**Environmental drivers of intertidal communities along Southeast Brazil**

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**Abstract**

**Introduction**

Coastal environments are natural transition zones between terrestrial, freshwater and marine ecosystems, working as an open laboratory to observe the functioning and integration of biological and abiotic drivers over shore communities. Rocky shores are coastal features of the seascape with a high diversity of organisms and species, constituting several ecological niches which make them model habitats for the study of ecological processes (Menge, 2000). The composition and dynamics of the communities in these habitats are directly influenced by physical (exposure to waves, temperature, salinity, tidal range) and biological (competition, predation, herbivory, settlement and colonization) factors. The integration of these factors results in ascending (bottom-up) and descending (top-down) ecological processes, which interact to regulate the diversity, abundance and distribution of producers and consumers (Menge, 2000; Jenkins et al., 2008). In addition, both processes vary at different spatial scales, from meters to hundreds of kilometers (Navarrete et al. 2005, Burrows et al. 2009).

Bottom-up processes influence coastal diversity by directly altering the functioning of ecosystems (Leonard et al. 1998). Biofilms play an important role in benthic ecology on rocky shores (Underwood 1979), being primary producers (Bustamante et al. 1995), serving as food for grazing herbivores (Thompson et al. 2004, Christofoletti et al. 2011) and influencing settlement of seaweed propagules and larvae of marine invertebrates (Wahl 1989). Bottom-up processes on rocky shores emerge from the effect of consumers on prey populations. Such processes have been studied since the 1960s and can be divided into herbivory and predation systems. Experimental works throughout the world report the influence of herbivores on the dynamics of macro and microalgae in the intertidal (Apolinário et al. 1994; Menge et al. 1999; Williams et al. 2000; Aguillera & Navarrete 2007; Jenkins et al. 2008). The abundance and growth of primary consumers is directly related to food, through variations in the primary productivity of phytoplankton; and recruitment, through the relationship between pelagic larval stages and coastal advective processes (e.g., Connolly et al. 2001; Leslie et al. 2005). In this context, variations in food and propagule supplies are seen as the basis for trophic interactions (Menge et al. 2003, Navarrete et al. 2005) and the transfer of energy to the upper links of the trophic chain (Bustamante et al. 1995, Nielsen & Navarrete 2004). Additionally, in coastal marine environments, the importance of these concepts must be observed in systems with contrasting oceanographic regimes, such as areas of high and low resurgence on the continental margin (Menge et al. 1997, Broitman et al. 2001), and comprising wide variations gradients for a better understanding of the relative importance of the regulatory mechanisms involved in the modulation of rocky shore communities.

**Material and Methods**

*Study area*

Between April and September 2015, a descriptive survey was carried out in 62 rocky shores along Southeast coast of Brazil (Fig. 1), comprising a linear length of ~530 km. The whole region studied is dominated by a microtidal regime, with mean sea level around 0.70 m and tidal range about 1.4 m (DHN 2018). Biological data were haphazardly sampled in intertidal zone along an area of approximately 100 m horizontal distance during low tides. Locations were selected within six main regions with distinct natural conditions and anthropogenic influence: (i) metropolitan region of Baixada Santista (MRBS), (ii) São Sebastião Channel (SSCh), (iii) Ubatuba (*i.e.*, north coast of São Paulo State), (iv) south coast of Rio de Janeiro state (SCRJ), (v) metropolitan region of Rio de Janeiro city (MRRJ), and (vi) Lakes Region in Rio de Janeiro (LRRJ, northeast coast of Rio de Janeiro State) (Table S1, Fig. 1). Details of each region can be found in Pardal *et al.* (*submitted*), but briefly, the metropolitan regions of São Paulo and Rio de Janeiro concentrate the largest anthropically influenced sites due to higher degree of urbanization of the two most populated cities in Brazil. The Ubatuba region and SCRJ have the least human influence and largest freshwater discharges, while SSCh and LRRJ are highly touristic but with an intermediate level of anthropic influence when comparing to the other regions sampled here. There are also gradients in temperature and productivity along the studied regions, where colder waters are found towards north due to upwelling events in the LRRJ, and higher productivity is commonly found associated to large bays in MRBS and SCRJ.

