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Influence of environmental variables over multiple spatial scales on the population structure of a key marine invertebrate

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Highlights

- Population structure of the barnacle varied mostly at small spatial scales
- Population structure was clearly related to environmental predictors
- Chlorophyll-a concentration was positively related with barnacle size
- Greater barnacle density occurred in wave-exposed sites
- Benthic patterns are coupled to scale-dependent oceanographical variation

Abstract

Quantifying scale-dependent patterns and linking ecological to environmental variation is required to understand mechanisms regulating biodiversity. We conducted a large-scale survey in rocky shores along the SE Brazilian coast to examine spatial variability in body size and density of an intertidal barnacle (*Chthamalus bisinuatus*) and its relationships with benthic and oceanographic predictors. Both the size and density of barnacles showed most variation at the smallest spatial scales. On average, barnacle body size was larger on shores located in areas characterised by higher chlorophyll levels, colder waters, low wave action and low influence of freshwater. Barnacles were more abundant at wave-exposed shores. We identified critical scales of spatial variation of an important species and linked population patterns to essential environmental predictors. Our results show that populations of this barnacle are coupled to scale-dependent oceanographic variation. This study offers insights into the mechanisms regulating coastal populations along a little studied coastline.

Keywords: benthic-pelagic coupling, chlorophyll-a, large-scale, rocky shore, sea temperature, wave exposure.

1. Introduction

Predicting ecological changes to varying environmental context has become a fundamental goal in ecology. Predictive models of species distribution and abundance are an important tool in the management of endangered populations, exotic species or those of economic importance (Mouquet et al., 2015). While the effect of single local factors on populations and communities has long been inferred (e.g., Elton, 1927), less is understood on the influence of simultaneous environmental predictors over multiple spatial scales. This is at least partly a consequence of financial and logistical constraints of gathering data from many sites over broad geographical extents. The increase in availability of satellite imagery products over the past two decades has facilitated macroecological approaches, bridging ecological and environmental variation over large scales of space and time (Lathlean et al., 2015; Scrosati and Ellrich, 2016; Giménez et al., 2017). Although this approach does not determine causation in the environment-species relationships, it allows identification of potential drivers of species distribution and abundance (Underwood et al., 2000; Thrush et al., 2003).

Debate on the scale-dependence of ecological patterns (Levin, 1992) has led to interest in identifying scales of variation in diverse marine organisms (Thrush et al., 1997; Jenkins et al., 2001; Giménez et al., 2014). This is an important practice since resolving scales of variation in natural populations is an important first step in determining the proximate processes causing them (Underwood and Chapman, 1996). Whilst abundant information and studies quantifying scale-dependence are available for temperate regions, there is still limited data elsewhere, for example in the subtropical Southwestern Atlantic. Reaching such a knowledge is desirable since understanding variation in natural populations from local to global scales is a prime research concern (Miloslavich et al., 2018; Bax et al., 2019) and the lack of such data may compromise initiatives towards the management of ecosystems (Ryabinin et al., 2019).

At small spatial scales, environmental variation has an important impact on population and community structure of rocky shores. Within-habitat variability such as substrate roughness or inclination, can affect recruitment, mobility and mortality of species by altering the availability of refuges and other relevant variables such as sediment deposition, water flow, wave force and temperature (Underwood and Chapman, 1989; Whorff et al., 1995; Westerbom et al., 2008; Meager et al., 2011). At a slightly wider scale, variation in wave action is an important predictor of intertidal patterns. Differences in the delivery of food and larvae, and dislodgment of individuals generate different patterns of abundance and size of organisms along gradients of wave exposure (Southward and Orton, 1954; Menge, 1978; Christofoletti et al., 2011). Greater water flow driven by stronger wave action increases recruitment rate and growth of individuals (Leonard et al., 1998). In addition, at these scales the influence of freshwater input can also alter structure of communities due to changes in physical-chemical conditions and sources of nutrients (Tallis, 2009; Giménez et al., 2010). Species under freshwater influence can experience different rates of recruitment, growth and mortality (Berger et al., 2006; Dias et al., 2018).

Efforts in scaling-up ecological data to broader spatial extents, for example over regional scales, have revealed major shifts in intertidal biota linked to ocean conditions worldwide (e.g., Bustamante et al., 1995; Menge et al., 1997b; Menge and Menge, 2013; Lathlean et al., 2015; Hacker et al., 2019). At such spatial scales, variability in populations and communities is related to different regimes of availability and supply of ecological subsidies (i.e., nutrients, detritus, phytoplankton, larvae) driven by oceanographic processes (Menge, 2000). Amongst these, coastal upwelling has a fundamental role in the regulation of benthic ecosystems; regional decreases in sea surface temperature may disrupt latitudinal gradients and alter the physiology of organisms, affecting structure and functioning of ecosystems (Sanford, 1999; Sellers et al., 2021). In addition, the enhanced availability of nutrients affects phytoplankton biomass that generally cascades-up through the food chains affecting growth and density of species (Menge et al., 2003). The incorporation of larger-scale perspective on quantifying ecological variation, in addition to local-scale investigations, is fundamental to better understanding coastal ecology.

Intertidal barnacles have been used extensively as biological models for ecological research. They are abundant and ubiquitous worldwide and respond to environmental variation over several spatio-temporal scales (e.g., Jenkins et al., 2000; Burrows et al., 2010; Scrosati and Ellrich, 2016; Giménez et al., 2017). Along the rocky coastline of the South-west Atlantic, the barnacle *Chthamalus bisinuatus* (Pilsbry, 1916) is the main species occupying the upper limits of the intertidal zone. Recent work has confirmed this species as a good indicator of environmental variability related to benthic-pelagic processes (e.g., Pardal-Souza et al., 2017; Mazzuco et al., 2018; Kasten et al., 2019). Here, we conducted a large-scale survey in rocky shores along the SE Brazilian coast to examine spatial variability in population structure of this intertidal barnacle and its relationship with relevant environmental predictors. A large-scale survey was implemented to quantify density and body size of *C. bisinuatus* at several local populations and to quantify key habitat characteristics of the studied shores (roughness, inclination and spatial extent). Large scale environmental predictors were obtained from satellite images (i.e., chlorophyll-a concentration, sea surface temperature and a freshwater discharge index) and a topographical index derived from coastline data (i.e., wave fetch as a proxy for wave exposure) (Burrows, 2012). Our first goal was to identify spatial variability in size and density of the barnacle *C. bisinuatus* and environmental predictors over a wide range of scales (from meters to > 500 km). We then evaluated the role of benthic and oceanographical environmental variables as predictors of barnacle density and body size. Because food availability, delivery rate and temperature should affect growth rate we expected barnacles to achieve larger size at sites characterised by higher phytoplankton density (using chlorophyll-a as a proxy), higher wave exposure and warmer waters. In addition, we expected that higher water flow would increase larval supply and thus recruitment rate; hence we hypothesised that that barnacle density would be greater at more wave-exposed sites.

