Capítulo ***4***

## **Biotic and physical effects on rocky intertidal populations along the Southwestern Atlantic**

**Abstract**

Bottom-up and top-down processes, set in the context of the physical environment, interact to regulate the abundance and distribution of species. Due to spatial dependence, there is a need for better situating the spatial context at which such processes act on. Through a large-scale observational study, we assessed the spatial scales of variation and contribution of biotic and physical influences on components of rocky intertidal communities from the Southeastern Brazil. We found that most of the variability in the population structure of all species occurred at small spatial scales (i.e., within- and among-sites). Further, we found little evidence of direct bottom-up and top-down influences on the populations but strong associations to physical indicators. Most species were bigger where seawater was colder likely explained by the temperature-size rule. Likewise, most species were more abundant at wave-exposed sites probably because of higher supply of larvae and food. Freshwater input also predicted population structure of species, but the direction of the effect was variable. These intertidal populations seem to be under strong physical control which affects physiological rates and modulates bottom-up inputs and top-down effects.

**Key words:** benthic-pelagic coupling, consumers, grazers, spatial-scales, temperature.

* 1. **Introduction**

The structure and dynamics of communities are influenced by the physical environment (e.g., wave exposure, temperature, salinity) and species interactions (e.g., competition, predation). The balance of the effects of consumers and producers in the context of abiotic heterogeneity results in bottom-up and top-down processes, which interact to regulate the diversity, abundance, and distribution of species (Menge 1992, 2000; Power 1992; Menge et al. 1997; Menge and Menge 2013, 2019; Bakker et al. 2015; Hacker et al. 2019; Sellers et al. 2021). Despite general importance, bottom-up and top-down processes are highly dependent on spatial scales, varying from meters to thousands of kilometres (Menge and Lubchenco 1981; Chapman 1994; Nielsen and Navarrete 2004; Navarrete et al. 2005; Coleman et al. 2006; Christofoletti et al. 2010; Whalen et al. 2020). There is, therefore, a need for better situating the spatial context in which such processes act on.

Manipulative experiments offer a strong approach to assess the role of top-down and bottom-up forces on shaping communities (Menge 1992, 2000; Power 1992; Underwood 1996). In addition to that, correlative studies grounded on large-scale research programs have also proved to be a powerful tool (e.g., Bustamante et al. 1995; Broitman et al. 2001; Thrush et al. 2003; Schoch et al. 2006; Giménez et al. 2010; Lathlean et al. 2015; Scrosati and Ellrich 2018). With due caution in making inferences (Eberhardt and Thomas 1991), the latter approach allows scaling-up ecological understanding on the seek for general mechanisms regulating distribution and abundance of taxa (Hewitt et al. 2007; Witman and Roy 2009). Rather being of less merit, observational studies have long offered key evidence towards comprehending natural phenomena (Underwood et al. 2000).

Based on a large-scale sampling along the Southeastern Brazil marine ecoregion (Spalding et al. 2007), we assessed the spatial scales of variation and contribution of bottom-up/top-down and physical influences on components of rocky intertidal communities. Bottom-up and top-down influences were evaluated based on models including resources/prey variables (i.e., abundance, size) as predictors of population structure of the predators and vice-versa. We hypothesised that the populations of the intertidal species are affected by both bottom-up and top-down processes. Therefore, we expected that greater availability of producers would increase the abundance and size of their consumers (i.e., bottom-up model). Further, we expected that abundance and size of prey would be smaller where predators are more numerous and bigger (i.e., top-down model). We also measured several other predictors representing heterogeneity in physical context at different spatial scales (e.g., shore topography, wave exposure, sea temperature). We predicted that the abiotic factors would affect the population structure of the intertidal species as they can have direct and indirect effects on recruitment, survival, growth and behaviour (see Introduction in **Chapters 2** and **3**). Finally, we predicted that variability in the abundance and size of species will be greater at small spatial scales assessed (Fraschetti et al. 2005).

* 1. **Material and Methods**

*Study area*

The study area and sampling design of this study were the same described in **Chapters 2** and **3**. See the Material and Methods section from these chapters for a detailed description and maps.