*Preys and predators sampling*

Preys (mussel *Mytilaster solisianus* and barnacle *Tetraclita stalactifera*), predators (whelk *Stramonita haemastoma*) and grazers (limpet *Lottia subrugosa* and periwinkle *Echinolittorina lineolata*) were sampled through photos, scraping or by manual collection in the meso and supralittoral of each location. Mussel abundance was estimated as percentage cover in photos of 625 cm² (n = 10), using a 100 regular intersection grid. In laboratory, mussels scraped from 10 x 10 cm parcels in each location were photographed for measuring, and then weighted. The density of the barnacle and limpets was measured from images of 100 cm² (n = 15). In each image, whenever possible 15 individuals of barnacles and all limpets were measured. Total abundance of the whelk per location was estimated collecting specimens in quadrats of 625 cm² (n = 20), and periwinkles were accessed by one person picking specimens by hand for five minutes. All collected individuals were after measured in laboratory, where the largest length of shell and operculum were the representative measure of size for mollusks and the barnacle, respectively.

*Acquisition of oceanographic data*

Nearshore oceanographic data was obtained from satellite images distributed by NASA Ocean Biology Processing Group (https://oceancolor.gsfc.nasa.gov). Ecological research has been taken great advances from such approach (e.g. Burrows et al. 2010, Cole et al. 2011, Mazzuco et al. 2015, Scrosati & Ellrich 2016, 2018), since measuring such environmental variables in situ over large spatial scales and at multiple locations is difficult and expansive. We used level-2 images from the Moderate Resolution Imaging Spectroradiometer (MODIS) aboard the Aqua satellite (1-km resolution). Chlorophyll-a concentration (Chla) and sea surface temperature (SST) were estimated from images within the 1-year period before field samplings at each location. We discarded distorted images or those with clouds covering the interest region. MODIS data were extracted in SeaDAS software (version 7.5.3) (https://seadas.gsfc.nasa.gov/) for a 5x5 spatial window where central pixel was the coordinates of each rocky shore (Table S1, Fig. 1). Pixels with valid values were aggregated as median to each image (= date) to characterize the different products for each location. For SST, we used data derived from long wave thermal radiation (11-12 μm) and pixels with quality flags 3 (bad) or 4 (failed) were not considered. Since we obtained few SST data for some location in 5x5 spatial buffer (n < 15), we increased it to 9x9 (see Appendix I). Furthermore, remote sensing reflectances (Rrs) at some bands (Rrs443, 469, 488 and 555 nm) were used for calculating a proxy for freshwater discharge (fwd). As Chla and colored dissolved organic matter (CDOM) optical signatures cannot be fully separated, CDOM:Chla ratio (calculated as: R\_469^443/R\_555^488) (Morel & Gentili 2009) has been proposed to indicate relative proportions of such particles. CDOM concentration is greater were there are freshwater influence, the same occurs for such index. Before all analysis with remote sensing reflectance, we excluded pixels with negative values and then calculated the coefficient of variation for each reflectance band considered for each image. Images with coefficient of variation of Rrs ≥ 100% were discarded. This criterion was established because we considered values larger than that you contain unreliable estimates. We chose to extract data from images selected by us instead using averaged images (level-3) because low-resolution interpolation may generate unrealistic values based on unknown number of replicates for interested spatial and temporal window (Appendix I). We draw caution on interpretation of such values since differential sediment loads and bathymetry along study area may have influenced nearshore estimates of Chla and Rrs. Despite of values being overall overestimated, magnitude differences among groups in comparison are preserved.

*Shore topography*

In each location, we characterized shore topography by measuring roughness, extension and inclination. For estimating substrate roughness, we used the chain method, a cheap and quick technique that generates reliable estimative (Frost et al. 2005). We laid chains of 3 m length from the upper limit of the infralittoral fringe up in a straight-line over the rock surface allowing it to follow all contours and crevices. The ratio between the known length of chain and distance covered over the ground resulted in the roughness index. Extension was measured as the distance between lower limit of mesolittoral and the upper limit of supralittoral, following the limits of distribution of dominant species *Chthamalus bisinuatus* (supralittoral) and *Tetraclita stalactifera* (lower mesolittoral). Finally, we performed measurements of substrate inclination with an inclinometer in the middle of the supralittoral, superior and inferior mesolittoral fringe range. For all variables (roughness, extension and inclination), five replicates were haphazardly measured in each shore.