2. Material and methods

2.1. Study area

Between April and September 2015, we carried out surveys at 62 rocky shores along the coast of South-east 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 0.7 m above local chart datums and an average tidal range of approximately 1.4 m. Sites were selected at least 1 km apart within two main regions: the state of São Paulo where the coastline has a northwest-southeast orientation (Region 1) and the state of Rio de Janeiro where the coastline changes to a west-east disposition (Region 2). Each region was subdivided into three sub-regions: Region 1: (i) Baixada Santista, (ii) São Sebastião Channel, and (iii) Ubatuba; Region 2: (i) Green Coast, (ii) Rio de Janeiro, and (iii) Lakes (Fig. 1; Appendix A, Table A.1.).

The coast of South-east Brazil is a complex system comprising areas under strong human pressure interspersed with relatively unoccupied ones. On the central coast of the state of São Paulo, the metropolitan region of Baixada Santista is an important urban centre, with ca. 1.8 million inhabitants, several industrial complexes and the biggest port of Latin America (Oscar Júnior et al., 2019). This sub-region is thereby under strong human influence (Braga et al., 2000; Martinez et al., 2019). An extensive estuarine system is found in Baixada Santista, influencing coastal waters (Lana et al., 2018). The São Sebastião Channel and Ubatuba sub-regions are both located in the north coast of the state of São Paulo, a region under less human influence, with several governmental protected areas. Rocky shores and sandy beaches are widespread in this region, while large freshwater discharge and estuarine ecosystems are not present. Further east, the Green Coast is also a less populated area located in the southern part of the state of Rio de Janeiro. Shores here are relatively protected from ocean swell due to a large number of islands and they are also under higher fluvial influence. The metropolitan region of Rio de Janeiro is the second most important urban centre of Brazil, with a population of 12 million people. This metropolitan area is located around Guanabara bay, one of most polluted areas in Brazil (Kjerfve et al., 1997). Guanabara bay waters are rich in chlorophyll-a and nutrients and the plume from the bay can extend 100s of kilometres (Takanohashi et al., 2016). Finally, located in the northeast coast of the state of Rio de Janeiro, the Lakes subregion is under less anthropic influence. A coastal wind-driven upwelling regime is established in this area, with cold waters reaching up to the surface and being transported 10s to 100s kilometres away (Valentin, 2001; Coelho-Souza et al., 2012).

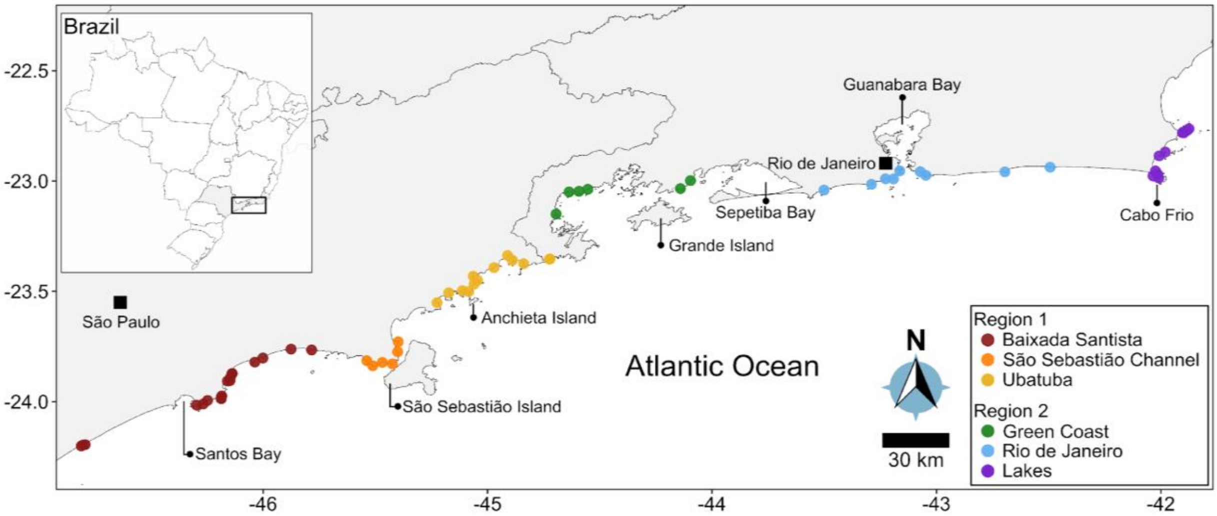


Fig. 1. Map of the study area along the South-east coast of Brazil (SW Atlantic). Circles represent surveyed sites and different colours identify different sub-regions within the two main regions. The cities of São Paulo and Rio de Janeiro and important geomorphological features are also shown.

2.2. Population structure of Chthamalus bisinuatus

A section of rocky shore of approximately 100 m horizontal length was selected at each site. Fifteen 25 cm^2 quadrats were then haphazardly located within the *Chthamalus bisinuatus* zone and a digital image taken. Total barnacle density was assessed and the opercular length of ~15 randomly selected individuals determined in each quadrat. For the analyses, size was averaged by replicate (see Appendix A, Table A.2 for details).