*Sampling of intertidal species*

Intertidal populations of different species (the mussel *Mytilaster solisianus*, the barnacle *Tetraclita stalactifera*, the dogwhelk *Stramonita brasiliensis*, the limpet *Lottia subrugosa*, and the periwinkle *Echinolittorina lineolata*) were sampled through photos, scraping, or by manual collection in the midlittoral and supralittoral zones of each site. All samplings were haphazardly done in the tidal zone of higher abundance of each species (Christofoletti et al. 2011b). Mussel abundance was estimated as percentage cover in photos of 625 cm² (n = 10), using a 100 regular intersection grid. Small clumps of mussels were scraped off from the substrate. In the laboratory, the size of the mussels randomly chosen was measured through photos. The densities of the barnacle and the limpet were also measured from images (100 cm², n = 15). In each image, 15 individuals were randomly measured whenever possible. The total abundance of the dogwhelk was estimated by collecting specimens in quadrats of 625 cm² (n = 20 per site). The total abundance of the periwinkle per site was accessed by hand sampling specimens for five minutes. The dogwhelks and periwinkles were measured in the laboratory with calliper or in digital images. The largest length of the shell or the operculum was the representative measure of size for molluscs and the barnacle, respectively.

*Abiotic environmental predictors*

The abiotic environmental predictors used here were: topographical features of the shores (inclination and roughness), wave fetch (as a proxy to wave exposure) (Burrows et al. 2008), satellite chlorophyll-a (Chla, as a proxy to phytoplankton biomass), satellite freshwater discharge index (FwD, based on reflectance band ratios) (adapted from Morel and Gentili 2009), satellite sea surface temperature (SST) and the Normalized Difference Vegetation Index (NDVI, as a proxy to biofilm biomass). Except for NDVI, all other predictors were measured, acquired, and processed as presented in **Chapters 2** and **3** (see the Material and Methods section and Appendices of these chapters).

NDVI measurements were done using the same technique applied by Pardal-Souza et al. (2017). The NDVI values were based on the analysis of 15 digital images (15 x 15 cm), taken randomly at the lower and upper midlittoral level of each site. The NDVI value is an indirect measure of biofilm biomass from a ratio between absorbed and reflected light spectrum by chlorophyll-a molecules (Murphy et al. 2005; Murphy and Underwood 2006). 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). To avoid the influence of the rock background colour, we took pictures before and after cleaning the sampling areas with bleach. We used the difference between the initial and final NDVI estimates. Negative values were discarded as they indicated water excess and a false estimation of biofilm biomass.

*Data analysis*

*Spatial scales of variation*

We used estimates of variance components for identifying spatial scales of variability in the size and abundance of intertidal species (as in Fraschetti et al. 2005; Giménez et al. 2017). For each response variable, we fitted a fully nested random model considering the factors representing variation at different spatial scales: region (100s of kilometres), subregion (10s of kilometres) and site (kilometres). Residual variance represented variability among quadrats (meters to 10s of meters). Models were fitted in R software (R Core Team 2020) using the package ‘lme4’ (Bates et al. 2015). Data was not transformed to guarantee comparability of variance estimates across all data.

*Predictive models*

We only included non-collinear variables in the predictive models based on variance inflation factor (cut-off: VIF > 3) (Zuur et al. 2009). The models were fitted through generalised linear mixed models with Gaussian (identity link), negative binomial (log link) or binomial (logit link) distribution. Models were also fitted in R software with packages ‘lme4’ and ‘glmmTMB’ (Brooks et al. 2017). All models were built including a random term and the abiotic predictors (Chla, SST, FwD, wave fetch, shore inclination and roughness). In addition to that, the model for the predator dogwhelk *Stramonita brasiliensis* included the preys’ parameters (abundance and size), while the models for the filter-feeders (*Tetraclita stalactifera* and *Mytilaster solisianus*) included the parameters of the predatory dogwhelks as predictors. The presence or absence of the mussel *Perna perna* was also used as a predictor of the dogwhelk’s population structure. We did not build models to predict the abundance and size of *P. perna* because this species is harvested along the study area (Carranza et al. 2009). For the grazers *Lottia subrugosa* and *Echinolittorina lineolata*, the models also included NDVI estimates from lower and upper midlittoral, respectively, as predictors. We did not build models for NDVI because the temporal scales of variability of biofilms are finer than that we measured the environmental predictors. These models were built to depict the relative contribution of physical control and bottom-up and top-down influences.