*Wave exposure*

The likely level of wave exposure of the shores was based on the model of Burrows (2012), and was used to produce a wave exposure map for coastline of Southeast Brazil (Fig. 2B) based on total wave fetch. For every coastal cell, wave fetch was calculated as the distance to the nearest land around each point on the map for up to 200 km away from coastline. The distance to the nearest land was determined in 32 (11.25°) angular sectors for each 200-m grid cell in the model domain. For each cell, the final wave fetch value was the sum of the fetch values across all 32 sectors. Therefore, such value may be expressed as number of cells (0 to 32,000 cells), distance in kilometers (0 to 6,400 km) or as log10 of number of cells (0 to 4.5). We use the latter unity in this study. Summed wave fetch was extracted for a circular area of 500-m radius centered on the coordinates of each location.

*NDVI - Normalized Difference Vegetation Index*

The estimates of biofilm biomass were derived from NDVI (Normalized Difference Vegetation Index) measurement using the same technique applied by Pardal-Souza et al. (2016). The NDVI values were based on the analysis of 15 digital images (15 x 15 cm), taken randomly at the low midshore level of all 62 shores. The NDVI value is an indirect measure of biofilm biomass from a ratio between absorbed and reflected light spectrum by chlorophyll molecules (Bryson et al. 2013). The result is an index from -1 to 1, where positive values are related to microalgae biomass, 0 is the absence of chlorophyll-a in biofilm (*i.e.* non detectable microalgae), and negative values indicated high absorption (*e.g.* values obtained in the water).

*Analysis*

The variables analyzed were grouped in three datasets representing environmental characteristics and biotic components. All variables were checked for distribution characteristics using visual inspection of frequency plots (function *chart*.*Correlation* from package *PerformanceAnalytics*) and the Shapiro-Wilks normality test (function *shapiro.test* from package *stats*). Also, collinearity between variables was tested checking correlation matrices (Pearson correlation coefficient) and applying the VIF (variance inflation factor, *corvif* function). Variables with VIF > 4 were not included in models (Zuur et al. 2009).

We applied Redundancy Analysis (RDA) to biotic data in function of environmental drivers to depict general patterns along spatial scales using average values per location, where populational parameters were standardized by their range, and environmental drivers were centered and scaled prior to run the RDA. The significance of axes and the relative contribution of each environmental variable were tested with a Monte-Carlo test (Reduced model, 4999 permutations) using ‘vegan’ package (Oksanen et al. 2019) tools ‘anova.cca’ and ‘ordistep’.

We address our objectives by using generalized linear mixed models and estimates of variance components. All analyses were performed in R software (R Core Team 2018), using the ‘nlme’ (Pinheiro et al. 2018), ‘lme4’ (Bates et al. 2015) and ‘glmmTMB’ (Brooke et al. 2017) packages. Theoretic information measures (Akaike’s Information Criterion, corrected for sample size: AICc) and likelihood ratio test (LR) were used for model selection whenever needed. Models were ranked and compared according to differences between AIC values (ΔAIC). If ΔAIC > 3, we selected the model with lower AIC; otherwise, LR tests were applied for comparing models nested in each other. In these cases, model with lower AIC score were selected if there was significant difference (p < 0.05); when there was not, we selected model with less parameters following the principle of parsimony. We fitted models by either restricted maximum likelihood method (REML) or maximum likelihood (ML), depending on selection of random or fixed structure, respectively (Zuur et al. 2009). In all cases involving model selection, appropriate family distribution was assessed though visual inspection of residuals plots and AIC score. Final mixed models were always refitted with REML for obtaining parameters estimates. Figures were made using R packages ‘ggplot2’ (Wickham 2016), ‘ggpubr’ (Kassambara 2018), ‘gridExtra’ (Auguie 2017), ‘cowpot’ (Wilke 2019), ‘lattice’ (Sarkar 2008), ‘rgdal’ (Bivand et al. 2018), ‘sp’ (Pebesma & Bivand 2005) and ‘raster’ (Hijmans 2019).

All models were built including a random term and the environmental drivers, but for the predator species (*Stramonita* *haemastoma*), the preys’ parameters (size, density, and cover) were also included in the models. Similarly, for prey species (*L. subrugosa* and *E. lineolata*) the mean values of size and density of predator species were also included in models to depict the relative contribution of bottom-up or top-down influence.

