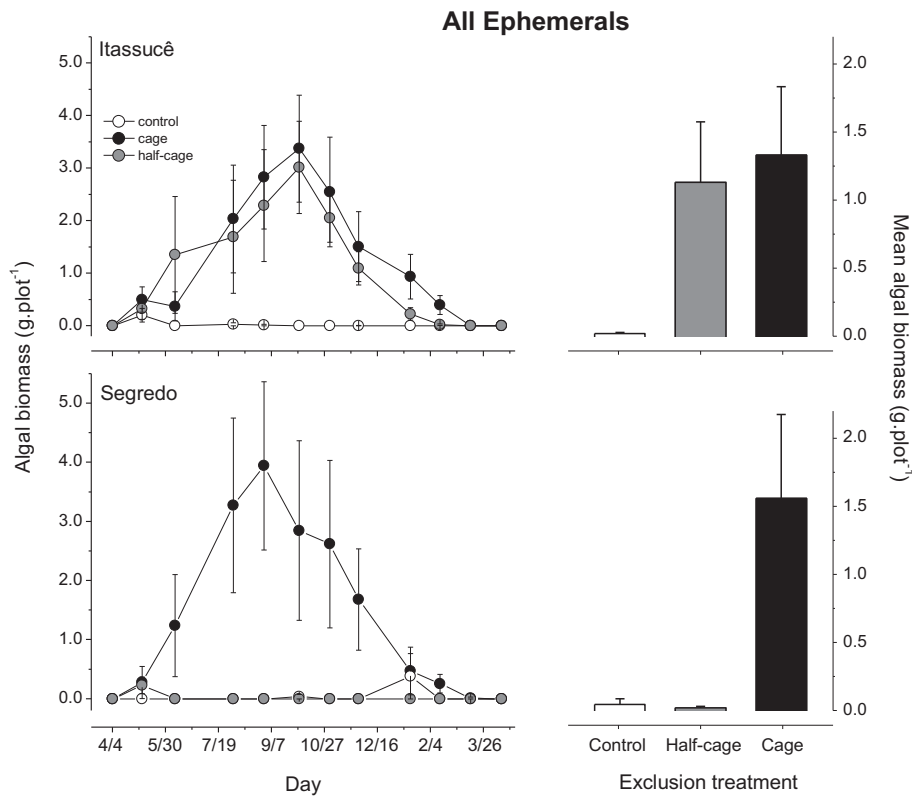
Fig. 4. Temporal variation of total biomass of ephemeral algae on experimental plots cleared in April 2008 at Itassucê and Segredo, under different conditions of consumer exposure (control and half-cage vs cage plots) and shading (control vs. half-cage and cage plots), and respective estimates of weighed mean algal biomass, as a proxy of integrated algal yield. Statistical results are described in Table 1. Whiskers indicate 1 SE around or above average values.

of environmental stress, through provision of shade, has no consistent effect on overall biomass or temporal persistence of the blooms in these shores. But at nearby shores moderately exposed to waves, grazers have no measurable effect on algal biomass and shading rock substrates from direct solar radiation can have positive effects on some years, but not on others. Because the development of ephemeral algae is often limited by nutrient flux (Barr et al., 2008; Wheeler, 1980), and because nitrate supply in the SCC is remarkably low, we submit that differences in macroalgal production across wave exposure and between years can be partly explained by small variation in nutrient fluxes. Other processes, such as interannual differences in propagule supply and selective herbivory could have also played an important role .

Enhanced water motion at sites few kilometers apart within the channel caused a great increase of algal biomass and primary production. Although the amelioration of desiccation and temperature stresses

Table 1
Summary results of the two-way analysis of variance, and orthogonal planned contrasts, for the effect of shading and herbivory ('treatment'). Data obtained from May 2008 through April 2009 at Segredo and Itassucê. Bold values indicate statistical significance at alpha = 0.05. Data were log-transformed.

Source	df	MS	F	p
Shore	1	0.021	1.06	0.3133
Treatment	2	0.327	16.50	**<0.0001**
Sh X Tr	2	0.103	5.20	**0.0137**
Residual	23	0.020		

Planned comparisons

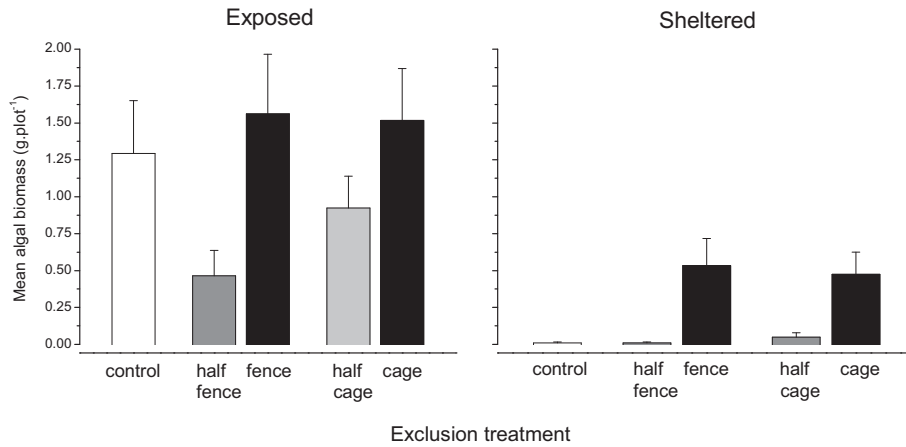|	Segredo		Itassucê	
	F	p	F	P
a) control vs. half-cage (shading)	0.01	0.923	7.05	**0.021**
b) cage vs. half-cage (grazing)	46.10	**<0.001**	0.09	0.764