2.3. Acquisition of oceanographic data

Chlorophyll-a concentration (Chla, as a proxy for phytoplankton biomass) and sea surface temperature (SST) were obtained from MODIS-Aqua satellite images (level-2, 1-km resolution) (https://oceancolor.gsfc.nasa.gov) covering the 1-year period prior to field sampling at each site. Chla and SST (quality flags 0, 1 or 2) were extracted for a spatial window of 5 x 5 and 9 x 9 pixels, respectively, centred on the coordinates of sites. We used a larger spatial buffer for SST since we obtained little data using 5 x 5 pixels (Appendix A, Table A.3).

Rivers and estuaries introduce waters rich in organic matter into the sea. The optically active component of such materials (CDOM, coloured dissolved organic matter) can be quantified through remote sensing and applied as a proxy for freshwater discharge (e.g., Schroeder et al., 2012). Chla and CDOM bio-optical signals cannot be truly separable because of similar spectral absorption properties (Morel and Gentili, 2009). Hence, applying a CDOM:Chla ratio is a way to estimate relative proportions of both absorbing substances (Morel and Gentili, 2009), providing a proxy for fluvial water input. We extracted remote sensing reflectances at 443, 469, 488 and 555 nm bands to calculate the ratio $R_{469}^{443}/R_{555}^{488}$ (adapted from Morel and Gentili, 2009). This ratio was used as a positive indicator of freshwater influence. We excluded pixels with negative values and then calculated the coefficient of variation for each band considered for each image. Images with coefficient of variation of bands ≥ 100% were discarded.

2.4. Wave exposure index

Estimates of wave exposure for every 200 m coastal cell along the coastline of South-east Brazil were made based on the model of Burrows (2012). Wave fetch was calculated as the distance, up to a maximum of 200 km, to the nearest land over 32 (11.25°) angular sectors. The final wave fetch value for each coastal cell represents the sum of the fetch values across all 32 sectors expressed as $\log_{10}$ of the number of 200 m cells (ranging from 0 to 4.5). The summed wave fetch was extracted for every cell within a circular area of 500 m radius centred on the coordinates of each site.

2.5. Shore characteristics

At each shore, the roughness of the substrate was established as a proxy for habitat complexity (Frost et al., 2005). Roughness was calculated as the ratio between the linear distance occupied by a 3 m chain applied to the rock surface such that it followed all contours and crevices and its maximum length (Frost et al., 2005). The extent of the *C. bisinuatus* zone was established as the linear distance between the lower and upper limit of distribution of *the species.* Substrate inclination was determined using an inclinometer. Five measurements of roughness, extent and inclination were haphazardly made at each shore.

2.6. Data analysis

2.6.1. Spatial scales of variation of population structure and environmental predictors

We used estimates of variance components for identifying spatial scales of variability in population structure of *Chthamalus bisinuatus* 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 kilometres), sub-region (10s of kilometres) and site (kilometres). Models were fitted in R software (R Core Team, 2020) using the package 'nlme' (Pinheiro et al., 2021). For barnacle size and density, residual variance accounted for variability within-sites (among replicates). For environmental variables, it accounted for variability among-sites since we used averaged data. Data was not transformed to guarantee that variance estimates were comparable across all data.

2.6.2. Relationships between environmental predictors and population structure

Before investigating relationships between environmental predictors and population structure, collinearity among variables was tested applying the VIF (variance inflation factor). Variables with VIF > 3 were not included in the models (Zuur et al., 2009). The effect of averaged values for environmental predictors on size and density was tested through (generalized) linear mixed models with Gaussian (identity link) or negative binomial (log link) distribution, respectively. We used the packages 'nlme' (Pinheiro et al., 2021) and 'glmmTMB' (Brooks et al., 2017). First, we selected the best random structure of the full model (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 (Appendix A, Table A.6). Once we selected the best random structure for models, fixed structure was selected through ML estimation. We performed a backwards stepwise removal of non-significant fixed effects. 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 (see Appendix B). The validation of the models also included testing for spatial autocorrelation. Where spatial autocorrelation was detected, spatial models were fitted to test robustness of the predictive models; such models where fitted through the package

‘INLA’, modelling residuals from a gaussian spatial random field using the Matérn autocorrelation function (details in Appendix C). Spatial structure of residuals was successfully minimized (see details in Appendix C.)

3. Results

3.1. Spatial patterns of environmental predictors

Average sea surface temperature (SST) for the 1-year period ranged from 23.04 to 26.17°C. At Baixada Santista, São Sebastião Channel and Ubatuba sub-regions, average SST was about 25°C, reaching higher values in the Green Coast (SST > 26 °C). From the Green Coast towards the Lakes sub-region, an SST gradient occurred, with values decreasing to ~23°C (Fig. 2A). Patterns of average chlorophyll-a concentration (Chla) also varied among sub-regions. Values higher than 6 $mg.m^{-3}$ were found in the Baixada Santista, Green Coast and Rio de Janeiro. Chla peaked in sites near to the entrance of Santos and Guanabara bays (Baixada Santista and Rio de Janeiro sub-regions, respectively; Fig. 1). A negative gradient of Chla was observed from the Baixada Santista towards São Sebastião Channel and Ubatuba sub-regions. Lowest Chla occurred in the Lakes sub-region (Fig. 2B). Average freshwater discharge index had patterns similar to Chla. Baixada Santista and Rio de Janeiro sub-regions had higher values of freshwater discharge, with peaks at sites near to the entrance of large bays. Moreover, freshwater discharge decreased from the Baixada Santista towards São Sebastião Channel and Ubatuba reaching intermediate values in the Green Coast and the Lakes sub-regions (Fig. 2C).

Most wave-exposed sites occurred in the Baixada Santista and Rio de Janeiro sub-regions. Wave fetch was intermediate at most sites from the São Sebastião Channel and Lakes sub-regions. In Ubatuba and Green Coast sub-regions, variability in wave fetch among sites was high due to an intricate coastline and protection from islands resulting in a mix of wave-sheltered and exposed areas (Fig. 2D). Descriptive statistics of these environmental variables are shown in supplementary material (Appendix A, Table A.4; see also Appendix D, Fig. D1 for raw data).