First, we selected the best random structure of the full model using REML estimation. The different models included all main effects of non-collinear variables and all possibilities of random effects (intercept only). We selected the model with the lowest AICc score excluding those with singular fit. Once we selected the best random structure for the models, the fixed structure was selected through ML estimation (Zuur et al. 2009). We performed a backwards stepwise removal of non-significant fixed effects (as in Burrows et al. 2010 and **Chapter 2**). In each run, the term with the biggest p-value was removed. The final model was selected once we could not drop any other term. The final best model was then refitted with REML and validated through inspection of residual plots (Zuur et al. 2019).

* 1. **Results**

*Abiotic environmental predictors*

The abiotic environmental predictors used in this Chapter are the same used in the **Chapters 2** and **3**. See the Results section of such chapters for a detailed description. NDVI was the only new predictor, which was used as a proxy for biofilm biomass. The mean NDVI values in the lower midlittoral tended to increase from south to north with the highest values in the Rio de Janeiro (0.17 ± 0.08; mean ± SD) and Lakes (0.15 ± 0.07) subregions. As for the lower midlittoral, NDVI values was the lowest in the Baixada Santista subregion (0.09 ± 0.07) but with similar values for the other subregions (mean 0.13 to 0.14) (Fig. 1). NDVI from both tidal levels varied mostly within-sites (~75%), with remaining variability concentrated at the among-sites scale (Fig. 1).

Diagram

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**Fig. 1.** NDVI estimates (as a proxy to biofilm biomass) in lower and upper midlittoral along the South-east coast of Brazil and spatial scales of variation. Small symbols are raw data, and large symbols with error bars are mean ± 2SE. UTM easting coordinates were used as *x*-axis as the studied coast runs mostly from west to east.

*Carnivorous predator*

The size of the dogwhelk *Stramonita brasiliensis* ranged from 6.1 to 59.2 mm, with larger and smaller average values found at sites from Lakes (28.6 ± 6.8 mm, mean ± SD) and Green Coast subregions (22.4 ± 7.1 mm), respectively (Fig. S1-A). *S. brasiliensis* was absent from samples on few sites of all subregions, except for Baixada Santista. Abundance values fluctuate from 0 to 94 individuals per site, but no general pattern was observed at all the scales assessed (Fig. S1-B). The dogwhelk abundance was positively associated to wave fetch and also was greater the mussel *Perna perna* was present (Table 1, Fig. 2A-B). *S. brasiliensis* size, in turn, was negatively related to the cover of the mussel *Mytilaster solisianus*. Larger part of variation occurred among-sites for abundance (~75%), and within- and among-sites for size (respectively, ~50% and ~40%) (Fig. 2D).

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**Fig. 2.** Environmental predictors (**A-C**) and scales of variation (**D**) of the abundance and size of the dogwhelk *Stramonita brasiliensis* along the South-east coast of Brazil. Black lines and shaded areas represent predictive values ± 95% confidence interval. Small circles are raw data. Graph **B** is a boxplot.

