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1	Local and large-scale spatial variation in a marine predator-prey interaction in the
2	Southwestern Atlantic
3	
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16	manuscript.

17

18 Abstract

19 Predator-prey interactions are a key ecological process which can be modified by 20 environmental conditions over a range of spatial scales. Through two complementary short-21 term experiments, we assessed how local and large-scale environmental conditions affect a 22 subtropical intertidal predator-prey interaction. At a local scale, we evaluated the effects of the 23 degree of exposure to wave action and prey density on consumption rate and interaction 24 strength using a whelk-barnacle system. Consumption rate decreased with wave exposure at 25 experimentally reduced prey density but did not change at ambient density. Such an 26 interactive effect occurred due to shifts in the whelk's feeding behaviour, likely linked to 27 encounter rate and stress amelioration underpinned by prey density. Per capita interaction 28 strength of the whelk on the barnacle weakened along the wave exposure gradient, but to a 29 greater degree at reduced compared to ambient prey density. This confirms that 30 environmental harshness can decrease the importance of predators, but the magnitude of 31 change may be modified by density-dependent effects. A large-scale experiment did not reveal 32 spatial patterns in the whelk-barnacle interaction, nor relationships to chlorophyll-a 33 concentration or the minor change in sea temperature across the study area. Patterns in the 34 size of consumed barnacles along the chlorophyll-a gradient suggest changes in food choice 35 related to prey quality and size. We conclude that disentangling the effects of wave exposure 36 and prey density revealed important potential mechanisms driving species locally. Large-scale 37 variation in the whelk-barnacle interaction appeared to be linked to species' traits shaped by 38 the environmental context.

39

40 **Keywords**: chlorophyll-a concentration, interaction strength, spatial scales, wave exposure.

41

42 Introduction

43 Species interactions have long been recognised to play a role in the organization of 44 communities (e.g., Elton 1927). Influential work from the 1960's put a spotlight on predation 45 as a main driver of community dynamics (Hairston et al. 1960; Connell 1961; Paine 1966). 46 Predators were shown to control their prey's population size and in so doing have knock-on 47 consequences for other trophic levels (i.e., top-down control) (Menge 1992; Power 1992). 48 Experimental work over subsequent decades expanded top-down theory by accounting for 49 the effects of environmental stress (Dayton 1971, 1975; Menge 1976, 1978a, b). The 50 'environmental stress hypothesis' predicted that the importance of predation decreases with 51 increasing environmental harshness because a high frequency of disturbance impairs the 52 foraging ability of mobile predators (Menge and Sutherland 1976, 1987). Such 53 conceptualizations were important to integrate mechanisms shaping communities and 54 strengthen the search for general principles driving biodiversity.

55 Menge and Sutherland's (1976) 'environmental stress hypothesis' was grounded in 56 experiments assessing the effects of wave exposure on rocky intertidal communities. In this 57 ecosystem, increasing wave action can limit the feeding of predatory whelks due to the risk of 58 dislodgement and death (Menge 1976, 1978a, b). Criticism of the generality of this hypothesis 59 has drawn attention to covarying factors along such environmental gradients (Underwood and 60 Denley 1984). Apart from affecting the foraging of consumers, wave exposure in intertidal 61 habitats generates consistent gradients in the abundance of sessile species. Higher delivery 62 of larvae and food generally increases the density of filter-feeders (e.g., barnacles, mussels) 63 towards more dynamic wave and flow conditions (Leonard et al. 1998; Burrows et al. 2010). 64 Variable densities of such organisms, in turn, can affect important parameters such as encounter probability of prey by predators (Holling 1965), prey handling (Wieters and 65 Navarrete 1998), feeding rate (Moran 1985) and availability of refuges (Davenport et al. 1998). 66 67 Therefore, wave exposure and prey density are key covarying factors affecting species 68 interactions. Progress in understanding the role of environmental variability on the dynamics 69 of coastal communities depends on disentangling the effects of these factors, a goal we 70 address here.