Average Chla at surveyed sites was correlated to freshwater discharge index (Spearman’s correlation coefficient, $r = 0.63$). The slope of the supralittoral fringe correlated positively with the roughness index ($r = 0.54$) and negatively with extent ($r = -0.53$). The remaining correlations among environmental variables were weak.

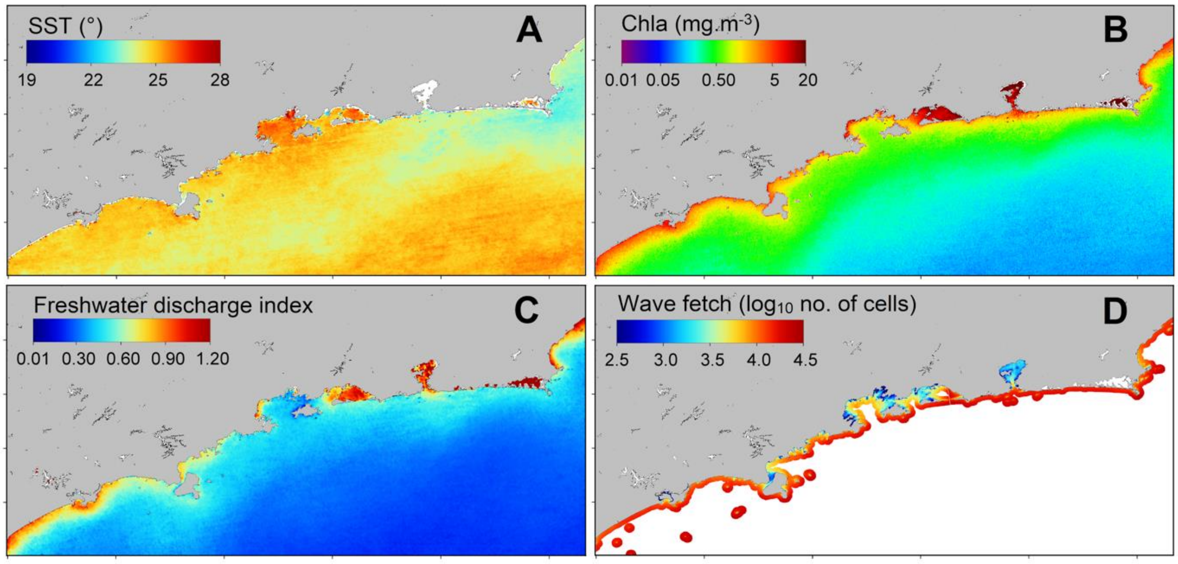


Fig. 2. Maps of satellite sea surface temperature (SST), chlorophyll-a concentration (Chla), freshwater discharge index and wave fetch for the South-east coast of Brazil (SW Atlantic). SST, Chla and freshwater discharge are average values for 1-year period before samplings (from May/2014 to September/2015). For wave fetch, each pixel represents the summed value.

For average estimated Chla, the freshwater discharge index and wave fetch, variability occurred mainly at the scales of sub-region and sites. For SST, besides sub-region, a large portion of variation occurred between regions (Fig. 3A). At the sub-region scale, variance amounted to 57% for SST, ~50% for both Chla and wave fetch, and 35% for the freshwater discharge index. Variation among sites was important for the freshwater discharge index (60%), followed by wave fetch (53%) and Chla (49%). For SST, 37% of variation was due to regions and only 6% to sites. Topographical features of substrate (extent, inclination and roughness) did not show consistent patterns among sub-regions or regions (Appendix A, Table A.5; Appendix D, Fig. D.1). Such factors varied almost exclusively at the scale of site (87-94%). The remaining variability occurred among sub-regions for inclination or between regions for inclination and roughness (Fig. 3A).

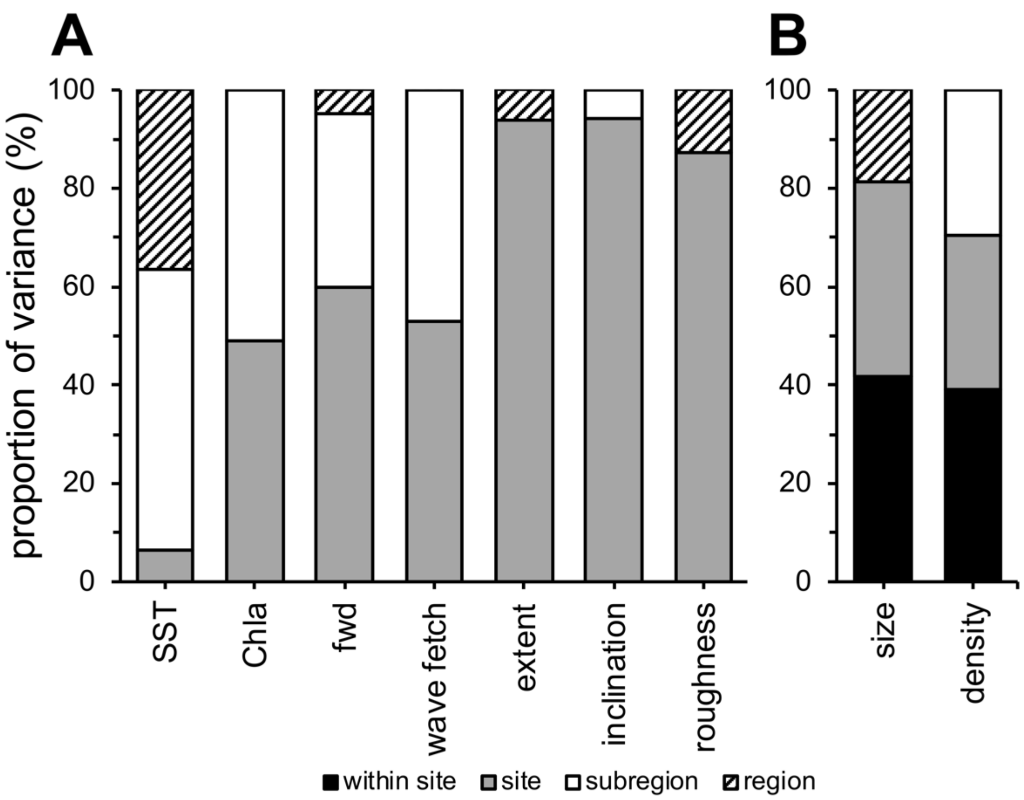


Fig. 3. Estimates of variance components for (A) the environmental predictors and (B) size and density of the barnacle *Chthamalus bisinuatus* in rocky shores along the South-east coast of Brazil (SW Atlantic). Variance components for environmental data were calculated based on average values per site; therefore, there is no data on variation within site. SST = satellite sea surface temperature; Chla = satellite estimated chlorophyll-a concentration; and fwd = freshwater discharge index.

