Marine Environmental Research xxx (xxxx) 106646

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Environmental factors have stronger effects than biotic processes in patterns of intertidal populations along the southeast coast of Brazil

Cesar A.M.M. Cordeiro [a,*], André Pardal [b,c], Luis Giménez [d], Áurea M. Ciotti [e], Stuart R. Jenkins [d], Michael T. Burrows [f], Gray A. Williams [g], Ronaldo A. Christofoletti [c]

[a] *Laboratory of Environmental Sciences, Universidade Estadual do Norte Fluminense (UENF), Av. Alberto Lamego 2000, 28013-602, Campos dos Goytacazes, RJ, Brazil*
[b] *Center of Natural and Human Sciences, Federal University of ABC (CCNH/UFABC), Rua Santa Adélia 166, Santo André, SP, 09210-170, Brazil*
[c] *Institute of Marine Science, Federal University of São Paulo (IMar/UNIFESP), Rua Dr Carvalho de Mendonça 144, Santos, SP, 11070-100, Brazil*
[d] *School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, LL59 5AB, UK*
[e] *Center for Marine Biology, University of São Paulo (CEBIMar/USP), Rod. Manoel Hipólito do Rego, km 131.5, São Sebastião, SP, 1160-000, Brazil*
[f] *Department of Ecology, Scottish Association for Marine Science, Scottish Marine Institute, Oban, Argyll, PA37 1QA, UK*
[g] *The Swire Institute of Marine Science and Area of Ecology & Biodiversity, School of Biological Sciences, The University of Hong Kong, Pokfulam Road, Hong Kong SAR, China*

ARTICLE INFO

Keywords:
Rocky shore
Population ecology
Species interactions
South atlantic
Spatial scales

ABSTRACT

Rocky shore communities are shaped by complex interactions among environmental drivers and a range of biological processes. Here, we investigated the importance of abiotic and biotic drivers on the population structure of key rocky intertidal species at 62 sites, spanning ~50% of the Brazilian rocky shoreline (i.e., ~500 km). Large-scale population patterns were generally explained by differences in ocean temperature and wave exposure. For the gastropod species *Lottia subrugosa*, differences at smaller scales (i.e., 0.1–1 km) were better explained by other abiotic influences such as freshwater discharge and substrate roughness. Based on the general population patterns of intertidal species identified, three main oceanographic groups were observed: a cold-oligotrophic grouping at northern sites (Lakes sub-region), a eutrophic group associated with large estuaries and urban zones (Santos and Guanabara bays); and a transitional warm-water group found between the two more productive areas. Larger individuals of *Stramonita brasiliensis*, *L. subrugosa* and *Echinolittorina lineolata* were generally found in the cold-oligotrophic system (i.e., upwelling region), while small suspension feeders dominate the warm-eutrophic systems. Evidence of bottom-up regulation was not observed, and top-down regulation effects were only observed between the whelk *S. brasiliensis* and its mussel prey *Perna*. Environmental drivers as compared to biotic interactions, therefore, play a key role determining the population structure of multiple intertidal species, across a range of spatial scales along the SW Atlantic shores.

1. Introduction

Rocky intertidal habitats are situated at the transition between terrestrial and marine domains, providing an open laboratory for gaining insights into factors regulating biodiversity. As a result, research over the past century has acknowledged the role of abiotic disturbance, species interactions, and the supply of resources in shaping the structure and dynamics of intertidal communities (reviewed by Connell, 1972; Underwood, 2000; Schiel, 2004; Hawkins et al., 2020). The further integration of ecological processes such as recruitment, competition, and predation has resulted in recognition of the importance of bottom-up and top-down mechanisms of regulation (Menge, 1995; 2000). These mechanisms are known to be modified by abiotic factors such as substrate topography, wave exposure, and ocean and air temperatures, determining the distribution, abundance, and diversity of species within coastal ecosystems (Underwood, 1984a; Benedetti-Cecchi, 2000; Seabra et al., 2016; Menge, 2000, 2023).

While ecological processes and abiotic gradients are undisputedly recognised as factors shaping rocky intertidal communities, their relative importance varies across spatial scales, ranging from centimetres to thousands of kilometres. Species interactions are more likely to influence biota locally (Paine, 1966; Menge and Olson, 1990), whereas abiotic variables affect organisms at a greater variety of scales. For example, substrate topography can influence recruitment and mortality by providing access to shelter and food, as well as by modulating environmental stress at small spatial scales (Underwood and Chapman, 1989;

* Corresponding author.
E-mail address: cesarcordeiro@uenf.br (C.A.M.M. Cordeiro).

https://doi.org/10.1016/j.marenvres.2024.106646
Received 26 March 2024; Received in revised form 2 July 2024; Accepted 15 July 2024
0141-1136/© 20XX

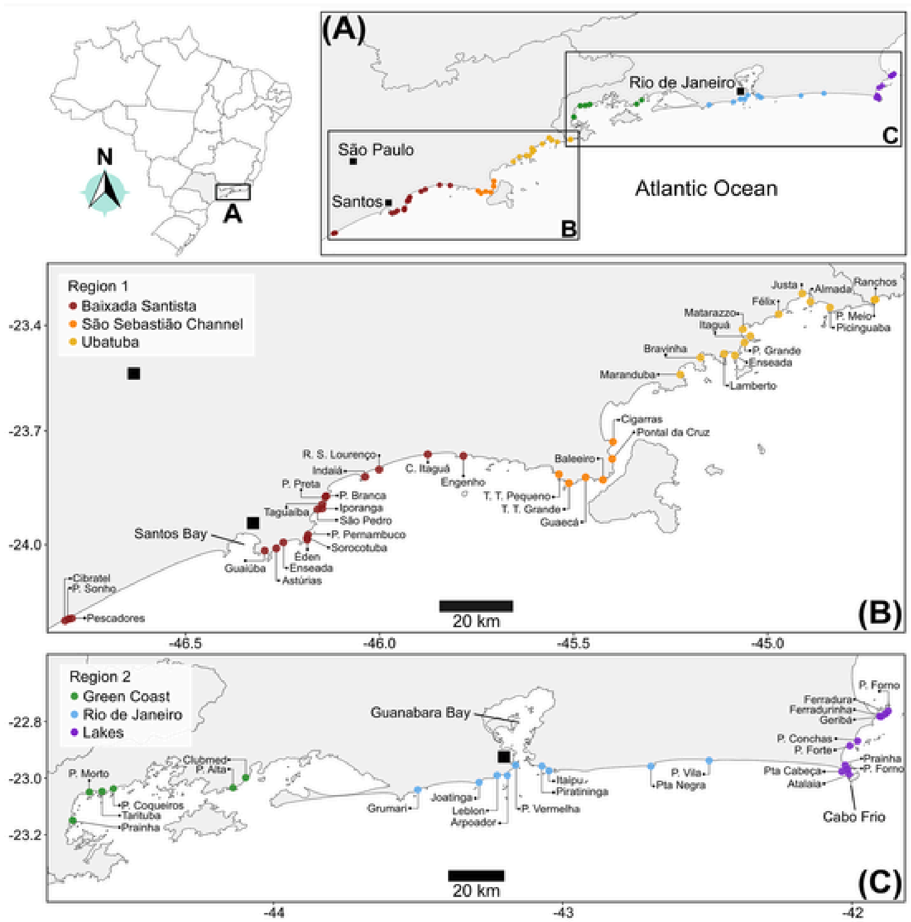

Fig. 1. Study area along the southwestern Atlantic (SE Brazil), depicting the coastline of São Paulo and Rio de Janeiro states (**A**). The circles represent the sixty-two surveyed sites, while the colours indicate the six sub-regions within the two main regions (**B** and **C**). The map also includes important urban centres (black squares: São Paulo, Santos, and Rio de Janeiro cities), Santos and Guanabara bays, and Cabo Frio.

Meager et al., 2011). Over broader spatial extents, however, oceanographic conditions such as upwelling, seawater temperature, estuarine plumes, and wave exposure are expected and can affect the recruitment, growth, and abundance of species by governing the supply of nutrients and propagules, and influencing organisms' physiology (Sanford, 1999; Navarrete et al., 2005; Burrows et al., 2009; Helmuth 2009; Giménez et al., 2010; Menge and Menge, 2013; Hacker et al., 2019). As a result, spatial dependence is a persistent question in ecology (Levin, 1992; Thorson et al., 2015), emphasising the necessity for studies that address the links between biotic variation and abiotic drivers across multiple scales.

Top-down mechanisms of regulation result from the effects of consumers on prey populations, influencing the structure of communities and, ultimately, the functioning of ecosystems (Menge, 1995; 2000; O'Connor et al., 2011). In rocky intertidal habitats, the influence of herbivores on micro- and macroalgae can be a major structuring factor (Menge et al., 1999; Aguillera and Navarrete, 2007; Jenkins et al., 2008). Likewise, carnivores have been shown to strongly influence their prey, often leading to trophic cascades (Paine, 1966; Wootton, 1995; Menge, 1995; Ng and Gaylord, 2020). Bottom-up mechanisms also play a fundamental role in regulating rocky intertidal communities (Underwood, 1979; Bustamante et al., 1995). For instance, biofilms can be a limiting resource for grazing herbivores (Underwood, 1984a; Mak and Williams, 1999; Thompson et al., 2004), while influencing settlement of seaweed propagules and invertebrate larvae (Wahl, 1989). Importantly, the abundance and growth of sessile suspension feeders are strongly linked to phytoplankton biomass in the nearshore ocean, as well as the supply, transport, and settlement of pelagic larval stages (Connolly et al., 2001; Leslie et al., 2005). Thus, variations in the influx of food and propagules are considered the basic drivers of trophic interactions and the transfer of energy to the upper links of the food web (Menge, 2003; Nielsen and Navarrete, 2004; Menge and Menge, 2013, 2019).

Here, we aimed to determine the importance of selected abiotic and biotic variables on the population structure of multiple rocky intertidal species of the southwestern Atlantic coast. This research is the fourth in a series of recent publications (Pardal et al., 2021, 2022, 2023) on large-scale variation in intertidal components and their links to environmental variables. We explored abiotic influences on intertidal populations while also considering the relationships between consumers and the characteristics of their food species (abundance/biomass and body size). With this approach, we quantified scale-dependent variation and identified abiotic variables which are potential drivers of density or cover of intertidal species at different spatial scales, and thereby the relative influence of potential effect of top-down and bottom-up processes (Christofoletti et al., 2011a; Pardal et al., 2022). We expected to find positive effects of abundance and/or size of prey/food on the abundance and/or size of their consumers (a bottom-up effect) and abundance and/or size of food species to be reduced where consumers are more numerous and/or bigger (a top-down effect). We also measured variables representing physical heterogeneity which may influence biotic interactions according to environmental stress at different spatial

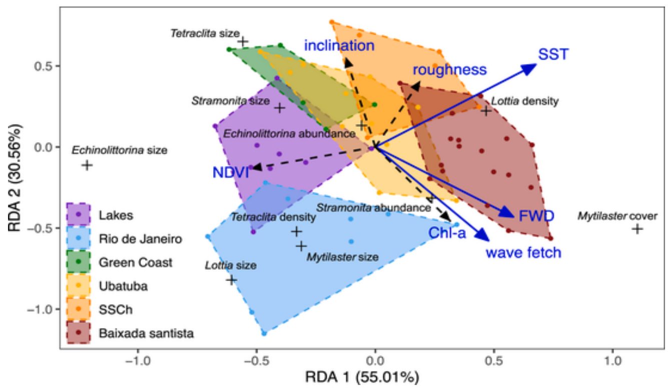

Fig. 2. Redundancy Analysis (RDA) of environmental variables and biological indicators of intertidal communities surveyed at sixty-two rocky intertidal habitats along the southwestern Atlantic coast (SE Brazil). Dashed vectors were not significant in the reduced model. $R^2_{adjusted}$ = 0.24 for reduced model. SSCh = São Sebastião Channel.