*Spatial scales of variation of population parameters and environmental predictors*

We used estimates of variance components for testing spatial scales of variability in populational parameters of investigated species and environmental predictors. For each response variable, we fitted a fully nested random model considering the factors representing variation at different spatial scales: region (100s of kilometers), subregion (10s of kilometers) and location (kilometers) (figure 1). For size and density, residual variance accounted for variability within location (among replicates). For environmental variables, however, it accounted for variability among locations since we used averaged data. Models were fitted by REML since sampling design was unbalanced due to different number of locations at each subregion. Such approach has been considered appropriated for dealing with unbalanced designs (Robison 1987). Data was not transformed in order to guarantee that variance estimates are comparable across all data. After that, we selected the best random model for spatial patterns of variability of population parameters. Models started with the fully nested random model and included all combinations of random effects with two or only one term. Gaussian (identity link) was used for size analysis, while negative binomial (log link) was applied for density, and binomial (logit link) for cover data. Size was log-transformed for analysis to meet assumptions. We did not consider models with singular fit on model selection.

*Effect of environmental predictors on population parameters*

Before investigating relationships among environmental variables on population parameters, we checked for collinearity among variables using correlation matrices (Spearman’s correlation coefficient) and applying the VIF (variance inflation factor, corvif function). Variables with r ≥ 0.65 and/or VIF > 4 were not included in models (Zuur et al. 2009). Effect of environmental predictors (averaged values) on size, density or cover (depending on species) were tested through generalized linear mixed models with Gaussian (identity link), negative binomial (log link) and binomial (logit link) distributions, respectively. First, we selected the best random structure of the full model using REML method. The different models included all main effect of non-collinear predictors and all possibilities of random effects (random intercept only) (Table S6). Once we selected the best random structure for models, fixed structure was selected through ML estimation. To do so, we performed a backwards stepwise removal of non-significant fixed effects. In each run, the term with biggest p-value or lowest t-value (abundance) was removed. The final mixed model was selected once we could not drop any other term. Final best model was then validated though inspection of residual plots against fitted values and selected environmental variables as well as residuals histogram (Appendix A).

*Spatial models*

The last step was testing for spatial autocorrelation through visual plots of model residuals versus spatial coordinates and model selection. Models accounting or not for spatial autocorrelation (fitted with REML) were compared through AIC score and LR test when needed. For almost all variables, there was no spatial patterns on residuals (models fitted in R package ‘nlme’ and ‘glmmTMB’), i.e. including a term for spatial autocorrelation did not improve models. We found spatial patterns on the residuals corresponding to *T. stalactifera* density. We therefore checked if the best model explaining variations in barnacle density was robust to spatial autocorrelation in the residuals. We did so by building several spatial models based on the location averaged density estimates. We first fitted spatial models using general least squares (Zuur et al. 2009, R package ‘glmmmTHB’), but such models did not improve nor removed the spatial patterns in the residuals (Appendix III, Table S2).

**Results**

*Environmental drivers*

Average sea surface temperature (SST) ranged from 23.04 to 26.17°C along sampled locations. A south-north gradient may be observed on SST (figure S1), with higher temperatures in MRBS, SSCh and Ubatuba subregions (SST ~ 25 °C), and a drop on mean values at MRRJ (~24 °C), and lowest values found at LRRJ (23.1 ± 0.07 °C).

Chlorophyll concentration values showed two peaks on south-north range with highest means at MRBS (6.53 ± 2.07 mg.m-3) and MRRJ (6.83 ± 2.65 mg.m-3) subregions (figure S1). Lowest and less variable [Chl-a] averages were observed at the LRRJ (2.37 ± 0.36 mg.m-3), followed by Ubatuba (3.29 ± 1.53 mg.m-3). The mean NDVI values increased from south to north with the highest and less variable values associated with sites in LRRJ (0.15 ± 0.03 SD, figure S1). Ubatuba (0.07 ± 0.06) and SCRJ (0.08 ± 0.06) subregions showed a high variability in NDVI values (figure S1). NDVI and [Chl-a] showed significative negative correlation (rho=-0.34, p<0.01).

Roughness was highly variable across sampled sites ranging from 1.03 to 3.01, with extreme values at Enseada (Ubatuba) (figure S1). A positive correlation was found between rocky shore inclination and roughness (rho=0.54, p<0.001). Inclination and extension of shores were negatively correlated (Spearman’s correlation coefficient, rho=-0.54, p<0.001). Both drivers had lower and less variable values at northern sites (figure S1), and higher values in Ubatuba and SCRJ (figure S1), associated with the complex costal contour of those subregions. Most wave-exposed locations (higher averaged wave fetch) occurs in MRBS and MRRJ subregions, and sheltered sites were associated to Ubatuba and SCRJ subregions, where variability in wave fetch is high because of the complex coastline and sheltering islands.