3.2. Spatial patterns of population structure of Chthamalus bisinuatus

Size of barnacles *Chthamalus bisinuatus* ranged, on average, from 0.21 to 6.44 mm of operculum length, while density varied from 0 to 292 individuals in 25 cm^2 (Appendix A, Table A.2). There was no clear pattern in barnacle size over the study area although barnacles tended to be larger in Region 2 than Region 1 (Fig. 4; Appendix D, Fig. D.2). Density, however, decreased from the Baixada Santista towards Ubatuba and Green Coast sub-regions, with intermediate values in the Rio de Janeiro and Lakes sub-regions (Fig. 4; Appendix D, Fig. D.2). Barnacle size varied mainly within- and among-sites (~40% of variance component for each); the remaining variance (19%) is attributed to region-scale variation. For density, most variability occurred again within-sites (39%), with similar amounts for scales of sites and sub-region (31 and 30%, respectively) (Fig. 3B).

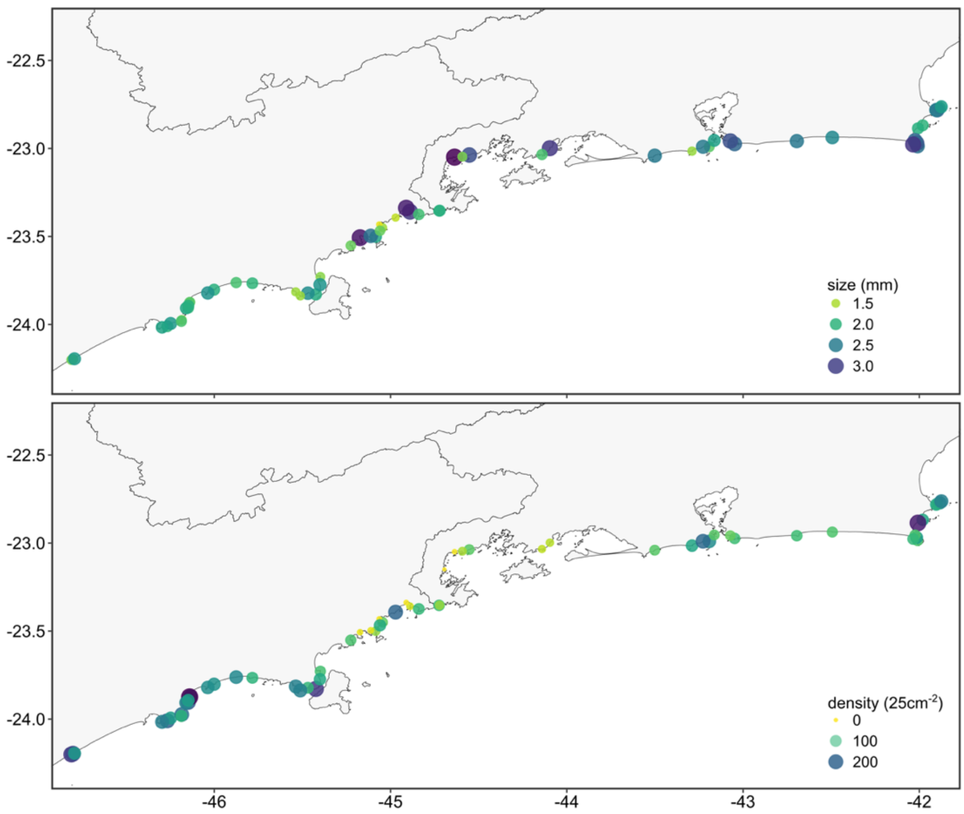


Fig. 4. Mean size and density of the barnacle *Chthamalus bisinuatus* assessed in rocky shores along the South-east coast of Brazil (SW Atlantic).

3.3. Relationships between environmental predictors and population structure

For both barnacle size and density, small-scale environmental variables (inclination, roughness and extent) were not selected as predictors in the best models (Table 1). Size was best predicted by a model including SST, Chla, freshwater discharge index and wave fetch. Barnacles were larger in areas with higher concentrations of Chla. In contrast, size related negatively with SST, freshwater discharge and wave fetch. Barnacles were predicted to be smaller in warmer waters, wave-exposed sites and areas under higher fluvial influence (Table 1, Fig. 5A-D). Furthermore, the final predictive model for size retained "site" as part of the random effect. The best model for population density included only wave fetch as an environmental predictor, with predicted density increasing with wave fetch (Fig. 5E). The model also included random variability at sub-region and site scales (Table 2). Spatial models retained wave fetch as a predictor (Appendix C, Tables C.2 and C.3) irrespective of the type of model. However, only those models based on the INLA approach minimised the spatial structure in the residuals (Appendix C, Fig. C.3).