Table 1
Summary of all biological indicators measured at 62 rocky intertidal habitats along southwestern Atlantic coast (SE Brazil). #Biofilm biomass was proxied by NDVI values (see section 2.3).

Variable	Midlittoral level	Variable usage	Potential predictor of	Regulation model
Whelk (*Stramonita brasiliensis*)				
1. Total abundance	low/mid	Response/predictor	3, 4, 6 and 7	Top-down
2. Body size		Response/predictor	3, 4, 6 and 7	
Mussel (*Mytilaster solisianus*)				
3. Percentage cover	mid	Response/predictor	1 and 2	Bottom-up
4. Body size		Response/predictor	1 and 2	
Mussel (*Perna*)				
5. Presence/absence	low	Predictor	1 and 2	Bottom-up
Barnacle (*Tetraclita stalactifera*)				
6. Density	low	Response/predictor	1 and 2	Bottom-up
7. Body size		Response/predictor	1 and 2	
Limpet (*Lottia subrugosa*)				
8. Density	low	Response	–	–
9. Body size		Response	–	–
Periwinkle (*Echinolittorina lineolata*)				
10. Total abundance	high	Response	–	–
11. Body size		Response	–	–
12. Biofilm biomass#	low	Predictor	8 and 9	Bottom-up
	high	Predictor	10 and 11	

scales (Menge and Sutherland, 1987). At the site level, we surveyed intertidal habitats to quantify substrate roughness and inclination. Large-scale oceanographic variables were obtained from satellite images and wave fetch derived from a topographical model (Burrows, 2012). We predicted that such variables would also affect the population structure of the intertidal species as they can directly and indirectly influence their recruitment, survival, growth, and behaviour. Evaluating the combined effects of these abiotic and biotic influences on the population structures of key intertidal species allowed us to elucidate the scales at which they were important and contribute to patterns seen around the Brazilian coast.

2. Material and methods

2.1. Study area

Between April and September 2015, surveys were carried out at 62 rocky intertidal sites spanning ~530 km of the SE coast of Brazil (Fig. 1). This extent consists of roughly 50% of the continuous rocky coastline of Brazil. The study area is dominated by a microtidal regime, with a mean sea level ~0.7 m above local Chart Datum and an average tidal range of ~1.4 m. We considered two main regions which are divided in six sub-regions with distinct natural conditions and anthropogenic influences (see details in Pardal et al., 2021, 2023): Region 1 – (i) Baixada Santista, (ii) São Sebastião Channel, (iii) Ubatuba; and Region 2 – (iv) Green Coast, (v) Rio de Janeiro, and (vi) Lakes (Fig. 1). Sites were hierarchically selected within sub-regions. Briefly, Baixada Santista and Rio de Janeiro sub-regions are two of the most important metropolitan centres of Brazil, which are under high anthropogenic influence due to intense urbanisation and the presence of ports, shipyards, and industrial complexes and also experience higher primary productivity associated with the large, urbanised bays. Ubatuba and Green Coast sub-regions have the least populated areas, while São Sebastião Channel and Lakes are under an intermediate level of anthropogenic influence. Along the study area, colder waters are found northwards due to upwelling events in the Lakes sub-region (Valentin, 2001).

2.2. Sampling of intertidal species

At each site, the intertidal zone (usually <5 m wide) was sampled along ~100 m of coastline during low tides. Populations of sessile suspension feeders (the mussels *Mytilaster solisianus* and *Perna*, and the barnacle *Tetraclita stalactifera*), grazers (the limpet *Lottia subrugosa* and the littorinid *Echinolittorina lineolata*) and a predatory whelk (*Stramonita brasiliensis; previously Stramonita haemastoma*) were sampled along the midlittoral zone (Table 1). Intertidal levels were sampled within the three visible distribution strata associated with the main sessile organisms occupying the primary substrate and shore height (see detailed description and photos in Pardal et al., 2023). The vertical extent of each stratum varies with local topography and wave conditions, but the low-level is mostly occupied by the barnacle *T. stalactifera*, the mid-level by the mussel *M. solisianus*, and the high-midlittoral level by the barnacle *Chthamalus bisinuatus*. The mussel *P. perna* is found from the low-midlittoral to the infralittoral fringe (Pardal et al., 2023). The limpet L. *subrugosa* and the whelk *S. brasiliensis* are common inhabitants of the mid- and low-midlittoral (Tanaka et al., 2000; Pardal et al., 2022), while the littorinid *E. lineolata* is found predominantly at the high-midlittoral and supralittoral fringe levels (Christofoletti et al., 2011a).

The abundance of the mussel *M. solisianus* was estimated as relative cover using a 100 regular intersection grid from 25 × 25 cm (n = 10) photos taken at the mid-midlittoral level. Individuals of *M. solisianus* were scraped from 10 × 10 cm areas (n = 15) and later photographed for measurement (±mm) in the laboratory. The presence of the mussel *P. perna* was verified in quadrats (25 × 25 cm, n = 6–11) at the low-midlittoral. The density of the barnacle *T. stalactifera* and the limpet *L. subrugosa* were measured from images of 10 × 10 cm areas (n = 15) taken from the low-midlittoral. In each image, whenever possible, 15 barnacles and all limpets were measured. The total abundance of whelks at each site was estimated through collections of 20, 25 × 25 cm quadrats in the low-midlittoral. The total abundance of littorinids was determined at the high-midlittoral by hand-collecting for 5 min by the same person. The whelks and littorinids were measured in the laboratory with callipers (accuracy = ± 0.03 mm) and from digital images, respectively. Body size was measured as the largest shell length for molluscs and the largest opercular length for the barnacle *T. stalactifera*. Images of *M. solisianus* and *E. lineolata* were calibrated using a micrometre slide (accuracy = ± 0.01 mm) and specimens were individu-

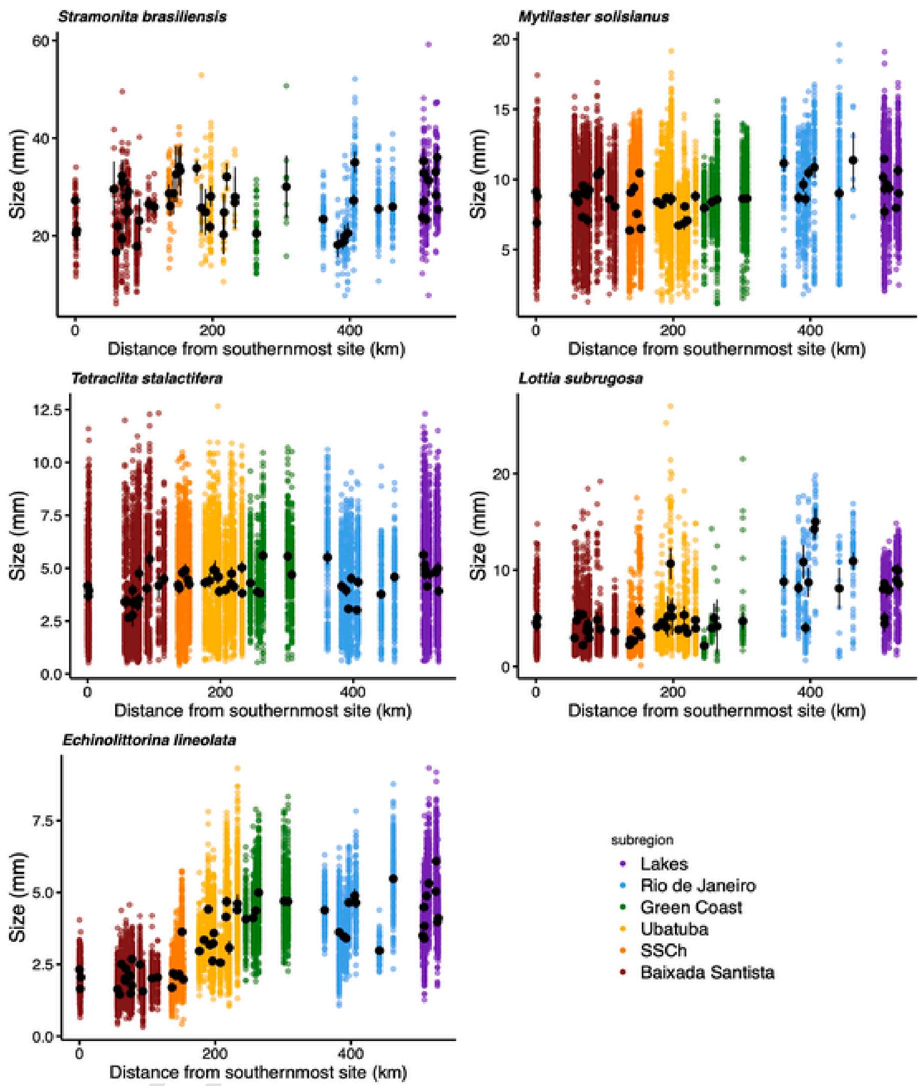

Fig. 3. Latitudinal variation in body size of rocky intertidal species (predatory whelk *Stramonita brasiliensis*, barnacle *Tetraclita stalactifera*, mussel *Mytilaster solisianus*, limpet *Lottia subrugosa*, and periwinkle *Echinolittorina lineolata*) surveyed at sixty-two sites and six sub-regions along the southwestern Atlantic coast (SE Brazil). Black circles with error bars represent site mean ± SE, while small coloured circles are raw data coded by sub-region.

ally measured using ImageJ software (Schneider et al., 2012). Barnacles and limpets were individually measured using ImageJ calibrated with the lower quadrat edge as reference (accuracy = ± 0.05 mm).

2.3. Biofilm biomass

Estimates of biofilm biomass were proxied by the NDVI (Normalized Difference Vegetation Index) using the techniques applied by Pardal-Souza et al. (2017). NDVI values were based on the analysis of 15 digital images (15 × 15 cm), taken randomly at the low- and high-midlittoral levels at each shore using a near-infrared-enabled digital camera (Canon PowerShot ELPH 110 modified by MaxMax.com). The NDVI for each image pixel was calculated from the difference in blue, green, and near-infrared measurements in photos (Murphy et al., 2009). The NDVI index is an indirect measure of the abundance of photosynthetic organisms present in the biofilm based on the ratio between absorbed and reflected light in bands influenced by chlorophyll molecules (Bryson et al., 2013). It ranges from −1 to 1, representing an increasing importance of the chlorophyll-a signal. The few negative NDVI values observed in samples (9.6% of total) were excluded from the analyses, as 0 was assumed to represent the absence of chlorophyll in the biofilm.