produced by incoming waves cannot be ruled out as a factor favoring algal productivity, the generally moderate and constant air temperatures across shores and years suggest that a main effect of waves at mid shore levels is to modulate nutrient regimes. Since nutrient concentration in surface waters within the channel is probably similar among all study shores, differences in the wave action at mid shore levels can probably lead to large differences in the nutrient fluxes to which sessile organisms are exposed. Ephemeral algae are characterized for their ability to rapidly capture nutrients (Steneck and Dethier, 1994) and, therefore, this algal group may be particularly favored by the pulsed nutrient inflows. This is achieved by creating turbulence and reducing the thickness of the boundary layer over the plant surface, thus increasing the flux of molecules from the external fluid to plant cells (Hurd, 2000; Wheeler, 1980). Lower on the shore, effective immersion time is increasingly dominated by tides and less by waves (Harley and Helmuth, 2003) and, therefore, nutrient fluxes among shores of different wave exposure should be more similar and more dependent on local currents and turbulence. *In situ* measurements of nutrients and experimental manipulations (e.g. nutrient additions) are indeed needed to test these propositions. Inter-annual differences in algal biomass, in both control and grazer exclusion plots, are also best explained by between-year differences in nutrient concentration in surface waters within the channel. Average and extreme air temperatures were very similar between years, suggesting that stress regimes perceived by intertidal algae were also similar during the course of long and short-term experimental trials. Instead, between-year variation in SST was important and supported the idea that increased nutrient availability led to increased overall algal biomass.

Despite the significantly higher biomass of benthic grazers at the wave exposed shores, grazing effects on algal biomass were consistently non-significant on these shores. Many experimental studies, mostly in temperate systems, have shown that grazer effects can be constrained by algal growth rates and frond size (e.g. Aguilera and Navarrete,

Fig. 5. Effects of herbivore exclusion on the development of ephemeral algae at replicate shores within levels of wave exposure (Jul.-Nov. 2010). Cages and fences excluded grazers with and without shading; half-cages and half-fences are respective procedural controls. Statistical results are described in Table 2. Bars and whiskers indicate average values +1 SE.

2012; Underwood, 1985). The null control exerted by mesoherbivores at wave exposed shores in our study is probably not related to the overall biomass of grazers, but to their small size in combination with increased algal growth rates. Intertidal molluscs in southeastern Brazilian shores are considerably smaller than the size of their counterparts in temperate regions, where top-down effects are much higher than those reported herein (e.g. Aguilera and Navarrete, 2007; Bustamante et al., 1995; Hawkins and Hartnoll, 1983b). In temperate shores of central Chile, the effects of the small sized molluscs within the guild (*Siphonaria* G. B. Sowerby, *Scurria* Gray, still larger than the species observed in Brazil) were restricted to the initial stages of algal succession conformed by biofilm and germlings of ephemeral algae (Aguilera and Navarrete, 2012). Larger fronds, as well as late successional algae, were consumed only by the larger species. Seemingly, differences in algal growth and frond size between shores exposed to different wave action along the SSC can probably make a great difference in the grazing effects of these small benthic consumers. Increased effects of herbivores when algal growth rates are reduced by environmental stress, or nutrient limitation, and null effects at high algal growth rates, are in general accordance with the model proposed by Underwood (1985) in his review on the mediation of biological interactions by physical factors in rocky shores.

The much higher biomass of mesoherbivores in exposed shores, where their effects were not detected, suggest a positive effect of the macroalgal standing stock on limpet and periwinkle populations, with no coupled top-down effects on these macroalgae (Menge, 2000). Contrasting herbivore biomass, however, could also be related to spatial

variation of the recruitment intensity of these consumers among shores (Nielsen and Navarrete, 2004), a possibility that should be investigated.

Results suggest that slower development of foliose algae enable a more substantial establishment of smaller filamentous species, as observed at Segredo and Saco Grande. Since filamentous algae contributed little to overall primary production, we focus this discussion on the changes observed between the foliose forms *Ulva* and *Porphyra*. It is still unclear to us what factors drove the striking inter-annual differences in composition of foliose algae, from the *Ulva* dominated state in 2008/9 to *Porphyra* domination in 2010, but such differences can help explaining mechanisms controlling the establishment of ephemeral macroalgae in our study region. In 2008/9, when *Ulva* prevailed, there was no

Table 2
Summary results of analyses of variance and planned comparisons testing the effects of grazing, with and without shading, at both sheltered and exposed shores. Data obtained from July to November 2010, at Segredo, Itassucê, Saco Grande and Feiticeira. Bold values indicate statistical significance. Data for sheltered shores were log-transformed.