**Table 1.** Summary of the final generalised mixed models for the relationships between the population structure of the intertidal species and environmental predictors (biotics and abiotic). Statistic values were *t-* (size) and *z-value* (abundance, density and cover). Transformations are indicated where applied.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Dependent variable | Fixed effects | Estimate | SE | Statistic value | P | N | Random  effects | Variance | SD |
| *Stramonita brasiliensis* |  |  |  |  |  |  |  |  |  |
| size | intercept | 29.44 | 1.31 | 22.46 | \*\*\* | 1,643 | site | 20.64 | 4.54 |
|  | *M. solisianus* cover | -0.58 | 0.02 | -2.70 | \*\* |  | residual | 27.98 | 5.29 |
| abundance | intercept | -0.84 | 0.79 | -1.05 |  | 59 | none |  |  |
|  | wave fetch | 0.90 | 0.22 | 4.00 | \*\*\* |  |  |  |  |
|  | *P. perna* presence | 0.85 | 0.20 | 4.15 | \*\*\* |  |  |  |  |
| *Tetraclita stalactifera* |  |  |  |  |  |  |  |  |  |
| log(size) | intercept | 1.86 | 0.09 | 19.09 | \*\*\* | 857 | site | 0.02 | 0.13 |
|  | FwD | -0.58 | 0.13 | -4.47 | \*\*\* |  | residual | 0.05 | 0.24 |
| density | intercept | 11.55 | 2.50 | 4.60 | \*\*\* | 945 | site | 0.41 | 0.64 |
|  | wave fetch | 0.42 | 0.19 | 2.22 | \* |  |  |  |  |
|  | SST | -0.40 | 0.09 | -4.43 | \*\*\* |  |  |  |  |
| *Mytilaster solisianus* |  |  |  |  |  |  |  |  |  |
| size | intercept | 20.34 | 4.17 | 4.87 | \*\*\* | 9,170 | site | 1.21 | 1.10 |
|  | SST | -0.46 | 0.17 | -2.74 | \*\* |  | residual | 6.35 | 2.52 |
| cover | intercept | -8.05 | 1.99 | -4.04 | \*\*\* | 620 | site | 2.28 | 1.51 |
|  | FwD | 3.30 | 1.53 | 2.16 | \* |  |  |  |  |
|  | wave fetch | 1.50 | 0.51 | 2.93 | \*\* |  |  |  |  |
| cover1 | intercept | 0.26 | 1.40 | 0.18 | ns | 550 | site | 1.34 | 1.16 |
|  | *S. brasiliensis* size | -0.11 | 0.03 | -2.85 | \*\* |  |  |  |  |
|  | FwD | 3.68 | 1.27 | 2.90 | \*\* |  |  |  |  |
| *Lottia subrugosa* |  |  |  |  |  |  |  |  |  |
| log(size) | intercept | 9.23 | 1.29 | 5.08 | \*\*\* | 677 | site | 0.03 | 0.17 |
|  | SST | -0.17 | 0.05 | -3.36 | \*\* |  | subregion | 0.01 | 0.12 |
|  | FwD | 0.59 | 0.23 | 2.59 | \* |  | residual | 0.08 | 0.29 |
|  | roughness | -0.57 | 0.21 | -2.63 | \* |  |  |  |  |
| density | intercept | 1.12 | 0.40 | 2.74 | \*\* | 772 | site | 0.25 | 0.50 |
|  | Chla | -0.12 | 0.04 | -3.11 | \*\* |  |  |  |  |
|  | FwD | 1.38 | 0.69 | 1.98 | \* |  |  |  |  |
|  | shore inclination | -9.29E-03 | 4.21E-03 | -2.20 | \* |  |  |  |  |
| *Echinolittorina lineolata* |  |  |  |  |  |  |  |  |  |
| sqrt(size) | intercept | 1.82 | 0.12 | 14.39 | \*\*\* | 9,709 | site | 0.03 | 0.17 |
|  |  |  |  |  |  |  | subregion | 0.09 | 0.30 |
|  |  |  |  |  |  |  | residual | 0.05 | 0.22 |
| sqrt(size)2 | intercept | -4.49 | 0.43 | -102.2 | \*\*\* | 9,709 | none |  |  |
|  | northing | 6.30E-06 | 5.93E-08 | 106.3 | \*\*\* |  |  |  |  |
| abundance | intercept | 5.27 | 0.07 | 68.84 | \*\*\* | 59 | subregion | <0.001 | <0.001 |

**Full model for the carnivore** (*S. brasiliensis*): *dependent variable* ~ Chla + SST + FwD + wave fetch + shore inclination + roughness + *T. stalactifera* density + *T. stalactifera* cover + *M. solisianus* cover + *M. solisianus* size + *P. perna* presence + *random* term; **Full model for the prey** (*M. solisianus* and *T. stalactifera*): *dependent variable ~* Chla + SST + FwD + wave fetch + shore inclination + roughness + *S. brasiliensis* abundance + *S. brasiliensis* size + *random* term; **Full model for the grazers** (*L. subrugosa* and *E. lineolata*): *dependent variable* ~ Chla + SST + FwD + NDVI + wave fetch + shore inclination + roughness + *random term*

1 separate GLMMmodel including dogwhelk size as a predictor (due to missing data); 2 linear effect of northing coordinates on periwinkle size

*Filter-feeders*

The size of the barnacle *Tetraclita stalactifera* ranged from 0.40 to 12.67 mm, and the highest means were found at the Lakes subregion, while lowest values were found at Baixada Santista and Rio de Janeiro (Fig. S1-C). Although variation within sites and subregions was high, locations within Region 2 had lower variation (Fig. S1-C). On the other hand, *T. stalactifera* mean density was higher towards the north (Rio de Janeiro and Lakes subregions) (Fig. S1-D). Barnacle density was higher and more variable at sites from Rio de Janeiro and Lakes, being negatively associated to SST, and positively to wave fetch (Table 1, Fig. 3A-B). The size of barnacles was negatively associated with freshwater input (Fig. 3C). Large portion of variance occurred within-and among-sites for density. For size, variability within-sites and among-sites amounted to ~75% and ~20%, respectively (Fig. 2D).