2.4. Environmental variables

2.4.1. Oceanographic data from satellite images

Estimates of chlorophyll-a concentration (Chl-a) and sea surface temperature (SST) were acquired from MODIS-Aqua satellite images (level-2, 1-km resolution) using standard algorithms. Chl-a was considered an indicator of food available for invertebrate suspension feeders. The satellite images covered a one-year period before field sampling at each site. We also extracted specific bands of the remote sensing reflectance derived from satellite images for determining a proxy for an increase in estimated freshwater discharge (freshwater discharge, herein), calculated as the ratio $\frac{R_{469}^{443}}{R_{555}^{488}}$ (adapted from Morel and Gentili, 2009). More details on imagery processing are available in Pardal et al. (2021).

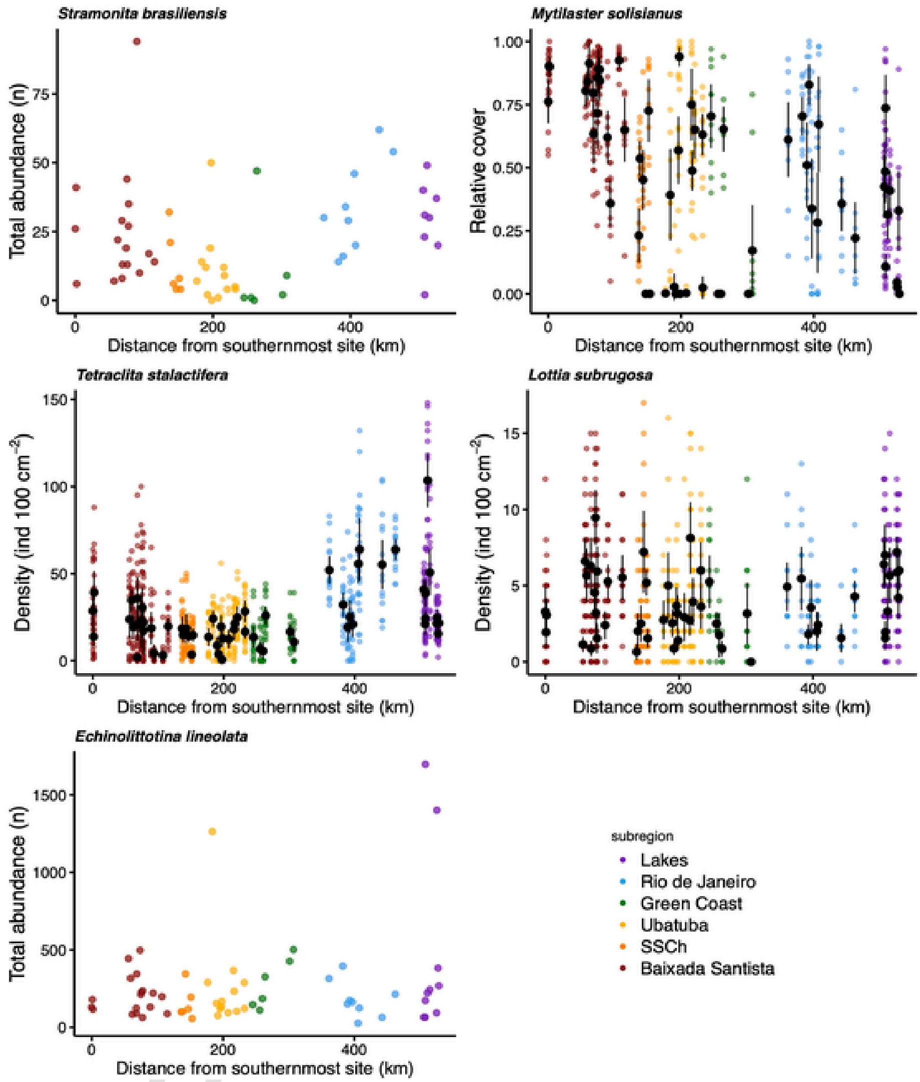

Fig. 4. Latitudinal variation in abundance (total abundance, percentage cover or density) of rocky intertidal species (predatory whelk *Stramonita brasiliensis*, barnacle *Tetraclita stalactifera*, mussel *Mytilaster solisianus*, limpet *Lottia subrugosa*, and periwinkle *Echinolittorina lineolata*) surveyed at sixty-two sites and six sub-regions along the southwestern Atlantic coast (SE Brazil). Black circles with error bars represent site mean ± SE, while small coloured circles are raw data coded by sub-region.

2.4.2. Wave fetch

Wave fetch was used as a proxy for wave exposure at each shore using the model of Burrows (2012). For every 200 m along the coastline of SE Brazil, wave fetch was calculated as the distance to the nearest land around each point on the map up to 200 km away from the 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 and expressed as $\log_{10}$ of the number of cells (see Pardal et al., 2021). The summed wave fetch was extracted for a circular area of 500 m radius centred on the coordinates of each site. In general, samples sites avoided exposed and so included sheltered to semi-exposed sites which allowed safe working conditions.

2.4.3. Shore topography

Within the same area where intertidal species were sampled, we demarcated five vertical profiles across the intertidal zone (i.e., from the low water level up to the upper limit of the midlittoral). The vertical profiles were placed approximately 10–15 m apart from each other. The substrate roughness, as a proxy for habitat complexity, was quantified along the vertical profiles using the chain method (Frost et al., 2005). This uses the ratio of a linear distance occupied by a 3 m-long chain (ø = ~10 mm), when placed to follow the contour of the rock surface, to its maximum length (i.e., 3m). The substrate inclination was determined by using an inclinometer held against the substrate along the vertical profiles. We took three measurements of inclination along each vertical profile by placing the inclinometer in the middle of each shore level (i.e., low-, mid-, and high-midlittoral).

2.5. Data analysis

2.5.1. Relationships among environmental variables and population parameters of intertidal species

All analyses were done in R software (R Core Team, 2020). First, we applied a Redundancy Analysis (RDA) to biotic data (i.e., population parameters of all sampled intertidal species) in relation to environmental variables to depict general patterns along spatial scales using site-averaged values. Population parameters of intertidal species were standardised by their range (*i.e.*, transformed in values between 0 and 1 based on the difference between each value and the minimum value of

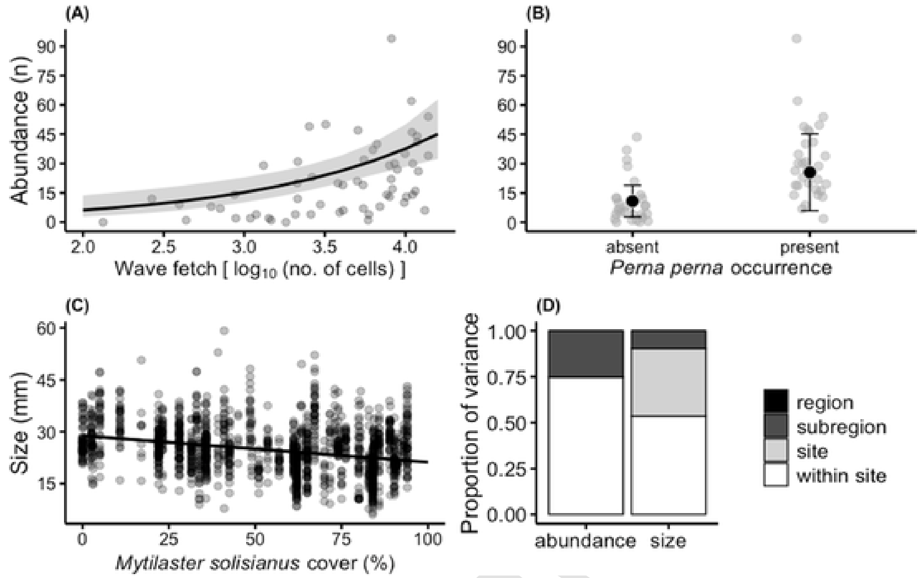

Fig. 5. The effect of environmental drivers on populational parameters and estimates of relative variance components for population parameters of the intertidal predatory whelk *Stramonita brasiliensis* along SE coast of Brazil. Black lines and shaded area represent predictive values of the response ±95% confidence interval. Dot and whiskers represent the mean and standard deviation.

each variable, divided by the difference between the maximum and minimum values of each variable), and environmental variables were scaled to zero mean and unit variance using the *decostand* function from the *vegan* package (Oksanen et al., 2019). The significance of axes and the relative contribution of each environmental variable were tested with a Monte-Carlo test (4999 unrestricted random permutations under the reduced model) using the functions *anova.cca* and *ordistep*.

2.5.2. Spatial scales of variation of intertidal species

The first step for building the models was to evaluate the best fit of random components of analyses. Thus, estimates of variance components were used for testing spatial scales of variability in population parameters of species. For each response, we fitted a fully nested random model considering the factors representing variation at scales of region (100s of kilometres), sub-region (10s of kilometres), and site (kilometres). Models started with the fully nested random model and included all combinations of random effects with two (sub-region and site) or one term. Models were estimated through restricted maximum-likelihood (REML) (Zuur et al., 2009) using *nlme* package (Pinheiro et al., 2023), and the best model was chosen based on AIC scores. No transformation was applied to guarantee that variance estimates were comparable across all data and we did not consider models with singular fits in model selection.

2.5.3. Predictive models

After testing random components (i.e., spatial scales) best fitting, we tested full models including the fixed variables. For that, 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 (GLMM) with Gaussian (identity link), negative binomial (log link), or binomial (logit link) distribution. Models were fitted in R software with the package *glmmTMB* (Brooks et al., 2017). All models were initially built including a random term and the fixed effects of the abiotic predictors (Chl-a, SST, freshwater discharge, wave fetch, shore inclination and roughness). For the predatory whelk, *S. brasiliensis*, the models also included the density, size and cover of its prey as predictors. Likewise, the models for the sessile suspension feeders *T. stalactifera* and *M. solisianus* included the abundance and size of the predatory whelk (Table 1). We did not build models to predict the abundance and size of *P. perna* because this mussel is harvested along the study area, and we could not quantify the extent of human intervention. For the grazers (*L. subrugosa* and *E. lineolata*), the models also included NDVI estimates from the low- and high-midlittoral, respectively, as predictors (Table 1). We did not build models to predict NDVI values because the temporal scales of variability of biofilms are finer than those over which environmental predictors were measured. These models were built to depict the relative contributions 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 maximum-likelihood (ML) estimation (Zuur et al., 2009). We performed a backwards stepwise removal of non-significant fixed effects. In each run, the term with the largest 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., 2009). When residuals indicated poor fit, models were reduced to mean values of dependent variables at the site level and run without the random term. We detected non-linear relationships between dependent variables and predictors for *M. solisianus* size and cover, and *L. subrugosa* size. These models were fitted using generalised additive models (GAM) using the *mgcv* package (Wood et al., 2016) following the same model selection procedure. The final best model was then validated through inspection of residuals histogram and residual plots against fitted values and selected variables (see 'Model selection and validation' in the Supplementary Material). All model selection procedures were based on the best model adjustment and parsimony.