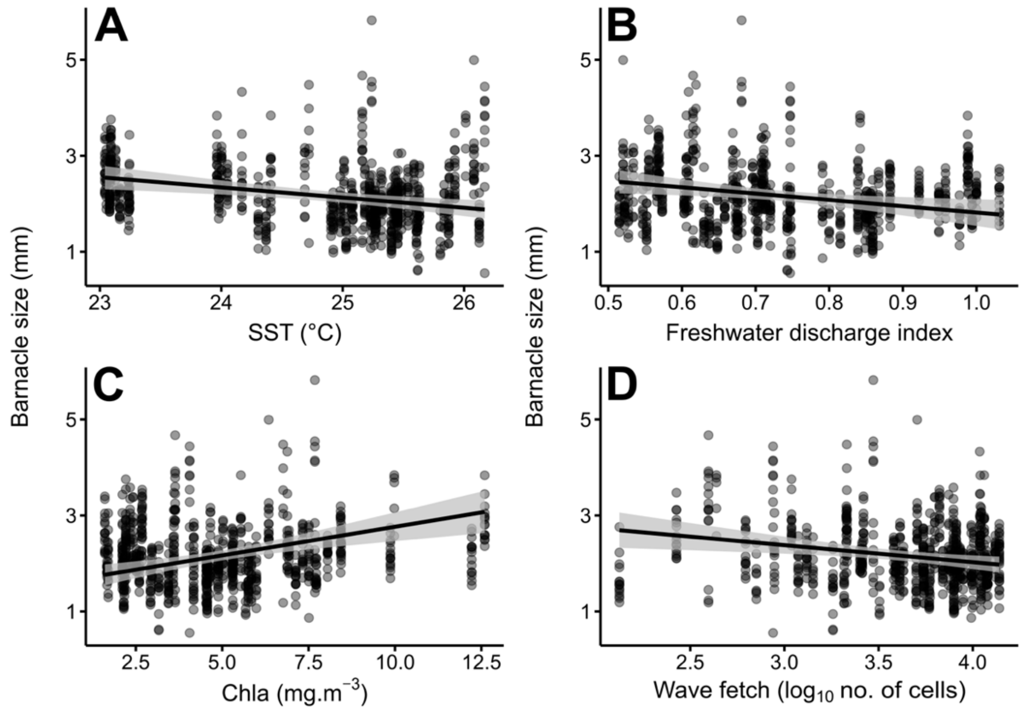
Table 1. Summary of the best model for the relationships of environmental variables and size and density of the barnacle *Chthamalus bisinuatus* along the South-east coast of Brazil (SW Atlantic). Abbreviations: SST = sea surface temperature; Chla = chlorophyll-a concentration; fwd = freshwater discharge index; *P<0.05, **P<0.01, ***P<0.001.

Size							
Fixed effects					**Random effects**		
Parameters	estimate	SE	t-value	P	Parameters	variance	SD
Intercept	9.078	1.628	5.576	***	Site	0.159	0.398
SST	-0.212	0.061	-3.476	**	Residual	0.206	0.454
Chla	0.119	0.028	4.178	***			
fwd	-1.311	0.495	-2.650	*			
wave fetch	-0.352	0.121	-2.900	**			

Density							
Parameters	estimate	SE	z-value	P	Parameters	variance	SD
Intercept	2.192	1.020	2.149	*	Site	0.480	0.693
wave fetch	0.600	0.275	2.180	*	Subregion	0.547	0.740

Full model: *size* ~ SST + Chla + fwd + wave fetch + inclination + roughness + extent + (1|site)

Full model: *density* ~ SST + Chla + fwd + wave fetch + inclination + roughness + extent + (1|subregion/site)



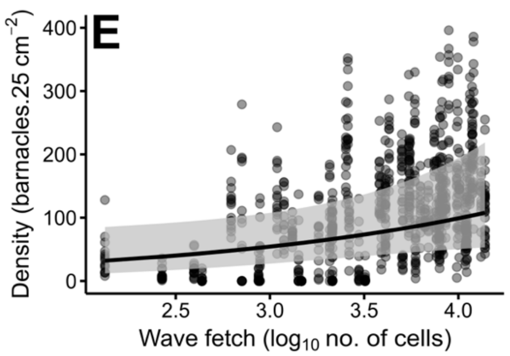


Fig. 5. Relationships among environmental predictors and size and density of the barnacle *Chthamalus bisinuatus* along the South-east coast of Brazil (SW Atlantic). Black lines and shaded areas represent predictive values of the response ± 95% confidence interval. SST = satellite sea surface temperature; Chla = satellite chlorophyll-a concentration.

3.4. Relationships between barnacle body size and density

Considering all data, barnacle body size and density were negatively related. Using data from each sub-region separately, there was a significant relationship at 4 out of 6 cases; the exceptions were São Sebastião Channel and Green Coast (Table 2, Fig. 6).

Table 2. Analysis of deviance table for the relationship between barnacle size and density along the South-east coast of Brazil and linear models for the relationship between size and density per sub-region. **P<0.01, ***P<0.001; ^{ns} = not significant.

A.	df	Chisq	P-value	
Intercept	1	1322.05	***	
Subregion	5	89.10	***	
Density	1	28.03	***	
Subregion*density	5	42.74	***	
B. Size *vs*. density per subregion				
Subregions	intercept	slope	R^2	N
Baixada Santista	2.104***	-0.0010**	0.046	266
São Sebastião Channel	2.149***	-0.0016^{ns}	0.076	86
Ubatuba	2.507***	-0.0054***	0.214	160
Green Coast	2.685***	-0.0046^{ns}	0.036	58
Rio de Janeiro	2.747***	-0.0038***	0.131	130
Lakes	3.145***	-0.0054***	0.299	147

Notes: **A**. Model fitted with 'gls' function from 'nlme' package accounting for the power of the variance of barnacle density (using 'weights' term). Significance of the terms was obtained with 'Anova' function (type III test) from 'car' package. **B**. Ordinary linear models fitted by sub-region. P-values were corrected with Bonferroni adjustment.

Including barnacle density as a predictor of barnacle size together with physical environmental variables resulted in a final predictive model retaining SST, Chla and density. The relationships among size and these variables were the same as the other models: negative association with SST and density and positive association to Chla. Including size as a predictor of density, in turn, resulted in a final model including SST, wave fetch and size as predictors. Density increased with wave fetch and decreased with SST and size (Appendix A: Table A.7).