A picture containing diagram

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**Fig. 3.** Environmental predictors (**A-C**) and scales of variation (**D**) of the density and size of the barnacle *Tetraclita stalactifera* along the South-east coast of Brazil. Black lines and shaded areas represent predictive values ± 95% confidence interval. Small circles are raw data. SST = sea surface temperature; FwD = freshwater discharge index.

The size of the mussel *Mytilaster* *solisianus* had low variation in general (8.64 ± 2.71 mm, mean ± SD), and the species was absent from nine sites, six of them between at São Sebastião Channel and Green Coast subregions (Fig. S1-E). The mean cover of *M. solisianus* decreased from southern to northern sites, with higher and less variable values on sites from Rio de Janeiro subregion (Fig. S1-F). The mean cover of *M. solisianus* was predicted to increase with wave fetch and freshwater input (Table 1, Fig. 3A-B). A second model including *Stramonita brasilensis* mean size as a predictor, revealed that mussel cover was lower where the dogwhelks were bigger (Table 1). Mussel size was negatively related to SST (Fig. 3C). Mussel cover had most variability at the among-sites scale (~50%); remaining variability was associated to the subregion and within-site scales. Mussel size varied mostly within-sites (80%) (Fig. 4D).

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**Fig. 4.** Environmental predictors (**A-C**) and scales of variation (**D**) of the cover and size of the mussel *Mytilaster solisianus* along the South-east coast of Brazil. Black lines and shaded areas represent predictive values ± 95% confidence interval. Small circles are raw data. FwD = freshwater discharge index; SST = sea surface temperature.

*Grazers*

The size of the limpet *Lottia subrugosa* ranged from 0.12 to 26.97 mm. Smaller and more variable averages were observed at sites from Green Coast and Ubatuba, increasing at Rio de Janeiro and Lakes subregions (Fig. S1-G). Densities of limpets were highly variable within and among sampled scales (Fig. S1-H), with no clear spatial patterns and values ranging from 0 to 17 limpets per 100 cm2. Limpet density was associated negatively with Chla and substrate inclination, and positively with freshwater input (Table 1, Fig. 5A-C). Limpet size, in turn, was predicted to increase towards sites with colder waters, low substrate roughness and closer to rivers (Fig. 5D-F). Limpet density varied most at the within- and among-sites scales, while limpet size varied mostly within-sites (~45%) and similarly at sits and region scales (~20% each) (Fig. 5G).

Another grazer, the periwinkle *Echinolittorina lineolata*, followed a similar pattern to the limpets concerning body size, with higher and more variable values at the northern sites (Fig. S1-I). Indeed, we found a positive correlation between the limpet and periwinkle sizes (rho = 0.53, P < 0.001). The average periwinkle size in the sites from Baixada Santista (1.95 ± 0.64 mm) and São Sebastião Channel (2.37 ± 0.98 mm) subregions were usually 50% smaller than the average of other subregions (4.19 ± 1.26 mm) (Fig. S1-I). None of the predictors was associated with the variation in either size or density of *E. lineolata* (Table 1). Periwinkle size, on the other hand, increased consistently with northing coordinates (northward) (LM: F1, 9707 = 11,290, P < 0.001, R2 = 0.54). Models for density had small number of replicates (n = 59), and we could not detect any trends (Fig. S1-J), or effects on the random structure of the models. The periwinkle abundance varied exclusively at the site scale, while size varied mostly at the region scale (~50%), followed by variability within-sites (~25%) (Fig. 5H).

Diagram

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**Fig. 5.** Environmental predictors (**A-F**) and scales of variation (**G**) of the density and size of the limpet *Lottia subrugosa* along the South-east coast of Brazil. **H.** Scales of variation of the periwinkle *Echinolittorina lineolata*. Black lines and shaded areas represent predictive values ± 95% confidence interval. Small circles are raw data. Chla = chlorophyll-a concentration; FwD = freshwater discharge index; SST = sea surface temperature.