The last step of modelling was testing for spatial autocorrelation through visual plots of model residuals versus spatial coordinates, predicted residuals (*DHARMa* package: Hartig, 2020), and selected variables. We found spatial patterns on the residuals corresponding to *L. subrugosa* and *T. stalactifera* densities. Therefore, we checked if the best model explaining variations in these responses was robust to spatial autocorrelation using spatial models fitted through INLA (Zuur et al., 2017). Those models were based on data averaged by site, Gaussian

Table 2
Summary of final models for size and abundance of the predatory whelk (*Stramonita brasiliensis*), using the whelk's prey (*Perna, Mytilus solisianus*) and environmental predictors. Whelk prey (*P. perna, M. solisianus*) and grazers (*Lottia subrugosa, Echinolittorina lineolata*) were included in further models as dependent variables tested for effects of biotic and abiotic factors (predictor variables). Spatial models (INLA) differed in the prior for the range of the Matérn spatial correlation function (i.e., the distance at which spatial autocorrelation becomes minimal, either 500 or 1000 km). SE = standard error, SD = standard deviation, N = number of observations in models, CI = credible interval, dev. exp. = deviance explained.

Dependent variable	Fixed effects	Estimate	SE	Statistic value	N	Random effects	Variance	SD
Stramonita brasiliensis								
size (LMM)	intercept	29.09	1.55	18.74	55	site	20.6	4.5
	M. solisianus cover	−0.05	0.03	-1.86^{M}		residual	27.9	5.3
abundance (GLM)	intercept	−0.84	0.79	0.29	59	none		
	P. perna presence	0.86	0.23	4.01***				
	wave fetch	0.90	0.21	4.16***				
Mytilaster solisianus								
size (LMM)	intercept	20.34	4.18	4.87***	9170	site	1.2	1.1
	SST	−0.46	0.17	−2.74**		residual	6.35	2.52
cover (GAM)	intercept	−0.33	0.28	−1.19	62	R^2adjusted = 0.29,		
	wave fetch	0.23	0.07	2.91**		dev. exp. = 32.4%		
	s(freshwater discharge)			6.38**				
Tetraclita stalactifera								
size (LM)	intercept	1.63	0.05	34.1***	604	site	0.003	0.06
	freshwater discharge	−0.23	0.65	−3.49***		residual		
density (INLA)		**β**	**CI 95%**		62			
Spatial 500	intercept	13.33	8.24, 18.62			σ_u = 0.15		
	SST	−0.41	−0.62, −0.20			range = 73		
Spatial 1000	intercept	13.53	8.38, 18.95			σ_u = 0.15		
	SST	−0.42	−0.63, −0.21			range = 314		
Lottia subrugosa								
size(LMM)	intercept	6.58	1.33	4.97***	677	sub-region	0.02	0.12
	SST	−0.18	0.05	−3.32***		site	0.03	0.17
	roughness	−0.57	0.22	−2.63**		residual	0.09	0.29
	freshwater discharge	0.59	0.24	2.51*				
density (INLA)		**β**	**CI 95%**					
Spatial 500	intercept	2.40	−0.83, 5.67		59	σ_u = 0.58		
	Chl-a	−0.55	−0.82, −0.55			range = 55.2		
	wave fetch	5.73	0.28, 11.19					
Spatial 1000	intercept	2.44	−0.86, 5.79			σ_u = 0.58		
	Chl-a	−0.55	−0.86, −0.25			range = 108.8		
	wave fetch	5.68	0.16, 11.20					
Echinolittorina lineolata								
size (LM)	intercept only	3.32	0.16	21.49***	60			
abundance (LM)	intercept only	5.28	0.08	69.37***	62			

Full model for the predatory whelk (*S. brasiliensis*): *dependent variable* ~ shore inclination + wave fetch + SST + roughness + Chl-a + *T. stalactifera* density + *T. stalactifera* cover + *M. solisianus* cover + *M. solisianus* size + *random term.* **Full model for whelk's prey** (*T. stalactifera* and *M. solisianus*): *dependent variable* ~ shore inclination + wave fetch + SST + roughness + Chl-a + NDVI + *S. brasiliensis* size + *S. brasiliensis* abundance + *random term.* **Full model for grazers** (*L. subrugosa* and *E. lineolata*): *dependent variable* ~ shore inclination + wave fetch + SST + roughness + Chl-a + NDVI + *random term.* s(.) = smooth term. GAM models for *L. subrugosa* size and *T. stalactifera* density were fitted to constrained smooth term 'monotone decreasing P-splines', while *M. solisianus* cover was fitted to 'monotone increasing P-splines'. ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, ^{M} $p = 0.06$.

residuals, and using a Gaussian Markov random field (GMRF) based on the Matérn correlation to model the spatial autocorrelation (procedures described in Pardal et al., 2021).

3. Results

3.1. Spatial patterns of biotic and abiotic variables

Abiotic characteristics of the sub-regions generally overlapped except for Rio de Janeiro and Lakes (Fig. 2) and, consequently, between Region 1 and Region 2. Wave fetch, SST, and freshwater discharge explained 17.4% (adjusted R^2) of constrained variance in the reduced model among sub-regions (Fig. 2 and Table S1), indicating the influence of oceanographic conditions over local characteristics (i.e., shore inclination and roughness, and NDVI). Baixada Santista and São Sebastião Channel sub-regions had warmer (SST) and more productive waters (Chl-a) as compared to the colder and more oligotrophic waters of Lakes and Rio de Janeiro. These later sub-regions, in turn, had higher NDVI values (i.e., biofilm biomass) (Fig. S2). Ubatuba and Green Coast were transitional sub-regions (Fig. 2), with high variability for most measured variables and higher shore complexity (i.e., shore roughness and inclination, Fig. 2 and Fig. S3).

We checked for explicit density-dependent effects by applying Spearman rank correlations between size and density/cover of all species averaged by site and no correlation was found ($p > 0.05$). The size (Fig. 3) and density (Fig. 4) of key species was variable along sampled sites, but larger limpets (*Lottia subrugosa*), whelks (*Stramonita brasiliensis*) and littorinids (*Echinolittorina lineolata*) were associated with cold-oligotrophic waters (Figs. 2 and 3). Local scale factors influenced the densities of whelks (prey presence - Fig. 5B, Table 2) and limpets (roughness - Fig. 6B, Table 2). Barnacle density (*Tetraclita stalactifera*) was also associated with cold-oligotrophic waters (Fig. 2), but mussel cover (*Mytilaster solisianus*) was higher in sub-regions with warmer waters and lower freshwater discharge and wave fetch (Fig. 2).

3.2. Population patterns and biotic interactions

Total whelk abundance (*S. brasiliensis*) ranged from 0 to 94 individuals per site, with the highest density found in Riviera de São Lourenço in Baixada Santista subregion (n = 94, Fig. 4). Whelk size was variable between sites, ranging from 6.1 to 59.2 mm, with larger averages in

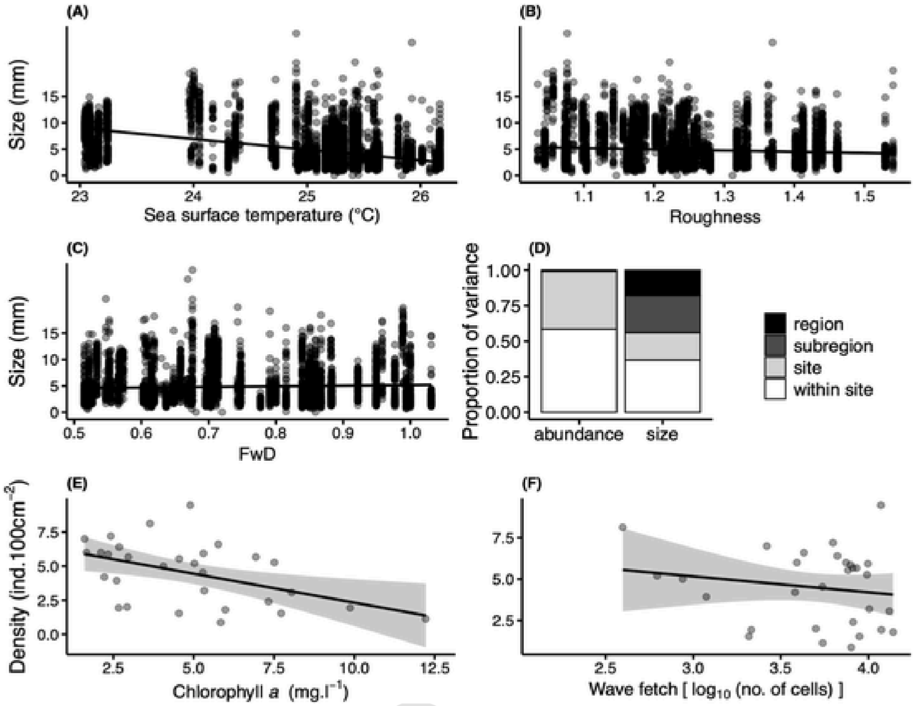

Fig. 6. The effect of environmental drivers on populational parameters (A – C, E – F) and estimates of relative variance components for population parameters (D) of the limpet *Lottia subrugosa* along SE coast of Brazil. Black lines and shaded area represent predictive values of the response ±95% confidence interval.

Lakes (28.6 ± 6.8 mm), and smaller average sizes in Green Coast (22.4 ± 7.1 mm) sub-regions (Fig. 3). Whelk size showed a negative, although marginally significant ($p = 0.06$), relationship with the cover of its prey, *M. solisianus*, while wave fetch and the presence of the mussel, *P. perna,* showed a positive effect on its density (Table 2, Fig. 5AandB). A larger variance portion of models could be attributed to site-level differences for size and density (Fig. 5D), indicating considerable changes in population structure among sites.

Limpet density (*Lottia subrugosa*) ranged from 0 to 17 individuals per 100 cm^2 and were highly variable within- and among sampled scales (Fig. 4). The best model retained Chl-a and wave fetch as predictors, with density increasing towards areas with lower Chl-a and higher wave fetch (Table 2, Fig. 5 and S8). Limpet size ranged from 1 to 26.9 mm across sites. Smaller and more variable average sizes were observed at sites in Green Coast and Ubatuba sub-regions, with size increasing at Rio de Janeiro and Lakes sites (Fig. 3). The best models predicted a decrease in limpet size in conditions of higher SST and substrate roughness (Table 2). The variance explained by random factors was mostly associated with the sub-region scale for limpet size and density (Fig. 6D), indicating similarities among neighbouring sites.