71 Models of community regulation considering consumer effects and environmental 72 stress have brought advances, but they have generally focused on organisms at local scales. 73 Investigations over larger spatial scales have shown that variation in nearshore oceanographic 74 conditions can have major effects on benthic biota (Menge 1992, 2000). Currently it is widely 75 accepted that distinct regimes of availability and delivery of nutrients, phytoplankton and larvae 76 along ocean discontinuities (e.g., upwelling, ocean currents) determine abundance of prey 77 and predators, setting the pace of trophic interactions (Bustamante et al. 1995; Menge et al. 78 1997, 2003; Menge and Menge 2013; Hacker et al. 2019; Sellers et al. 2021). Environmental 79 variation over large scales can also modify the behaviour and physiology of predators, altering feeding rates and hence the strength of top-down control. For example, variation in seawater temperature can be responsible for variation in the strength of interactions due to effects on predators' metabolism (Sanford 1999; O'Connor 2009; Kordas et al. 2011; Carr and Bruno 2013). Likewise, variation in nutritional quality of prey, which could be linked to large-scale variability in phytoplankton availability, can affect consumers' feeding choices (Palmer 1984; Simpson et al. 2010; Schmidt et al. 2012). Therefore, understanding variation in natural communities relies on integration of factors operating over both local and larger spatial scales.

87 Here, our aim was to evaluate how environmental conditions at different spatial scales 88 affect an intertidal predator-prey interaction in the subtropical rocky coast of the southwestern 89 Atlantic. This was done through two independent and complementary short-term studies. First, 90 we carried out field experiments over eight sites within a region (few kilometres apart) to 91 disentangle the effects of the degree of exposure to wave action and prey density on the 92 interaction between the whelk Stramonita brasiliensis and the barnacle Tetraclita stalactifera. 93 We measured the consumption rate and calculated the per capita interaction strength (PCIS) 94 (i.e., the per capita effects of one species on another's abundance) (Paine 1980) of predators 95 at experimentally reduced (hereafter 'reduced') and ambient prey density across a gradient of 96 wave exposure. We expected that consumption rate would decrease with increasing wave 97 exposure (environmental stress hypothesis; Menge and Sutherland 1976) but also predicted 98 a weaker negative effect of wave exposure on consumption rate at ambient compared to 99 reduced prey density due to greater encounter probability of the prey by the predator and 100 buffering from wave-induced stress. Also, we predicted that PCIS would be weakened by 101 increasing wave exposure, but with a stronger effect at reduced prey densities (density-102 dependent interaction strength; Berlow et al. 1999). Secondly, we carried out experiments 103 along over 450 km of coast to test for spatial patterns on the same whelk-barnacle system and 104 potential relationships to sea temperature and chlorophyll-a concentration (Chla, as a proxy 105 for food availability to barnacles). We predicted that consumption rate and PCIS would 106 decrease towards colder waters due to decreasing metabolism of the predator. Assuming 107 higher prey quality where phytoplankton is more abundant (Bertness et al. 1991; Dahlhoff and 108 Menge 1996), we expected both responses to decrease towards Chla richer waters as a result 109 of lower predation rates driven by higher energetic yield per unit of consumed prey compared 100 to sites with low Chla. In other words, we expected the predator to eat less in high Chla sites 111 since fewer prey would satisfy their energetic demands. In this experiment we also explored 112 relationships among prey size, predator responses and ocean conditions. Such analyses 113 allowed the inference of mechanisms explaining observed patterns of species interactions.

114

115 Material and Methods

116 Experiment 1: Effect of wave exposure and prey density on predator-prey interactions

117 Using a comparative experimental approach, we carried out field manipulations of 118 predator and prey in the lower midlittoral of the intertidal zone over eight sites in the north 119 coast of São Paulo State (Ubatuba, Southeast Brazil) (Fig. 1; see also Appendix A: Fig. A1). 120 This area is characterised by a microtidal regime, with mean sea level around 0.7 m above 121 local chart datums and an average tidal range of about 1.4 m. The lower midlittoral zone in 122 this area is dominated by the large barnacle *Tetraclita stalactifera* while other species such as 123 oysters and mussels can also be found, usually, in lower abundance (Pardal-Souza 2021). 124 Sites ranging from a few kilometres up to 20 km apart were chosen along a gradient of 125 exposure to wave action (Fig. 1) determined using wave fetch as a proxy applying Burrows' 126 (2012) model to the Southeast coast of Brazil (Fig. 1A). Briefly, the wave fetch was estimated 127 for every 200 m coastal cell as the distance, up to a maximum of 200 km, to the nearest land 128 over 32 angular sectors (11.25°). The final wave fetch value for each coastal cell represents 129 the sum of the fetch values across all 32 sectors expressed as log₁₀ of the number of cells 130 (Burrows 2012). The summed wave fetch was extracted for a 3 x 3 spatial buffer centred on 131 the coordinates of each site. Averaged wave fetch agreed with previous wave exposure 132 categorisations of the same sites based on maximum wave force (Bueno and Flores 2010).