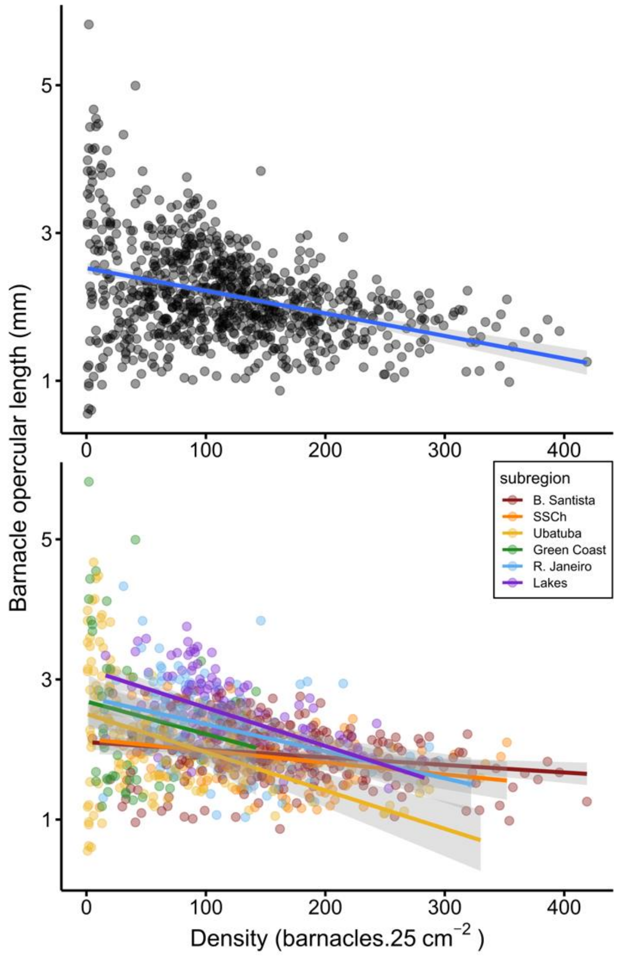


Fig. 6. Relationships between body size and density of the barnacle *Chthamalus bisinuatus* along the South-east coast of Brazil (SW Atlantic). Lines and shaded areas represent predictive values of the response ± 95% confidence interval. B. Santista = Baixada Santista; SSCh = São Sebastião Channel; R. Janeiro = Rio de Janeiro.

4. Discussion

This is one of the few broad-scale studies investigating spatial variation of intertidal rocky shore populations and environmental variables and their relationships in the Southwestern Atlantic (see also Borthagaray et al., 2009; Giménez et al., 2010; Cruz-Motta et al., 2020). Our results provide evidence of links between oceanographic conditions and ecological patterns and thus contribute to the discussion on benthic-pelagic coupling. Patterns of variability of environmental predictors met expectations given the dominant oceanographic processes along this coastline (e.g., upwelling, freshwater input). We found that both size and density of the barnacle *Chthamalus bisinuatus* varied mostly within- and among-shores. We also identified clear associations between population structure and environmental predictors. Barnacles reached larger sizes in areas with higher food availability, colder waters, wave-protected shores and under less fluvial influence. Barnacle density was greater in wave-exposed sites.

Most spatial variation in size and density of the barnacle *Chthamalus bisinuatus* occurred at the smallest scales (within- and among-shores) in agreement with several other studies done in the rocky intertidal (e.g., Underwood and Chapman, 1996; Fraschetti et al., 2005). Variability at small spatial scales is likely caused by a complex interplay of biotic (e.g., recruitment, competition, predation) and abiotic factors. Within abiotic factors, topographical features of shores (e.g., inclination, roughness) can be responsible for small-scale variation of benthic species (Underwood and Chapman, 1989; Chapman, 1994; Underwood, 2004). The quantification of topography in our study did not capture variation at the scale of centimetres to millimetres, which establishes the microhabitat conditions experienced by single individuals. Although average topographical features varied mostly among-sites, none of the tested variables (roughness, inclination, extent) related to population structure of *C. bisinuatus*.

We found that satellite estimated chlorophyll-a concentration predicted barnacle size, with larger individuals in locations of higher Chla. Comparisons between upwelling and non-upwelling areas worldwide have linked variation in intertidal suspension feeders to nearshore food availability (Menge, 2000). For instance, in locations with greater Chla along the northwest Pacific coast, barnacles grew faster, reached larger size and were more fertile (Menge et al., 1997a; Sanford and Menge, 2001; Leslie et al., 2005). Similar relationships have been described for barnacles on the east coast of the USA (Bertness et al., 1991; Sanford et al., 1994), Scotland (Burrows et al., 2010) and Galápagos archipelago (Witman et al., 2010) demonstrating strong bottom-up regulation. Along our studied area, phytoplankton biomass is generally low because waters tend to be meso-oligotrophic. The greatest values of Chla are situated in estuarine areas where nutrient input from natural and anthropogenic sources fertilise coastal waters (Oliveira et al., 2016). Nearshore, Chla was lowest at the sub-region where the Cabo Frio upwelling regime occurs. This counter-intuitive observation is probably a consequence of the south-westward advection of upwelled waters offshore (Gonzalez-Rodriguez et al., 1992; Calil et al., 2021). In fact, phytoplankton biomass can actually be lower at focal points of upwelling in comparison to sites some distance away from the upwelled waters (Wroblewski, 1977). Other possible causes are strong zooplankton grazing (Carbonel and Valentin, 1999) and seasonal variability (Moser and Gianesella-Galvão, 1997). As the upwelling regime occurs predominantly during the austral spring and summer (Valentin, 2001), using averaged Chla for 1-year dilutes the influence of seasonally intense upwelling. For the period considered here, average Chla in more urbanised areas were about 2-3 times higher than less urbanised ones. Our results suggest that the rate of benthic-pelagic processes may respond to such spatial heterogeneity and thus anthropogenic influences may overcome natural oceanic variation. Future research identifying the effect of different sources of nutrients on coastal species will elucidate the balance of natural and anthropic influences along such coast. In this regard, the application of stable isotopes techniques on species from intertidal rocky shores seems to be an alternative (e.g., Vinagre et al., 2015; Puccinelli et al., 2019).