The mean cover of the mussel, *M. solisianus,* decreased from southern to northern sites, with higher and less variable values in Baixada Santista (Fig. 4), where freshwater discharge was greater (Fig. S2). The mean cover of *M. solisianus* was positively related with wave fetch and freshwater discharge (Table 2, Fig. 7A and B). No effects of the abundance or size of its predator, the whelk *S. brasiliensis*, were observed on mussel cover (Table 2). The size of *M. solisianus* showed low variation (8.6 ± 2.7 mm, mean ± SD), and the species was absent from nine sites, six of them between São Sebastião Channel and Green Coast sub-regions (Fig. 3). Mussel size was negatively related to SST (Table 2, Fig. 7C) with an inflection for predicted values above 24 °C, and larger individuals were found at northern sites (Fig. 3). Most variability was concentrated at within-site levels for size and density (Fig. 7D), reflecting high variability in local populations.

The mean density of the barnacle, *T. stalactifera,* was highly variable (Fig. 4) at the site level (<60% of variability), but higher at northern sites (Fig. 4), peaking at Forte shore in Lakes sub-region (mean ± SD: 103.5 ± 30.8). Barnacle density was negatively associated with SST (best model: density fitted using gamma residuals Tables 2 and S5, Fig. 8 and S6). Barnacle size ranged from 0.4 to 12.7 mm, with larger individuals found in Lakes sub-region (Table S3). Barnacles were smaller in sites close to estuaries in Baixada Santista and Rio de Janeiro sub-regions (Fig. 3), reflecting the models' negative predicted association with freshwater discharge in models (Table 2, Fig. 8C). As with density values, sizes were highly variable within sites (~90% of variability) (Fig. 8D).

The total abundance of the littorinid *E. lineolata* varied between 27 and 501 (median = 167, Q1 = 107, Q3 = 255.5) individuals per site (Fig. 3). *E. lineolata* size followed a similar pattern to limpets, with higher and more variable values at the northern sites (Fig. 3). Mean littorinid size in sites from Baixada Santista (1.9 ± 0.6 mm) and São Sebastião Channel (SSCh) (2.4 ± 0.9 mm) sub-regions was usually 50% smaller than sites from other sub-regions (4.2 ± 1.3 mm, Fig. 3), which was reflected in differences between sub-regions (Fig. S4; $F_{5,56} = 35.33$, $p < 0.001$; Tukey test, Region 1: Baixada Santista = SSCh ≠ Ubatuba; Region 2: Green Coast = Rio de Janeiro = Lakes). Littorinid mean size, however, increased with latitude, i.e., towards northern sites ($n = 60$, $r = -0.84$, $p < 0.001$; Fig. 9A). None of the environmental variables were associated with the variation in either littorinid density or size (Table 2). Abundance values were highly variable within sites, but size was more variable at region scale (Fig. 9B).

4. Discussion

4.1. - spatial patterns of biotic and abiotic variables

Sea surface temperature (SST) and wave fetch (as a proxy for the degree of exposure to wave action) were the most important predictors of

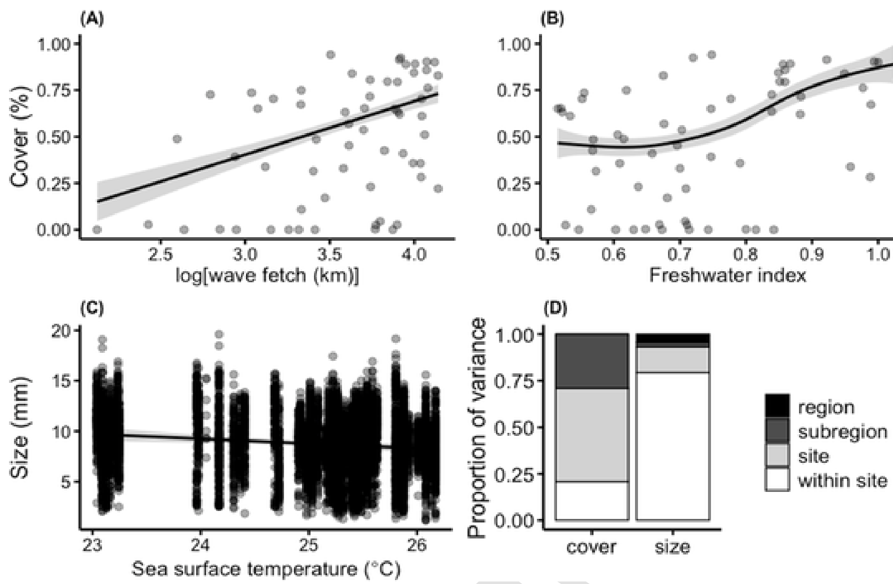

Fig. 7. The effect of environmental drivers on populational parameters and estimates of relative variance components for population parameters of the mussel *Mytilaster solisianus* along SE coast of Brazil. Black lines and shaded area represent predictive values of the response ± 95% confidence interval. Dot and whiskers represent the mean and standard deviation.

population parameters of the studied intertidal species along SE Brazil, indicating that such biota is under strong control of these abiotic variables. Although the explained variance of the multivariate model was below 20%, taking into consideration the scale and number of variables associated with the key species, we can consider those factors as of high importance to the intertidal populations investigated here. Out of five species evaluated, three (*L. subrugosa*, *T. stalactifera* and *S. brasiliensis*) were, on average, larger and more abundant at sites with lower SST and higher wave fetch. On the other hand, bottom-up and top-down processes appear to have little influence, and were only associated with site-level variation. Freshwater discharge was also correlated with population parameters of three species, but the direction of this effect was variable. Chlorophyll-a concentration (Chl-a, as a proxy for food availability for suspension feeders) and shore roughness affected only one species.

In the present study, sites were surveyed after the austral summer, the period of more frequent and intense upwelling events in the Cabo Frio system (Valentin, 2001), which may have enhanced SST effects. Larger sizes of most species were observed at sites with lower SST. Lower water temperatures are expected at higher latitudes, where species usually reach larger body sizes within their distributional ranges, but coastal upwelling in Cabo Frio creates an anomalous thermal gradient in SST across our study area. It is predicted that somatic growth and sexual maturity are predicted to slow down under lower temperatures, resulting in larger adults (Atkinson, 1994). Although our study area represents a fraction of the distributional ranges of the studied species, the limpet *L. subrugosa* and the mussel *M. solisianus* conformed to predictions of the temperature-size rule for ectotherms (Atkinson, 1994). This pattern was also described for the barnacle, *Chthamalus bisinuatus,* along this same study area (Pardal et al., 2021). Along this SST gradient, competition for resources would also favour populations of larger-bodied individuals which may better tolerate seasonal resource shortage (Kaspari and Vargo, 1995; Berke et al., 2012) or environmental stress (Benedetti-Cecchi et al., 2000). The average size of the littorinid, *Echinolittorina lineolata,* and the barnacle, *Tetraclita stalactifera,* were not associated with SST. *E. lineolata* inhabits the supralittoral fringe and is likely to be more influenced by air than water temperature (Marshall et al., 2010). Greater desiccation stress associated with higher air temperatures could also select larger shells due to optimised water storage (Vermeij, 1973; Tanaka et al., 2000) and, in fact, smaller individuals of this littorinid are found towards the equator along the Brazilian coast (Matos et al., 2020). *T. stalactifera* growth rates have been reported to be similar in sites under different temperature regimes (23.3 °C and 19.9 °C) within the Lakes sub-region (Skinner et al., 2005). Finally, as observed experimentally, larger barnacles *T. stalactifera* suffer higher predation rates by the whelk *Stramonita brasiliensis* (Pardal et al., 2022), which could contribute to smaller barnacles at southern sites, where whelks are more abundant, masking possible SST effects. The influence of differences in air temperature over regional scales in determining the distribution of rocky intertidal organisms has been demonstrated in a number of studies (e.g., Firth et al., 2011; Seabra et al., 2016), but equally there are numerous cases where this is not the case as air temperature is often not the primary driver of body temperatures in intertidal organisms (e.g., Marshall et al., 2010; Ng et al., 2017; Brahim and Marshall, 2020). We did not measure air temperature directly across our study site because mean satellite-borne air temperature is a very poor proxy for the temperature species experience on the rock surface (e.g., Lathlean et al., 2011) and also is known to vary at smaller scales due to local 'modifying factors' (sensu Helmuth et al., 2006) such as aspect and topography. Air temperature seems important as a driving factor of intertidal distribution when there are considerable differences with water temperatures, as in upwelling shores (Seabra et al., 2016) or high latitudes (Heaven and Scrosati, 2008). Along this part of the Brazilian coast, the lowest spring tides are nocturnal during the summertime, which helps buffering for effects of hot air temperatures during the day (Christofoletti et al., 2011b). The combined effect of hot water and hot air might be the worst scenario for intertidal organisms, which would be observed when low tides occur during the day (e.g., Little et al., 2021). Specially in the Lakes region, upwelling events are more frequent and intense during spring and summer months (Valentin, 2001), which also may have a refreshing effect over the hot air during daytime low tides. During the winter, we might expect that the daytime low tides potentially impose a lower temperature stress to intertidal organisms because of the smaller differences between air and water temperature. As a result, the importance of small-scale topographic features and the effect of thermal refuges needs to be further investigated in the thermal landscape along the studied shores

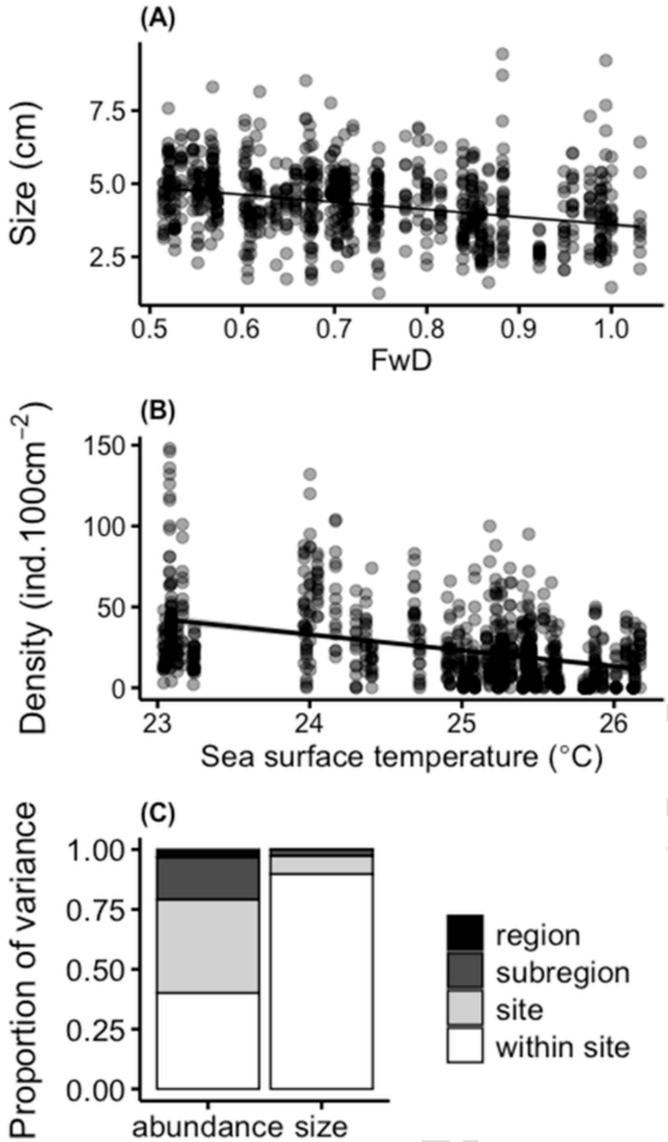

Fig. 8. The effect of environmental drivers on populational parameters and estimates of relative variance components for population parameters of the barnacle *Tetraclita stalactifera* along SE coast of Brazil. Black lines and shaded area represent predictive values of the response ±95% confidence interval.

to clarify those points, to help understanding the cumulative thermal stress historic (Rezende et al., 2014) of those intertidal organisms.