133 We used a 2-way factorial design with the treatments 'prey density' (ambient, reduced) 134 and 'predator' (inclusion, exclusion). At each site, we haphazardly selected 28 plots (625 cm²) 135 dominated by the barnacle T. stalactifera located at least one meter apart. Organisms other 136 than this barnacle were removed. Plots were randomly assigned to reduced or ambient prey 137 density treatments. In the reduced treatment, barnacles were removed to establish 15-20 138 individuals per plot, which is representative of low-density patches at sheltered sites across 139 the study area. Remaining barnacles in the plots of reduced treatment were clumped together. 140 Natural prey densities were used in the ambient treatment (Fig. 2). Half of the plots of each 141 density treatment were then randomly assigned to inclusion or exclusion of the predator. In 142 the inclusion treatment, one adult of the whelk *Stramonita brasiliensis* (shell length: 35-40 mm) 143 was confined inside cages (25 x 25 x 7 cm) of stainless-steel mesh (gauge 1.6 mm, mesh size 144 15 mm) fixed to the substrate. Our manipulated whelk density (1 individual per 625 cm² = 16 145 ind.m⁻²) was higher than densities recorded by Christofoletti et al. (2011) in the study area 146 which ranged from site averages of 0.1 to 4.4 individuals per m² but was in line with localised 147 densities at small spatial scales. Exclusion treatments were used for measuring mortality of 148 prey due to natural causes or cage artefacts (as in Sanford and Swezey 2008). Cages were 149 regularly cleaned of fouling.

150 This experiment started in June 2018 and lasted until August to October 2018 151 depending on site and plot, from 45 to 112 days (mean = 72 days) (Appendix A: Table A1). 152 The number of dead barnacles (i.e., empty shells or missing individuals) in both inclusion and 153 exclusion treatments were counted using photography or directly at the site, approximately 154 every 15-20 days. These regular visits ensured damaged cages were repaired and whelk 155 densities maintained regularly. Occasional invading predators, usually small gastropods, were 156 removed from the cages. Some plots were rejected where predators escaped more than once, 157 or the total fully caged period was less than 65% of the experiment duration (Appendix A: 158 Table A1). Due to cages lost to storms and escapes of whelks, the final number of replicates 159 per treatment was between 4 and 7 (Appendix A: Table A1).

160

161 Experiment 2: Large-scale variation in predator-prey interactions and relationships to 162 chlorophyll-a concentration and sea temperature

163 To test how the whelk-barnacle interaction varied over large-scales and determine any 164 potential relationships with chlorophyll-a concentration (Chla) and sea temperature, we carried 165 out caging experiments at ten sites spanning about 450 km of linear distance along the coast 166 of SE Brazil (Appendix A: Fig. A1). The same microtidal regime occurs along this whole region 167 (mean sea level = 0.7 m; tidal range = 1.4 m). The degree of exposure to wave action of the 168 sites ranged from intermediate to exposed based on wave fetch values (Appendix A: Fig. A2). 169 All shores were gently sloping and had similar assemblage structure in the lower midlittoral, 170 i.e., dominated by beds of the barnacle *T. stalactifera* (Pardal-Souza 2021).

171 In this experiment, 6 and 4 cages were randomly assigned, respectively, to inclusion 172 and exclusion of the predatory whelk S. brasiliensis (shell length: 30-35 mm). In the inclusion treatment, we included one whelk per cage. The density of *T. stalactifera* was manipulated to 173 174 maintain between 40-50 individuals per plot, a common prey density among all sites studied 175 (Fig. 3). We failed in achieving such target density in three out of the ten sites because of 176 rough weather. Barnacle density at these sites was higher (Fig. 3). Experiments lasted 177 between 55 and 62 days, starting in August 2019 and ending in September or October 2019, 178 depending on site. For a few plots (4 out of 51), experimental duration was about 30 days 179 because cages were lost. The number of live barnacles was quantified through digital images 180 taken at the beginning, middle and at the end of the experiment. We also used the images to 181 measure the size of barnacles available (opercular length; n = 16 to 28 per plot) and consumed 182 (n = 3 to 24 per plot) during the experiment.