* 1. **Discussion**

Our research reveals that, as expected (Underwood et al. 2000; Fraschetti et al. 2005), most of the variability in the population structure of key components of subtropical rocky shores occurred at small spatial scales, i.e., within- and among-sites (see discussions in **Chapters 2** and **3**). In addition to that, we found little evidence of direct bottom-up and top-down influences on the populations but strong associations to physical indicators. Consistently, three out of five species were bigger where seawater was colder and more abundant at wave-exposed sites. Freshwater input also predicted the population structure of most species, but the direction of the effect was variable. Chlorophyll-a concentration and topographical features of shores, on the other hand, affected only one species. This is one of the few large-scale work in rocky intertidal communities along the Southwestern Atlantic (see also Giménez et al. 2017; Cruz-Motta et al. 2020; Livore et al. 2021) and contributes to a better comprehension of the links between environmental variability and biological responses at several spatial scales.

Low SST in the Lakes subregion is associated to the Cabo Frio upwelling regime (Valentin 2001; Coelho-Souza et al. 2012). Here, we found that most species were bigger in colder waters. Although SST was not retained as a predictor of the size of the dogwhelk *Stramonita brasiliensis*, individuals were also bigger in sites from the Lakes subregion (Fig. S1-A). Such consistent pattern is likely linked to the temperature-size rule (Atkinson 1994), where low temperatures delay sexual maturity resulting in bigger adults. The same pattern was described for the barnacle *Chthamalus bisinuatus* along this study area (**Chapter 2**). The only exception was the periwinkle *Echinolittorina lineolata*, which size patterns were similar in the Region 2 (Green Coast, Rio de Janeiro and Lakes subregion) and independent of SST. *E. lineolata* inhabits the supralittoral fringe and it is probably more influenced by air than water temperature. Considering that air temperature along the SE Brazil increases northward (Alvares et al. 2013), patterns in periwinkle size could be linked to gradients in desiccation stress. Thus, it is reasonable that higher air temperature (and higher desiccation stress) could select larger shells due to optimised water storage (Vermeij 1973; Tanaka et al. 2002). Along the Brazilian coast (from 23° to 3°S), smaller individuals of this periwinkle are found equatorward (Matos et al. 2020). The strong association between periwinkle size and latitude in this study supports such hypothesis, which deserves further investigation.

Another consistent and expected pattern we found in this study was the positive influence of wave fetch on the abundance of most species. For the filter-feeders, the increase in hydrodynamics results in higher delivery of food and larvae (Leonard et al. 1998; McQuaid et al. 2005; Dias et al. 2018) and thereby higher densities (Burrows et al. 2010; Tam and Scrosati 2014). Such mechanisms are likely to explain the higher abundances of the barnacle *Tetraclita stalactifera* and the mussel *Mytilaster solisianus* in more wave-exposed sites, consistently with results reported for the barnacle *Chthamalus bisinuatus* (**Chapter 2**). For mobile consumers as *Stramonita brasiliensis*, the positive association between abundance and wave fetch might be linked to a greater availability of prey (Rilov et al. 2001; Christofoletti et al. 2011b) in addition to increased recruitment. In fact, we found that this dogwhelk was more abundant in sites with the presence of the mussel *Perna perna*. However, this relationship could be confounded as *P. perna* occurrence seems to be strongly determined by wave exposure (A. Pardal *pers. obs.*). These results suggest that wave exposure has a key role in modulating bottom-up inputs (i.e., food, larvae) along the studied area (see also Christofoletti et al. 2011b; Flores et al. 2015). On the other hand, the potential mediation of top-down effects by wave action (Menge and Sutherland 1976) is yet to be explored.

The influence of freshwater discharge (FwD) was another important predictor of population structure of investigated species although the direction of the effect was variable. The negative relationship between FwD and the size of the barnacle *Tetraclita stalactifera* can be due to reduced growth rate induced by low salinity (Simpson and Hurlbert 1998; Berger et al. 2006) and high turbidity (White 2008). Again, this result was consistent with patterns in size of the barnacle *Chthamalus bisinuatus* along the same studied area (**Chapter 2**). The positive association of FwD with the size of the mussel *Mytilaster solisianus*, in contrast, suggests that this species can cope well with the lower salinity and high turbidity of estuarine waters. In agreement with that, mytilids species can have great abundance associated to estuarine (Giménez et al. 2010) and polluted areas (López Gappa et al. 1990; Martinez et al. 2019). For the limpet *Lottia subrugosa* the positive effect of FwD on both size and density suggests that biofilm productivity could be greater near to bays fueled by eutrophic waters (e.g., Oliveira et al. 2016). We did not detect patterns of greater biofilm biomass (i.e., NDVI) in such areas which can be due to high grazing pressure keeping biofilm standing stock low.