Upwelling areas are also known for increased local productivity (Kämpf and Chapman, 2016), and the seasonal events in SE Brazil enhance nutrient concentrations in waters of northern sites (Coelho-Souza et al., 2017). The highest Chl-a values were, however, recorded around estuarine urbanised areas, where natural terrestrial run-off and organic pollutants are increased by sewage discharge (Oliveira et al., 2016). Our results did not, therefore, support the expected bottom-up regulation model linked to intermittent upwelling regimes (Menge, 2000), where higher food availability (i.e., Chl-a, biofilm, prey) would correlate with the size and abundance of consumers. Both limpet (*L. subrugosa*) size and biofilm biomass (proxied by NDVI) increased northwards, where there are lower SST averages, although this relationship was not significant. Even with the increase of nutrients fuelling growth (Oliveira et al., 2016), biofilm biomass may be highly variable over short time periods and high grazing pressure may keep biofilm standing stock low and mask physical influences (Christofoletti et al., 2011a). Pollutants in urbanised areas may influence the physiology of intertidal organisms, for instance, increasing the energetic costs of higher individual *Mytilaster solisianus* feeding rates at polluted sites and affecting individual growth (Martinez et al., 2019). The influence of pollutants, however, will need a deeper investigation and direct quantification as we did not measure them in the present study.

The positive influence of wave fetch on the abundance of most species was another well documented pattern found in this study. Higher wave action results in higher delivery of food and larvae to shores (Leonard et al., 1998; McQuaid and Lindsay, 2005; Dias et al., 2018) and, thereby, to higher densities of suspension feeders at wave-exposed locations (Jenkins et al., 2008; Burrows et al., 2010; Christofoletti et al., 2011b). Such mechanisms can explain the higher abundances of the barnacle, *T. stalactifera,* and the mussel, *M. solisianus,* on more wave-exposed sites, which is consistent with results reported for the barnacle *C. bisinuatus* (Pardal et al., 2021). The mussel *M. solisianus* was more abundant close to estuaries and polluted sites, possibly reflecting characteristics of local planktonic productivity, besides hydrodynamic factors. Particulate organic matter concentration is, for example, higher close to estuaries (e.g., Pardal et al., 2023) making these areas more suitable for fine-filter feeders (i.e., mussels), as compared to coarse filter feeders (i.e., barnacles, see Dubois and Colombo, 2014). Possibly, the energetic costs of higher individual feeding rates at polluted sites (Martinez et al., 2019) may affect individual growth, and influence mussel size close to urbanised estuaries.

Rock surface roughness can influence limpet foraging by limiting their access to biofilm and shelters (Erlandsson et al., 1999; Johnson et al., 2008). Smoother rocks facilitate access to biofilm and provide larger biofilm biomass to limpets (Hutchinson et al., 2006), influencing resource availability in some sites. In fact, the largest individuals (shell length >25 mm) were found on shores with more smooth rocks (e.g., Saquarema, Piratininga and Itaipú). Although the use of the chain method has been criticized for being too coarse to reflect shelter availability for small organisms, such as limpets and littorinids (Meager and Schlacher, 2013), the correlation observed here indicates that this easily obtained measurement was useful to identify patterns for *L. subrugosa*.

4.2. - population patterns and biotic interactions

A large part of the explained variability in size or density of the studied intertidal species occurred at within- and among-sites levels, reflecting the importance of processes operating at smaller spatial scales (i.e., between 0.1 and 10s of km). Variability at such scales is commonly linked to effects of biotic interactions (e.g., predation or competition, Schiel, 2004; Kunze et al., 2021). However, we found little evidence of effects of the predatory whelk, *S. brasiliensis,* on populations of its potential prey (*T. stalactifera* and *M. solisianus*). A possible top-down influence was only suggested by the negative correlation between whelk size and the presence of the mussel *P. perna*. In fact, large-sized whelks are effective in reducing the abundance of mussels (López et al., 2010). However, *S. brasiliensis* has a cryptical behaviour (e.g., hides inside crevices) and is harvested along the Brazilian coast for consumption and the aquarium trade (Silva and Martins, 2017; Gurjão and Lotufo, 2018), which could have influenced abundance in some populations.

The abundance of the predatory whelk, *S. brasiliensis,* and the cover of the mussel, *M. solisianus,* were both positively affected by wave fetch. This coincident pattern indicates that, at more wave-exposed shores, whelks have access to greater prey availability (Rilov et al., 2001; Christofoletti et al., 2011b). However, whelk abundance and mussel cover were not significantly correlated perhaps because at exposed shores whelks have mussels as alternative prey and because predation rates of whelks on barnacles are reduced by wave action (Pardal et al., 2022). The lack of predation effect increases the relative importance of competition among sessile organisms, affecting patchiness within- and

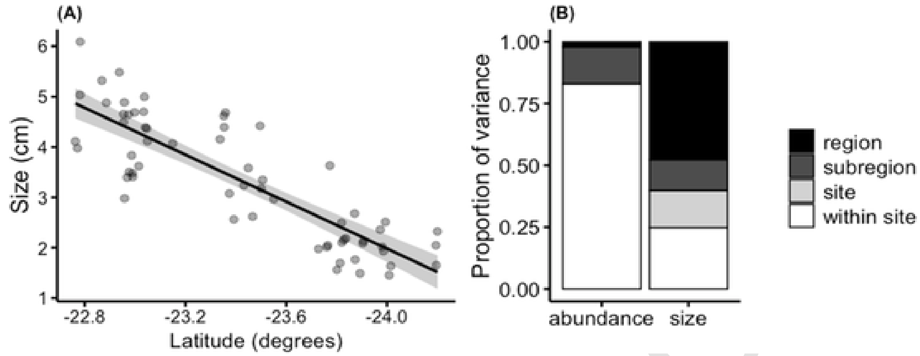

Fig. 9. The effect of environmental drivers on populational parameters and estimates of relative variance components for population parameters of the *Echinolittorina lineolata* along SE coast of Brazil. Black lines and shaded area represent predictive values of the response ±95% confidence interval.

between shore levels (Underwood, 1984b; Menge and Sutherland, 1987), and may have a larger influence on prey populations structure. Such synergistic effects may be more readily detected at the transitional zones because those sites offer natural combinations of local-scale influences within relatively homogeneous temperature and productivity conditions that are the main drivers at larger spatial scales. Due to its complex coastline, sites between Green Coast and Ubatuba sub-regions are ideal for future experimental approaches to unravel the relative contribution of wave exposure and biotic interactions on Brazilian rocky shore communities. Still, other biotic (recruitment and competition) and anthropogenic factors not evaluated here may also affect predator populations and should also be included in future research efforts.

4.3. - general patterns

Few studies have quantified large-scale patterns in rocky intertidal communities along the Southwestern Atlantic (but see Giménez et al., 2010; Miloslavich et al., 2016; Palomo et al., 2019; Cruz-Motta et al., 2020; Thyrring and Peck, 2021; Pardal et al., 2021, 2022, 2023), and the present study is the first dealing with multi-taxa population parameters, and the roles of environmental variability and biological responses at multiple spatial scales. Here, we observed the influence of lateral modifiers, i.e., abiotic drivers, and little evidence of top-down processes regulating rocky shore populations. Seawater temperature mostly influenced species size, acting at the regional scale (i.e., 100s of km) as a product of oceanographic processes from the SW Atlantic coast. Wave fetch is a product of coastal morphology and prevailing winds, mixing effects from sub-region (i.e, 10s of km) and site scales (i.e., 100s of m), influencing species abundance. Freshwater discharge had a sub-regional influence in sites close to estuaries, also affecting species abundance. Lastly, roughness only affected limpet size, indicating a site scale influence (i.e., 100s of m).

Overall, our results show that the investigated intertidal populations are spatially associated with three main trophic-oceanographic systems along the coast of Brazil over the latitudes between 22°S and 24°S: the colder upwelling area at the northern limit of sampled sites contrasts with the warmer southern limit, creating a gradient in SST; two large estuarine areas (Santos and Guanabara bays) form centres of elevated primary production (i.e., Chl-a) and freshwater discharge; the areas between these two centres are characterised by shores with variable degrees of wave exposure and topographic complexity (i.e., roughness and inclination). We could, therefore, identify three trophic-oceanographic domains: (i) a cold-oligotrophic system at northern sites (Lakes sub-region); (ii) an eutrophic systems associated to large estuaries and urban zones (Santos and Guanabara bays); and (iii) a transitional warm-water systems in between the eutrophic centres. These patterns reinforce the influence of estuaries on the dynamics of rocky shores, which may increase our understanding of multiple interacting factors, especially along South American shores. Thus, further investigation efforts should address experimental validation of the role of species interactions at broader spatial extents whilst accounting for the key role of abiotic processes.

Uncited References

; .

CRediT authorship contribution statement

Cesar A.M.M. Cordeiro: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **André Pardal:** Writing – review & editing, Writing – original draft, Validation, Methodology, Formal analysis, Conceptualization. **Luis Giménez:** Writing – review & editing, Visualization, Validation, Methodology, Formal analysis. **Áurea M. Ciotti:** Writing – review & editing, Visualization, Methodology. **Stuart R. Jenkins:** Writing – review & editing, Funding acquisition. **Michael T. Burrows:** Writing – review & editing, Methodology. **Gray A. Williams:** Writing – review & editing, Supervision, Funding acquisition. **Ronaldo A. Christofoletti:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

all data and codes used in this manuscript are fully available in public repositories

Acknowledgements

CAMMC was supported by post-doctoral fellowship (CNPq 163739/2014–5) and FAPERJ (JCNE E-26/200.215/2023). This research was also funded by the São Paulo Research Foundation (FAPESP), grants no. 2015/26859–3 (AP) and 2016/24551–4 (RAC). GAW was supported by a Special Visiting Researcher Fellowship (CNPq/MCTI 314060 2014–16). AMC was supported by CNPq 306591/2022–7. We are grateful to the lab technicians Carolina Chaaban and Nathalia Hespanhol and others who helped in the intensive field and laboratory work (Mariana Puga, Gerson, Deborah Gallo, Bruno Sayão and Celine Diogo).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106646.