Average freshwater discharge index (FWD) had patterns similar to [Chl-a] (figure S1). MRBS and MRRJ subregions had higher values of FWD, with peaks at locations near to bays entrance, indicating higher fluvial influence. Furthermore, average [Chl-a] at surveyed locations was correlated to FWD (rho = 0.63, p<0.001). Detailed descriptive statistic of these environmental variables for each location can be found on supplementary material from Pardal-Souza *et al*. (*submitted*).

Finally, multivariate analysis allowed a global view of environmental drivers’ range, indicating a gradient from north to south influenced by SST, and a division between MRBS site with more influence of freshwater input, wave fetch and chlorophyll-a (figure S2). Lastly, local factors such as roughness and inclination were associated with site from SSCh, Ubatuba and SCRJ, although only FWD, wave fetch and SST were significant (*F-value* 7,46 = 3.66, p <0.001).

*Preys and predator*

In general, the predator *S. haemastoma* shell size was variable along sampled sites, ranging from 6.1 to 59.2 mm, with larger and smaller mean sizes found at LRRJ (28.6 ± 6.8 mm, mean ± SD) and SCRJ (22.4 ± 7.1 mm) sites, consequently (figure 2). *Stramonita haemastoma* was absent from samples on few sites of all subregions, except for MRRJ subregion. Density values fluctuate from 1 to 172 (ind\*1.25m-2) per location (median=19, Q1= 6.75, Q3=29), with the two most extreme densities found at MRBS sites (Astúrias = 172, Riviera de São Lourenço = 94), but any general pattern was observed on the scale of sites, subregions or regions (figure 2, figure S2). Larger part of variation was associated with within site differences for size, and among sites for density (figure 6), reflecting the influence of local drivers on populational parameters. The size of *S. haemastoma* showed predicted negatively relationship with its prey cover (*M. solisianus*), while wave fetch showed predicted positive effects on density of this predator species (table 1, figure 4).

*Tetraclita stalactifera* size ranged from 0.4 to 12.67 mm for all sites, and the highest means were associated to LRRJ subregion, and lowest values were found at MRBS and MRRJ (figure 2). Although variation within sites and subregions was high, locations within Region 2 had lower variation (figure 2). On the other hand, *T. stalactifera* mean density was higher towards north (LRRJ and MRRJ subregions (figure 3), peaking at Forte shore (103.47 ± 30.27 mean ± SD). Barnacles’ size was associated negatively with the freshwater input index (table 1, figure 4). Barnacle densities were higher and more variable at MRRJ and LRRJ sites (figure 2), being negatively associated with SST, and positively with wave fetch (table 1, figure 4). As observed for its predator, there was a large portion of variance associated ‘within sites’ for size, and among and ‘within sites’ for density (figure 6). Spatial correlation was detected for *T. stalactifera* density values and was included in complementary analyses applying spatial correlation structure (Table A3). However, despite autoregressive model had improved model adjust, the spatial correlation on residuals remained with small trends for spatial correlation at location level (figure A4). This way, results from this model must be treated with care due to violation on analysis requirements, although the trends observed in predicted values were well fitted (Figure 4). Besides, that no association with predators’ abundance or size was found on barnacle size or density (table 1).

The size of *Mytilaster* *solisianus* had low variation in general (8.64 ± 2.71 mm, mean ± SD), and the species was absent from nine localities, six of them between SSCh and SCRJ (figure 2). The mean cover of *M. solisianus* decreased from southern to northern sites, with higher and less variable values on MRBS sites (figure 3). Again, most of variability was concentrated at within site level (figure 6), reflecting high variability in local populations. Mytilidae size was negatively related to SST (table 1, figure 4), and larger sizes were found at northern sites (figure 2). The mean cover of *M. solisianus* showed predicted positive effects from wave fetch (table 1, figure 4). No effect of predators was observed on *M. solisianus* cover (table 1).