The abundance and body size of consumers are key traits on predicting outcomes of species interactions (Menge 1983; Emmerson and Raffaelli 2004). Here, we found little evidence that the population structure of the predatory gastropod *Stramonita brasiliensis* affected populations of two of its main prey. The only case supporting evidence of direct top-down control was the lower cover of the mussel *Mytilaster solisianus* where the populations of *S. brasiliensis* were composed of bigger individuals. In fact, dogwhelks are effective in reducing the abundance of mussels, especially the bigger individuals (López et al. 2010). The erratic pattern of dogwhelk abundance and lack of effects on prey population could be because *S. brasiliensis* is harvested for consumption and aquarium trade along the studied area (e.g., Silva and Martins 2017; Gurjão and Lotufo 2018). Depending on the harvesting pressure, which we mostly lack data, the populations of this dogwhelk can be kept at low abundance or skewed to small individuals, thereby restricting top-down effects on prey. Moreover, our characterization of the dogwhelk populations was coarse and might have some influence on the observed patterns. The same is true for the periwinkle abundance. Such less detailed sampling, however, is part of large-scale research programs (Thrush et al. 2003).

Based on bottom-up regulation model (Menge 2000), we expected that higher availability of food (i.e., Chla, biofilm, prey) would correlate to consumers’ size and abundance. Overall, this prediction was not supported. Here, we found the highest Chla values in estuarine urbanised areas, certainly increased by untreated sewage discharge from cities (Oliveira et al. 2016). The subregion where the Cabo Frio upwelling occurs had low Chla, maybe explained by seasonal changes, since the upwelling occurs mostly during austral spring-summer (Valentin 2001), and the seaward advection of upwelled waters (Calil et al. 2021) (see a more detailed discussion in **Chapter 2**). Notwithstanding, Chla only related to the limpet abundance, which was predicted to decrease towards waters rich in Chla. Such pattern could be related to density-dependence (**Chapter 2**). Biofilm biomass also did not predict grazers’ population structure likely because grazing pressure masks biofilm standing stock. Alternatively, biofilm is highly variable in time and space (Jenkins et al. 2001; Christofoletti et al. 2011a) and possibly our sampling method did not capture the spatio-temporal scales in which biofilm and grazers are coupled.

Overall, our results show that investigated intertidal populations are spatially associated with three main trophic-oceanographic systems along the studied area: (i) a cold meso-oligotrophic system at the northernmost sites (Lakes subregion); (ii) a eutrophic system associated to large estuaries and urban zones (Santos and Guanabara bays; Baixada Santista and Rio de Janeiro subregions); and (iii) transitional systems between the two eutrophic bays (São Sebastião Channel, Ubatuba and Green Coast subregions). These three systems have contrasting oceanographical features that seem to exert strong physical control on the intertidal populations affecting physiological rates and modulating bottom-up inputs and top-down effects. Although species interaction (i.e., grazing, predation) has been demonstrated to have great importance on the dynamic of local intertidal communities (Christofoletti et al. 2010, 2011a; López et al. 2010), our results support that at the large-scale assessed here environmental mediation seem to play a key role. Further efforts should address the role of species interaction at broader spatial extents accounting for variability of key abiotic features (e.g., wave exposure and temperature).

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### **Appendix A:** Supplementary figure

Graphical user interface, text

Description automatically generated with medium confidence

Diagram

Description automatically generated

**Fig. S1.** Patterns of body size and abundance of intertidal species along the South-east coast of Brazil (SW Atlantic). **A-B** = dogwhelk *Stramonita brasiliensis*; **C-D** = barnacle *Tetraclita stalactifera*; **E-F** = mussel *Mytilaster solisianus*; **G-H** = limpet *Lottia subrugosa*; **I-J** = periwinkle *Echinolittorina lineolata*. Small symbols are raw data, and large symbols with error bars are mean ± 2SE. For **B** and **J** there is only one data per site. UTM easting coordinates were used as *x*-axis as the studied coast runs mostly from west to east.