References

Aguillera, M.A., Navarrete, S.A., 2007. Effects of *Chiton granosus* (Frembly, 1827) and other molluscan grazers on algal succession in wave exposed mid-intertidal rocky shores of central Chile. J. Exp. Mar. Biol. Ecol. 349, 84–98.

Atkinson, D., 1994. Temperature and organism size-a biological law for ectotherms? Adv. Ecol. Res. 25, 1–58.

Benedetti-Cecchi, L., 2000. Predicting direct and indirect interactions during succession in a mid-littoral rocky shore assemblage. Ecol. Monogr. 70 (1), 45–72.

Benedetti-Cecchi, L., Acunto, S., Bulleri, F., Cinelli, F., 2000. Population ecology of the barnacle *Chthamalus stellatus* in the northwest Mediterranean. Mar. Ecol.: Prog. Ser. 198, 157–170.

Berke, S.K., Jablonski, D., Krug, A.Z., Roy, K., Tomasovych, A., 2012. Beyond Bergmann's rule: size–latitude relationships in marine Bivalvia world-wide. Global Ecol. Biogeogr. 22 (2), 173–183.

Brahim, A., Marshall, D.J., 2020. Differences in heat tolerance plasticity between supratidal and intertidal snails indicate complex responses to microhabitat temperature variation. J. Therm. Biol. 91, 102620.

Brooks, M., Kristensen, K., van Benthem, K., Magnusson, A., Berg, C., Nielsen, A., Skaug, H., Maechler, M., Bolker, B., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modelling. Rom. Jahrb. 9, 378–400.

Bryson, M., Johnson-Roberson, M., Murphy, R.J., Bongiorno, D., 2013. Kite aerial photography for low-cost, ultra-high spatial resolution multi-spectral mapping of intertidal landscapes. PLoS One 8, 1–15.

Burrows, M.T., 2012. Influences of wave fetch, tidal flow and ocean colour on subtidal rocky communities. Mar. Ecol. Prog. Ser. 445, 193–207.

Burrows, M.T., Harvey, R., Robb, L., Poloczanska, E.S., Mieszkowska, N., Moore, P., Leaper, R., Hawkins, S.J., Benedetti-Cecchi, L., 2009. Spatial scales of variance in abundance of intertidal species: effects of region, dispersal mode, and trophic level. Ecology 90, 1242–1254.

Burrows, M.T., Jenkins, S.R., Robb, L., Harvey, R., 2010. Spatial variation in size and density of adult and post-settlement *Semibalanus balanoides*: effects of oceanographic and local conditions. Mar. Ecol. Prog. Ser. 398, 207–219.

Bustamante, R.H., Branch, G.M., Eekhout, S., 1995. Maintenance of an exceptional intertidal grazer biomass in South Africa: subsidy by subtidal kelps. Ecology 76, 2314–2329.

Christofoletti, R.A., Almeida, T.V.V., Ciotti, A.M., 2011a. Environmental and grazing influence on spatial variability of intertidal biofilm on subtropical rocky shores. Mar. Ecol. Prog. Ser. 424, 15–23.

Christofoletti, R.A., Takahashi, C.K., Oliveira, D.N., Flores, A.A.V., 2011b. Abundance of sedentary consumers and sessile organisms along the wave exposure gradient of subtropical rocky shores of the south-west Atlantic. J. Mar. Biol. Assoc. U. K. 91, 961–967.

Coelho-Souza, S.A., Pereira, G.C., Lopez, M.S., Guimaraes, J.R.D., Coutinho, R., 2017. Seasonal sources of carbon to the Brazilian upwelling system. Estuar. Coast Shelf Sci. 194, 162–171.

Connell, J.H., 1972. Community interactions on marine rocky intertidal shores. Annu. Rev. Ecol. Systemat. 3 (1), 169–192.

Connolly, S.R., Menge, B.A., Roughgarden, J., 2001. A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific Ocean. Ecology 82, 1799–1813.

Cruz-Motta, J.J., Miloslavich, P., Guerra-Castro, E., et al., 2020. Latitudinal patterns of species diversity on South American rocky shores: local processes lead to contrasting trends in regional and local species diversity. J. Biogeogr. 47, 1966–1979.

Dias, G.M., Christofoletti, R.A., Kitazawa, K., Jenkins, S.R., 2018. Environmental heterogeneity at small spatial scales affects population and community dynamics on intertidal rocky shores of a threatened bay system. Ocean Coast Manag. 164, 52–59.

Dubois, S.F., Colombo, F., 2014. How pick can you be? Temporal variations in trophic niches of co-occurring suspension-feeding species. Food Webs 1 (1–4), 1–9.

Erlandsson, J., Kostylev, V., Williams, G.A., 1999. A field technique for estimating the influence of surface complexity on movement tortuosity in the tropical limpet *Cellana grata* Gould. Ophelia 50 (3), 215–224.

Firth, L.B., Knights, A.M., Bell, S.S., 2011. Air temperature and winter mortality: implications for the persistence of the invasive mussel, *Perna viridis* in the intertidal zone of the south-eastern United States. J. Exp. Mar. Biol. Ecol. 400 (1–2), 250–256.

Frost, N.J., Burrows, M.T., Johnson, M.P., Hanley, M.E., Hawkins, S.J., 2005. Measuring surface complexity in ecological studies. Limnol Oceanogr. Methods 3, 203–210.

Giménez, L., Borthagaray, A., Rodríguez, M., Brazeiro, A., Carranza, A., 2010. Rocky intertidal macrobenthic communities across a large-scale estuarine gradient. Sci. Mar. 74, 88–100.

Giménez, L., Torres, G., Pettersen, A., Burrows, M.T., Estevez, A., Jenkins, S.R., 2017. Scale-dependent natural variation in larval nutritional reserves in a marine invertebrate: implications for recruitment and cross-ecosystem coupling. Mar. Ecol. Prog. Ser. 570, 141–155.

Gurjão, L.M.D., Lotufo, T.M.C., 2018. Native species exploited by marine aquarium trade in Brazil. Biota Neotropica 18, e20170387.

Hacker, S.D., Menge, B.A., Nielsen, K.J., et al., 2019. Regional processes are stronger determinants of rocky intertidal community dynamics than local biotic interactions. Ecology 100, e02763.

Hartig, F., 2020. DHARMa: residual diagnostics for hierarchical (Multi-Level/mixed) regression models. R package version 0.3.3.0. https://CRAN.R-project.org/package=DHARMa.

Hawkins, S.J., Pack, K.E., Hyder, K., Benedetti-Cecchi, L., Jenkins, S.R., 2020. Rocky shores as tractable test systems for experimental ecology. J. Mar. Biol. Assoc. U. K. 100 (7), 1017–1041.

Heaven, C.S., Scrosati, R.A., 2008. Benthic community composition across gradients of intertidal elevation, wave exposure, and ice scour in Atlantic Canada. Mar. Ecol.: Prog. Ser. 369, 13–23.

Helmuth, B., 2009. From cells to coastlines: how can we use physiology to forecast the impacts of climate change? J. Exp. Biol. 212 (6), 753–760.

Helmuth, B., Broitman, B.R., Blanchette, C.A., Gilman, S., Halpin, P., Harley, C.D., O' Donnell, M.J., Hofmann, G.E., Menge, B., Strickland, D., 2006. Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. Ecol. Monogr. 76 (4), 461–479.

Hutchinson, N., Nagarkar, S., Aitchison, J.C., Williams, G.A., 2006. Microspatial variation in marine biofilm abundance on intertidal rock surfaces. Aquat. Microb. Ecol. 42, 187–197.

Jenkins, S.R., Moore, P., Burrows, M.T., Garbary, D.J., Hawkins, S.J., Ingolfsson, A., Sebens, K.P., Snelgrove, P.V.R., Wethey, D.S., Woodin, S.A., 2008. Comparative ecology of North Atlantic shores: do differences in players matter for process? Ecology 89, S3–S23.

Johnson, M.P., Hanley, M.E., Frost, N.J., Mosley, M.W., Hawkins, S.J., 2008. The persistent spatial patchiness of limpet grazing. J. Exp. Mar. Biol. Ecol. 365 (2), 136–141.

Kämpf, J., Chapman, P., 2016. The functioning of coastal upwelling systems. In: Upwelling Systems of the World - Scientific Journey to the Most Productive Marine Ecosystems. Springer, Cham, Switzerland, p. 433p.

Kaspari, M., Vargo, E.L., 1995. Colony size as a buffer against seasonality: bergmann's rule in social insects. Am. Nat. 145, 610–618.

Kunze, C., Wölfelschneider, M., Rölfer, L., 2021. Multiple driver impacts on rocky intertidal systems: the need for an integrated approach. Front. Mar. Sci. 8, 667168.

Leonard, G.H., Levine, J.M., Schmidt, P.R., Bertness, M.D., 1998. Flow-driven variation in intertidal community structure in a Maine estuary. Ecology 79, 1395–1411.

Lathlean, J.A., Ayre, D.J., Minchinton, T.E., 2011. Rocky intertidal temperature variability along the southeast coast of Australia: comparing data from *in situ* loggers, satellite-derived SST and terrestrial weather stations. Mar. Ecol.: Prog. Ser. 439, 83–95.

Leslie, H.M., Breck, E.N., Chan, F., Lubchenco, J., Menge, B.A., 2005. Barnacle reproductive hotspots linked to nearshore ocean conditions. Proc Nat Acad Sci USA 102 (30), 10534–10539.

Little, C., Trowbridge, C.D., Williams, G.A., Hui, T.Y., Pilling, G.M., Morritt, D., Stirling, P., 2021. Response of intertidal barnacles to air temperature: long-term monitoring and *in-situ* measurements. Estuar. Coast Shelf Sci. 256, 107367.

López, M.S., Coutinho, R., Ferreira, C.E.L., Rilov, G., 2010. Predator-prey interactions in a bioinvasion scenario: differential predation by native predators on two exotic rocky intertidal bivalves. Mar. Ecol. Prog. Ser. 403, 101–112.

Mak, Y.M., Williams, G.A., 1999. Littorinids control high intertidal biofilm abundance on tropical, Hong Kong rocky shores. J. Exp. Mar. Biol. Ecol. 81–94.

Marshall, D.J., McQuaid, C.D., Williams, G.A., 2010. Non-climatic thermal adaptation: implications for species' responses to climate warming. Biol. Lett. 6 (5), 669–673.

Martinez, A.S., Mayer-Pinto, M., Christofoletti, R.A., 2019. Functional responses of filter feeders increase with elevated metal contamination: are these good or bad signs of environmental health? Mar. Pollut. Bull. 149, 110571.

Matos, A.S., Matthews-Cascon, H., Chaparro, O.R., 2020. Morphometric analysis of the shell of the intertidal gastropod *Echinolittorina lineolata* (d'Orbigny, 1840) at different latitudes along the Brazilian coast. J. Mar. Biol. Assoc. U. K. 100, 725–731.

McQuaid, C.D., Lindsay, J.R., 2005. Interacting effects of wave exposure, tidal height and substratum on spatial variation in densities of mussel *Perna perna* plantigrades. Mar. Ecol. Prog. Ser. 301, 173–184.