Contrary to our expectations, the size of *Chthamalus bisinuatus* was negatively related with sea surface temperature. We hypothesised larger individuals in warmer waters; temperature can for example affect growth rate of cirripedes by affecting cirral beating (Southward, 1955). However, the relationship between temperature and growth in intertidal barnacles may result from a complex effect of different factors (Sanford et al., 1994; Jenkins et al., 2001) and growth can actually be reduced at warmer temperatures (Lathlean et al., 2013; Leal et al., 2020). Also, our results only record barnacle size, not growth rate. Aquatic ectotherms generally reach a larger size in colder environments as a result of phenotypic plasticity in the growth-maturity relationship (Atkinson, 1994; Atkinson and Sibly, 1997). Furthermore, investigating the large-scale influence of air temperature on *C. bisinuatus* seems to be worthwhile as this species remains emersed for long periods. According to estimates made by Kasten and Flores (2013) for the same region, this barnacle is immersed for only 30 minutes every 12.4 hours, thereby remaining exposed to air more than 95% of the time in each tidal cycle. Over the study area, in contrast to sea temperature, both mean and maximum annual air temperatures increase northward (Alvares et al., 2013). Therefore, it is plausible that higher air temperature (and higher desiccation stress) could select larger individuals due to optimised water storage. Such patterns of bigger animals in up-shore direction has been shown for intertidal gastropods (Vermeij, 1973; Tanaka et al., 2002) and barnacles (Benedetti-Cecchi et al., 2000). Alternatively, the size of animals could be linked to different patterns of survivorship driven by seawater or air temperature (Benedetti-Cecchi et al., 2000; Lathlean et al., 2013) or both.

We also found a negative relationship between barnacle size and the freshwater discharge index. In our study area, sites under higher fluvial influence also had more Chla as a result of the input of nutrients through estuaries. The negative effect of freshwater discharge on barnacle size, however, suggests a possible trade-off. Despite increasing food availability, fluvial waters also introduce different types of materials and change local conditions (e.g., salinity, turbidity) (Giménez et al., 2010; Dias et al., 2018). Such shifts in the physical environment are likely to trigger complex responses in coastal organisms. For example, osmotic stress caused by low salinity may decrease growth rate and survivorship, as shown for barnacles in the laboratory (Simpson and Hurlbert, 1998; Qiu and Qian, 1999) and, in a more complex and variable way, under natural conditions (Berger et al., 2006). Furthermore, rivers and estuaries introduce different nutrients to the coast with the potential to affect the nutritional profile of prey and their consumers (Tallis, 2009; Puccinelli et al., 2016). Consuming prey with different nutritional quality, in turn, can affect growth and survival (Nasrolahi et al., 2007). Future efforts towards linking riverine and estuarine influence on ecological responses of coastal organisms will elucidate ecosystem functioning and connectivity along the coast of Southwestern Atlantic.

In this study, wave fetch was negatively related with size of the barnacle *Chthamalus bisinuatus*. Since elevated water flow increases food supply, it is expected that filter-feeders will reach greater sizes at more exposed locations (e.g., Leonard et al., 1998; McQuaid and Lindsay, 2000). Our contradictory result is probably a question of density-dependent growth (Jenkins et al., 2008; Dias et al., 2018) since higher densities of *C. bisinuatus* occurred at wave-exposed shores. Greater density or biomass of filter-feeders in response to wave exposure is a long known general pattern for the rocky intertidal (e.g., Southward and Orton, 1954). Such a pattern is linked to increased supply of larvae and food and affects both settlement and post-settlement processes (Sanford et al., 1994; Jenkins, 2005). These mechanisms are likely to explain the positive association between barnacle density and wave fetch along the South-east coast of Brazil. In fact, wave fetch was the only predictor of barnacle density, similar to results reported for *Semibalanus balanoides* around Scotland, where wave fetch was the main predictor of density of both juveniles and adults (Burrows et al., 2010).

Naturally, the patterns in density and size that we found in this study can be linked to covariation among the environmental predictors. For example, Chla, SST and freshwater discharge index are somewhat correlated and any relationships with barnacle population structure can originate from such correlations instead of an individual 'effect' of any particular predictor. Likewise, barnacle size and density are generally not independent. Density can drive body size due to density-dependent growth, while size can affect density through size-dependent survival (Hyder et al., 2001; Jenkins et al., 2008). In our study these variables are, overall, related: barnacles are smaller where they are more abundant. Populations consisting of larger individuals and lower densities could be a result of self-thinning (Hughes and Griffiths, 1988), as suggested for other intertidal species elsewhere in the Atlantic (O'Connor, 2010; Tam and Scrosati, 2014). Therefore, the effects of environmental predictors on population structure may occur via links of particular predictors to either size, density or both. For example, adding density as a predictor of size resulted in a final model that includes barnacle density as a predictor but not wave fetch. Although we identified useful environmental predictors of a key intertidal species, untangling their individual links to population structure will depend on manipulative work.

5. Conclusion

This study contributes toward understanding the associations between environmental and ecological variation over several spatial scales. Our results indicate that the dynamics of populations of the barnacle *Chthamalus bisinuatus* along the South-east coast of Brazil are linked to scale-dependent oceanographic variation. These findings agree with recent large-scale studies along the Brazilian coast that also found consistent links between ecological responses in intertidal species and oceanic forcing (Mazzuco et al., 2015, 2018; Kasten et al., 2019). Our results also suggest that the Cabo Frio upwelling does not affect the populations of this barnacle as predicted in a recent model of benthic-pelagic coupling (Menge and Menge, 2013, 2019). On the other hand, the high Chla around estuarine bays, likely influenced by pulses of human inputs (i.e., sewage), seems to function analogously to intermittent upwelling regimes affecting the size patterns in this barnacle. We expect that the patterns described, and proposed hypotheses will help guide future research in this understudied region particularly in understanding how community structure and species interactions respond to spatial variation in oceanic variables. This is the first of a series of studies linking large-scale variation in intertidal populations and communities to environmental variables along the South-east coast of Brazil. Altogether, these efforts will provide a robust comprehension of patterns of rocky shores along this coastline integrating benthic ecology and coastal oceanography.

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Data accessibility

http://ipt.iobis.org/wsaobis/resource?r=brazilianrockyshores&v=1.1

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