*Grazers*

The shell size of *Lottia subrugosa* ranged from 0.12 to 26.97 mm in total length across all sites. Smaller and more variable size averages were observed at sites on SCRJ and Ubatuba, increasing at MRRJ and LRRJ sites (figure 2). Densities of limpets were highly variable within and among sampled scales (figure 3), with no clear spatial patterns and values ranging from 0 to 17 limpets per 100 cm2 (Q1 = 1, Q3 = 6). Variance associated with random factors was almost equally associated with all scales for limpet size, but larger than 90% for density (figure 6). Best fitted models predicted a decrease in limpet size under the influence of temperature, freshwater influence and substrate roughness (table 1), indicating that larger limpets would be likely found at warm water and low relief shores far away from rivers. As for densities, only chlorophyll-a concentration was associated negatively in models (table 1), indicating predicted greater densities on more productive waters (figure 5).

The second grazing species, *E. lineolata*, followed a similar pattern to limpets concerning body size, with higher and more variable values at northern sites (figure 2), reflected at the positive correlation found for limpet and periwinkle sizes (rho = 0.53, p<0.001). Average periwinkle size from MRBS (1.95 ± 0.64 mm) and SSCh (2.37 ± 0.98 mm) sites was usually 50% smaller than the average of other sites (4.19 ± 1.26 mm) (figure 3). Despite of the clumped organization of smaller sizes on southern sites and higher variation associated with random factors at subregions (figure 6, figure S6), no spatial correlation was observed on model residuals (figure A10). None of the environmental drivers was associated with the variation in neither density, nor size of periwinkles (table 1). Density models had small number of replicates (n=62), and we could not detect any trends, or effects on models’ random structure (figures 3 and 6, figure S6).

Also, as observed on multivariate analysis for environmental drivers, there was indicated an overlap between regions and higher similarity among biotic components within subregion scale, where MRBS and SSCh were opposite to LRRJ, MRRJ and SCRJ, and Ubatuba as a transitional subregion (figure 7). Larger sizes of grazer species and preys were usually associated together and found associated with colder waters and higher NDVI in Region 2, while density of grazers was less influence by drivers (figure 7). Mytilidae cover was related to MRBS subregion which was more influenced by freshwater and wave fetch (figure 7). In summary, larger sizes of grazing, filter-feeding and predator species were related to oligotrophic colder waters, while densities were associated to local scale factors and more productive sites (figure 7).

Uma imagem contendo captura de tela

Descrição gerada automaticamente

**Figure 1.** Map of study area along Southeast coast of Brazil. Each coloured circle represents one of 62 surveyed rocky shores. Note the division of area into 2 main regions and 6 subregions. RMBS = Metropolitan Region of Baixada Santista; SSCh = São Sebastião Channel; SCRJ = south coast of Rio de Janeiro; and MRRJ = Metropolitan Region of Rio de Janeiro.



**Figure 2**. Body size variation (mean ± se) of the predator *Stramonita haemastoma* (a), the preys *Tetraclita* *stalactifera* (b) and *Mytilaster* *solisianus* (c) and the grazing species *Lottia* *subrugosa* (d) and *Echinolittorina* *lineolata* (e) in intertidal environments of 62 rocky shores from the southwestern Atlantic coast (Brazil).



**Figure 3**. Density (mean ± se) of the predator *Stramonita haemastoma* (a), the preys *Tetraclita* *stalactifera* (b) and *Mytilaster* *solisianus* (c) and the grazing species *Lottia* *subrugosa* (d) and *Echinolittorina* *lineolata* (e) in intertidal environments of 62 rocky shores from the southwestern Atlantic coast (Brazil).

|  |  |
| --- | --- |
| (a) | (b) |
| (c) | (d) |
| (e) | (f) |
| **Figure 4.** Effect of environmental drivers on populational parameters of the whelk Stramonita haemastoma (a, b), the barnacle Tetraclita stalactifera (c, d, e), and the mussel Mytilaster solisianus (f, g) along SE coast of Brazil. Black lines and shaded area represent predictive values of the response ± 95% confidence interval. | (g) |

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**Figure 5.** Effect of environmental drivers on populational size and density of the limpet *Lottia subrugosa* along southwestern Atlantic coast (Brazil). Black lines and shaded area represent predictive values of the response ± 95% confidence interval.



**Figure 6**. Estimates of relative variance component for population parameters (size, density or cover) of the whelk *Stramonita haemastoma* (Str hae), the barnacle *Tetraclita stalactifera* (Tet sta), the mussel *Mytilaster solisianus* (Mit sol), the limpet *Lottia subrugosa* (Lot sub), and the periwinkle *Echinolittorina lineolata* (Ech nil) in 62 rocky shores along southwestern Atlantic coast (Brazil). Variance components for environmental data were calculated based on averaged values per location for *S. haemastoma* and *E. lineolata* densities, then there is no data on variation within location.