Meager, J.J., Schlacher, T.A., 2013. New metric of microhabitat complexity predicts species richness on a rocky shore. Mar. Ecol. 34 (4), 484–491.

Meager, J.J., Schlacher, T.A., Green, M., 2011. Topographic complexity and landscape temperature patterns create a dynamic habitat structure on a rocky intertidal shore. Mar. Ecol. Prog. Ser. 428, 1–12.

Menge, B.A., 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. Ecol. Monogr. 65, 21–74.

Menge, B.A., 2000. Top-down and bottom-up community regulation in marine rocky intertida habitats. J. Exp. Mar. Biol. Ecol. 250, 257–289.

Menge, B.A., 2003. The overriding importance of environmental context in determining the outcome of species-deletion experiments. In: Kareiva, P., Levin, S.A. (Eds.), The Importance of Species. Princeton University Press, Princeton, NJ, pp. 16–43.

Menge, B.A., 2023. Community theory: testing environmental stress models. Ecol. Lett. 26, 1314–1324.

Menge, B.A., Daley, B.A., Lubchenco, J., Sanford, E., Dahlhoff, E., Halpin, P.M., Hudson, G., Burnaford, J.L., 1999. Top-down and bottom-up regulation of New Zealand rocky intertidal communities. Ecol. Monogr. 69, 297–330.

Menge, B.A., Menge, D.N., 2013. Dynamics of coastal meta-ecosystems: the intermittent upwelling hypothesis and a test in rocky intertidal regions. Ecol. Monogr. 83 (3), 283–310.

Menge, B.A., Olson, A.M., 1990. Role of scale and environmental factors in regulation of

community structure. Trends Ecol. Evol. 5 (2), 52–57.
Menge, B.A., Sutherland, J.P., 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Am. Nat. 130 (5), 730–757.
Miloslavich, P., Cruz-Mota, J.J., Hernandéz, A., Herrera, C., Klein, E., Barros, F., Bigatti, G., Cárdenas, M., Carranza, A., Flores, A., et al., 2016. Benthic assemblages in South American intertidal rocky shores: biodiversity, services, and threats. In: Rodrígues, R.R. (Ed.), Marine Benthos: Biology, Ecosystems, Functions and Environmental Impact. Nova Science Publishers, Hauppauge, NY.
Morel, A., Gentili, B., 2009. A simple band ratio technique to quantify the colored dissolved and detrital organic material from ocean color remotely sensed data. Rem. Sens. Environ. 113, 998–1011.
Murphy, R.J., Underwood, A.J., Jackson, A.C., 2009. Field-based remote sensing of intertidal epilithic chlorophyll: techniques using specialized and conventional digital cameras. J. Exp. Mar. Biol. Ecol. 380 (1–2), 68–76.
Navarrete, S.A., Wieters, E.A., Broitman, B., Castilla, J.C., 2005. Benthic-pelagic coupling and the oceanographic control of species interaction. Proc. Natl. Acad. Sci. U.S.A. 102 (50), 18046–18051.
Ng, G., Gaylord, B., 2020. The legacy of predators: persistence of trait-mediated indirect effects in an intertidal food chain. J. Exp. Mar. Biol. Ecol. 530–531, 151416.
Ng, T.P.T., Lau, S.L.Y., Seuront, L., Davies, M.S., Stafford, R., Marshall, D.J., Williams, G.A., 2017. Linking behaviour and climate change in intertidal ectotherms: insights from littorinid snails. J. Exp. Mar. Biol. Ecol. 492, 12–131.
Nielsen, K., Navarrete, S.A., 2004. Mesoscale regulation comes from the bottom-up: intertidal interactions between consumers and upwelling. Ecol. Lett. 7, 31–41.
O'Connor, N.E., Donohue, I., Crowe, T.P., Emmerson, M.C., 2011. Importance of consumers on exposed and sheltered rocky shores. Mar. Ecol. Prog. Ser. 443, 65–75.
Oksanen, J., Blanchet, F.G., Friendly, M., et al., 2019. Vegan: community ecology package. R package version 2, 5. 4.
Oliveira, E.N., Fernandes, A.M., Kampel, M., Cordeiro, R.C., Brandini, N., Vinzon, S.B., Grassi, R.M., Pinto, F.N., Fillipo, A.M., Paranhos, R., 2016. Assessment of remotely sensed chlorophyll-a concentration in Guanabara Bay, Brazil. J. Appl. Remote Sens. 10 (2), 026003.
Paine, R.T., 1966. Food web complexity and species diversity. Am. Nat. 100, 65–75.
Palomo, M., Bagur, M., Calla, S., Dalton, M., Soria, S., Hawkins, S., 2019. Biodiversity and interactions on the intertidal rocky shores of Argentina (South-West atlantic). In: Hawkins, S., Bohn, L., Firth, L., Williams, G. (Eds.), Interactions in the Marine Benthos: Global Patterns and Processes (Systematics Association Special Volume Series. Cambridge University Press, Cambridge, pp. 164–189.
Pardal, A., Cordeiro, C.A.M.M., Ciotti, A.M., Jenkins, S.R., Giménez, L., Burrows, M.T., Christofoletti, R.A., 2021. Influence of environmental variables over multiple spatial scales on the population structure of a key marine invertebrate. Mar. Environ. Res. 170, 105410.
Pardal, A., Jenkins, S.R., Christofoletti, R.A., 2022. Local and large-scale spatial variation in a marine predator–prey interaction in the southwestern Atlantic. Oecologia 199, 685–698.
Pardal, A., Martinez, A.S., Ciotti, A.M., Christofoletti, R.A., Cordeiro, C.A., 2023. Macroecology of rocky intertidal benthic communities along the southwestern Atlantic: patterns of spatial variation and associations with natural and anthropogenic variables. Mar. Environ. Res. 190, 106099.
Pardal-Souza, A.L., Dias, G.M., Jenkins, R.E., Ciotti, A.M., Christofoletti, R.A., 2017. Shading impacts by coastal infrastructure on biological communities from subtropical rocky shores. J. Appl. Ecol. 54 (3), 826–835.
Pinheiro, J., Bates, D., R Core Team, 2023. Nlme: linear and nonlinear mixed effects models. R package version 3, 1–163.
R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL. https://www.R-project.org/.
Rezende, E.L., Castañeda, L.E., Santos, M., 2014. Tolerance landscapes in thermal ecology. Funct. Ecol. 28 (4), 799–809.
Rilov, G., Benayahu, Y., Gasith, A., 2001. Low abundance and skewed population structure of the whelk *Stramonita haemastoma* along the Israeli Mediterranean coast. Mar. Ecol. Prog. Ser. 218, 189–202.
Sanford, E., 1999. Regulation of keystone predation by small changes in ocean temperature. Science 283 (5410), 2095–2097.
Seabra, R., Wethey, D.S., Santos, A.M., Gomes, F., Lima, F.P., 2016. Equatorial range limits of an intertidal ectotherm are more linked to water than air temperature. Global Change Biol. 22 (10), 3320–3331.
Schiel, D.R., 2004. The structure and replenishment of rocky shore intertidal communities and biogeographic comparisons. J. Exp. Mar. Biol. Ecol. 300, 309–342.
Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. Nat. Methods 9, 671–675.
Silva, E.J.D., Martins, I.X., 2017. A pesca de moluscos em ambientes intermareais no oeste do estado do Rio Grande do Norte, Brasil. Arq Ciên Mar Fortaleza 50, 110–118.
Skinner, L.F., Siviero, F.N., Coutinho, R., 2005. Comparative growth of the intertidal barnacle *Tetraclita stalactifera* (Thoracica: tetraclitidae) in sites influenced by upwelling and tropical conditions at the Cabo Frio region, Brazil. Rev. Biol. Trop. 55 (1), 71–78.
Tam, J.C., Scrosati, R.A., 2014. Distribution of cryptic mussel species (*Mytilus edulis* and *M. trossulus*) along wave exposure gradients on northwest Atlantic rocky shores. Mar. Biol. Res. 10, 51–60.
Tanaka, M.O., Duque-Estrada, T.E., Magalhães, C.A., 2000. Dynamics of the acmaeid limpet *Collisella subrugosa* and vertical distribution of size and abundance along a wave exposure gradient. J. Molluscan Stud. 68, 55–64.
Thyrring, J., Peck, L.S., 2021. Global gradients in intertidal species richness and functional groups. Elife 10, e64541.
Thompson, R.C., Norton, T.A., Hawkins, S.J., 2004. Physical stress and biological control regulate the producer-consumer balance in intertidal biofilms. Ecology 85 (5), 1372–1382.
Thorson, J.T., Skaug, H.J., Kristensen, K., Shelton, A.O., Ward, E.J., Harms, J.H., Benante, J.A., 2015. The importance of spatial models for estimating the strength of density dependence. Ecology 96 (5), 1202–1212.
Underwood, A.J., 1979. The ecology of intertidal gastropods. Adv. Mar. Biol. 16, 111–210.
Underwood, A.J., 1984a. Microalgal food and the growth of the intertidal gastropods *Nerita atramentosa* Reeve and *Bembicium nanum* (Lamarck) at 4 heights on a shore. J. Exp. Mar. Biol. Ecol. 79, 277–291.
Underwood, A.J., 1984b. Vertical and seasonal patterns in competition for microalgae between intertidal gastropods. Oecologia 64, 211–222.
Underwood, A.J., 2000. Experimental ecology of rocky intertidal habitats: what are we learning? J. Exp. Mar. Biol. Ecol. 250 (1–2), 51–76.
Underwood, A.J., Chapman, M.G., 1989. Experimental analyses of the influences of topography of the substratum on movements and density of an intertidal snail, *Littorina unifasciata*. J. Exp. Mar. Biol. Ecol. 134, 175–196.
Valentin, J.L., 2001. The Cabo Frio upwelling system, Brazil. In: Seeliger, U., Kjerfve, B. (Eds.), Coastal Marine Ecosystems of Latin America. Springer, Berlin Heidelberg, Berlin, Heidelberg, pp. 97–105.
Vermeij, G.J., 1973. Morphological patterns in high-intertidal gastropods: adaptive strategies and their limitations. Mar. Biol. 20, 319–346.
Wahl, M., 1989. Marine Epibiosis. I. Fouling and antifouling: some basic aspects. Mar. Ecol. Prog. Ser. 58, 175–189.
Wood, S.N., Pya, N., Saefken, B., 2016. Smoothing parameter and model selection for general smooth models (with discussion). J. Am. Stat. Assoc. 111, 1548–1575.
Wootton, J.T., 1995. Effects of birds on sea urchins and algae: a lower-intertidal trophic cascade. Ecoscience 2 (4), 321–328.
Zuur, A.F., Ieno, E.N., Saveliev, A.A., 2017. Spatial, Temporal and Spatial-Temporal Ecological Data Analysis with R-INLA, vol. 1. Highland Statistics Ltd.
Zuur, A.F., Ieno, E.N., Walker, N.J., Savelier, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York, USA, p. 574p.