Source	df	Sheltered shores			Exposed shores		
		MS	F	p	MS	F	p
Shores	1	0.140	3.45	0.075	0.262	0.26	0.615
Treatment	4	0.344	10.03	**0.023**	2.127	2.09	0.101
Sh X Tr	4	0.034	0.84	0.505	0.801	0.79	0.542
Residual	40	0.041			1.020		

Planned comparisons for 'treatment' at sheltered shores

	F	p
a) cage vs. fence (shading, no grazers)	0.173	0.699
b) control vs. half-cage (shading with grazing)	0.073	0.800
c) control vs. half-fence (fence artifacts)	0.000	0.999
d) cage vs. half-cage (grazing under shade)	8.727	**0.042**
e) control vs. fence (grazing without shade)	13.257	**0.022**
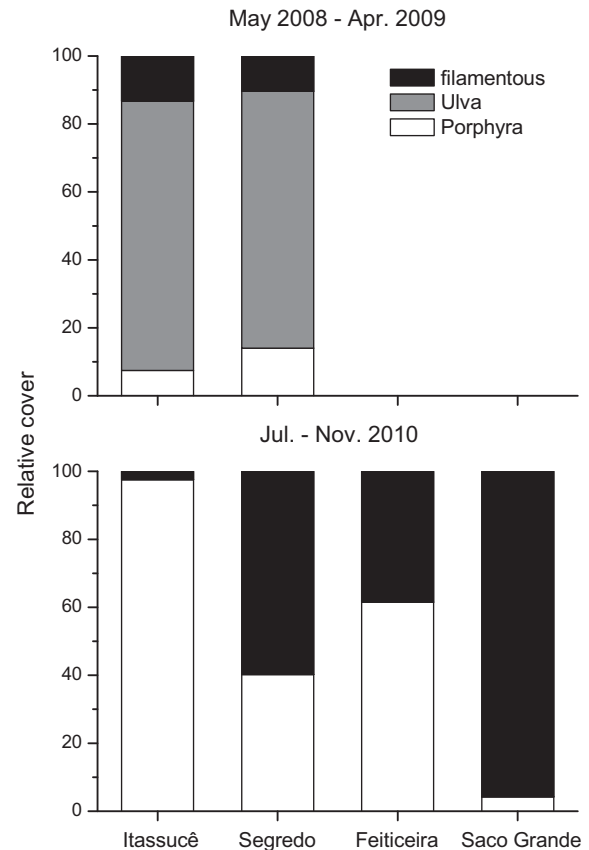
Fig. 6. Relative cover of foliose (*Ulva* and *Porphyra*) and filamentous ephemeral algae on experimental plots cleared in 2008 and 2010 at the study shores.

development of macroalgal patches in control plots suggesting a general effect of desiccation stress. Providing shade reduced physical stress, but this manipulation was however insufficient to increase algal biomass at Segredo, probably because poor water motion (low nutrient delivery) and grazing prevented biomass accretion. At Itassucê, however, shaded plants rapidly responded thanks to higher water flows and escaped grazing control. In 2010, when the more stress-resistant *Porphyra* prevailed (Blouin et al., 2011; Contreras-Porcia et al., 2011; Johnson et al., 1974), shading did not play any apparent role on total algal biomass at the wave protected shores. Blooms of similar magnitude were observed only when grazers were removed, with or without shading. At more exposed shores (Itassucê and Feiticeira) large algal blooms of similar magnitude were also observed with or without shading.

Spatially variable bottom-up inputs and top-down control, driven by variation in wave exposure, appear to be major drivers controlling midshore ephemeral biomass in our study area. Besides the well documented effect of waves on temperature and desiccation stresses, wave modulation of nutrient supply may be a very important factor controlling distribution patterns of intertidal macroalgae in this study system, and deserves more attention in the typically nutrient-depleted tropical and subtropical shores. Under increased water motion, ephemeral algae grew fast to safe canopy size, no longer controlled by the small benthic herbivores that prevail in this region. The effect of environmental stress was smaller in magnitude and more variable than what has been shown in other tropical shores (e.g. Moore, 1972; Williams, 1993), probably because aerial climatic conditions in southeastern Brazil are moderate compared to other tropical areas. Moreover, the effect of environmental stress apparently depends on the identity of species colonizing the midshore. Ecological knowledge of rocky shore intertidal communities, as well as oceanographic conditions in nearshore waters along Brazilian coastlines, are still scant. Therefore, while our experimental results are sound, we acknowledge that several aspects of our interpretation require further support. We hope that the present study will spur future ecological and oceanographic investigations in this region.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jembe.2014.11.001.

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