**Figure 7.** Redundancy Analysis (RDA) of environmental drivers and biological indicators of intertidal communities along 62 rocky shores from southwestern Atlantic coast (Brazil). Dashed vectors were not significant in reduced model. *R2adjusted* = 0.24 for reduced model.

**Table 1.** Summary of final models of generalized mixed effect models (GLMM) for predator, preys and grazers indicators (dependent variables) tested for effects of biotic and abiotic factors (predictor variables). Statistic value applied were the *t-value* for size, and the *z-value* for densities and cover. SE = standard error, N = number of observations in models.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Dependent variable** | **Fixed effects** | **Estimate** | **SE** | **Statistic value** | **N** | **Random effects** | **Variance** | **SD** |
| *Stramonita haemastoma* |  |  |  |  |  |  |  |  |
| size | intercept | 3.33 | 0.05 | 69.4 | 1650 | Location | 0.03 | 0.18 |
|  | *M. solisianus* cover | -0.002 | 0.00 | -2.53\* |  |  |  |  |
| density | intercept | -1.94 | 0.89 | -2.19 | 58 | Subregion | <0.001 | <0.001 |
|  | Wave fetch | 1.11 | 0.26 | 4.31\*\*\* |  |  |  |  |
| *Lottia subrugosa* |  |  |  |  |  |  |  |  |
| size | intercept | 9.12 | 2.04 | 4.47 | 772 | Location | 0.07 | 0.27 |
|  | SST | -0.29 | 0.08 | -3.48\*\*\* |  | Subregion | 0.04 | 0.21 |
|  | Freshwater index | 0.69 | 0.34 | 2.04\* |  |  |  |  |
|  | Roughness | -0.72 | 0.32 | -2.19\* |  |  |  |  |
| density | intercept | 1.53 | 0.17 | 9.26 | 784 | Location | 0.29 | 0.53 |
|  | Chlorophyll | -0.06 | 0.03 | -2.26\* |  |  |  |  |
| *Echinolittorina lineolata* |  |  |  |  |  |  |  |  |
| size | intercept | 1.16 | 0.14 | 7.77 | 9707 | Location | 0.12 | 0.36 |
|  |  |  |  |  |  | Subregion | 0.04 | 0.19 |
| density | intercept | 5.04 | 0.06 | 94.68 | 62 | Region | <0.001 | <0.001 |
| *Mytilaster solisianus* |  |  |  |  |  |  |  |  |
| size | intercept | 9.76 | 0.38 | 25.78\*\*\* | 52 | GAM |  |  |
|  | SST (edf = 2.02) ref.edf = 2.58 |  |  | 3.83\* |  | R2 = 0.14 | Dev. exp | 16.8% |
| cover | intercept | -6.69 | 1.98 | -3.39 | 1996 | Location | 2.95 | 1.72 |
|  | Wave fetch | 1.81 | 0.54 | 3.34\*\*\* |  |  |  |  |
| *Tetraclita stalactifera* |  |  |  |  |  |  |  |  |
| size | intercept | 1.59 | 0.04 | 36.94\*\*\* | 594 | Location | 0.002 | 0.05 |
|  | Freshwater index | -0.20 | 0.06 | -3.45\*\*\* |  |  |  |  |
|  |  |  |  |  |  |  |  |  |
| density | intercept | 39.84 | 3.53 | 11.28\*\*\* | 62 | GAM |  |  |
|  | SST (edf = 2) ref.edf = 2 | -0.31 | 0.07 | 14.94\*\*\* |  | R2 = 0.31 | Dev. exp | 33.6% |

**Full model for predator** (*S. haemastoma*): *dependent variable* ~ shore extension + shore inclination + wave fetch + SST + roughness + [Chl-a] + NDVI + *T. stalactifera* density + *T. stalactifera* cover + *M. solisianus* cover + *M. solisianus* size + *random term* / **Full model for preys** (*T. stalactifera* and *M. solisianus*): *dependent variable* ~ shore extension + shore inclination + wave fetch + SST + roughness + [Chl-a] + NDVI + *S. haemastoma* size + *S. haemastoma* abundance + *random term* / **Full model for grazers** (*L. subrugosa* and *E. lineolata*): *dependent variable* ~ shore extension + shore inclination + wave fetch + SST + roughness + [Chl-a] + NDVI + *random term*

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