183 Chla was obtained from level-3 MODIS-Aqua satellite images (4-km resolution; 184 https://oceancolor.gsfc.nasa.gov/l3/) extracted for a 3 x 3 spatial buffer centred on the 185 coordinates of sites over a period of 3-months, from one month prior to the start of the 186 experiment until its end. Chla data were obtained prior to the experiment because we

187 considered that barnacle quality at the start of the experiment was influenced by previous 188 patterns in Chla (at least over 30 days). Sea temperature were measured using temperature 189 loggers (iButton DS1921G-F5, Berkshire, UK) attached to a PVC plate and directly fixed to 190 the substrate inside the cages. Measurements were recorded every hour with a resolution of 191 0.5 °C. To extract only seawater temperatures from this intertidal dataset, we calculated the 192 average and standard deviation of all measurements for each site. Temperature values out of 193 the range of the site average \pm 1.5 SD were excluded. This approach successfully eliminated 194 air temperatures during low tides periods (see Appendix A: Fig. A3). At some sites, loggers 195 were damaged due to rough weather; in these cases, satellite-borne sea surface temperature 196 (SST) data were used. Data was extracted as described before, but only for the period of the 197 caging experiments at each site. In order to minimise errors at these sites, we corrected 198 satellite SST using the average difference between temperature logger derived sea 199 temperature and that based on satellites for the nearest site where we obtained both sets of 200 data. This was done by subtracting the daily sea temperature logger average from daily SST 201 average (Appendix A: Fig. A4, Table A2).

202

203 Consumption rate and interaction strength of predator on prey

In both experiments, we calculated the mortality rate of the barnacle prey for each cage *i* from the site *j* belonging to the treatments 'predator' k (k = 0: exclusion; k = 1: inclusion) and 'prey density' *l* (ambient, reduced: only for the Experiment 1) as the difference between the number of live barnacles in the beginning (B₀) and at the end of the experiment (B_t) divided by the time elapsed *t*:

209
$$MR_{ijk(l)} = \left(\frac{B_{0_{ijk(l)}} - B_{t_{ijk(l)}}}{t}\right)$$

210 (1)

Per capita consumption rate of barnacles by whelks $(CR_{ij(l)_{k=1}})$ was calculated by subtracting the average mortality rate of prey in the absence of predators $(\overline{MR}_{j(l)_{k=0}})$ from the mortality rate in the presence of the predator $(MR_{ij(l)_{k=1}})$ divided by the number of whelks *S*. *brasiliensis* inside the cages $(S_{ij(l)_{k=1}})$. Since inclusion and exclusion plots were not paired, $\overline{MR}_{j(l)_{k=0}}$ was obtained by averaging 1,000 averages calculated through bootstrapping. A few negative values due to lack of predation and subtraction of background mortality were replaced to zero since there cannot be a negative consumption rate.

218
$$\operatorname{CR}_{ij(l)_{k=1}} = \left(\frac{\operatorname{MR}_{ij(l)_{k=1}}}{\operatorname{S}_{ij(l)_{k=1}}}\right) - \overline{\operatorname{MR}}_{j(l)_{k=0}}$$

219 (2)

For calculating interaction strength, we assumed that the trajectory of the focal cohorts of prey could be expressed as an exponential function (as in Navarrete and Menge 1996):

B_t = B₀
$$e^{(-(m-\alpha S)t)}$$
,

223 (3)

where B_t is the number of live barnacles at time *t*, B_0 is the initial number of live barnacles, *m* is the mortality rate in the absence of predators, *S* is the abundance of the predatory whelk and α is the per capita interaction strength (PCIS) of the whelk on the barnacle cohort. Simplifying the formula by dividing both sides by B_0 and taking natural logarithms, we obtained that:

229
$$PCIS_{ij(l)_{k=1}} = \left[\frac{\ln\left(\frac{B_{t_{ij(l)_{k=1}}}}{B_{0ij(l)_{k=1}}}\right)}{S_{ij(l)_{k=1}} \cdot t}\right] - \bar{m}_{j(l)_{k=0}}$$

230

The mortality rate in the absence of predators for each cage belonging to each site and treatment (where pertinent) $(m_{ij(l)_{k=0}})$ was obtained using a similar formula to equation 4,

(4)

but without the term S. In both cases, B_t and B_0 were added to 1 to avoid natural logarithms of zero. As before, the mortality rate in the absence of predators $\overline{m}_{j(l)_{k=0}}$ was calculated by averaging 1,000 averages obtained through bootstrapping.

236

237 Data analysis

238 The main effects of wave exposure and prey density treatment (ambient, reduced) and 239 their interaction on per capita consumption rate (CR) and interaction strength (PCIS) of the 240 predator on prey (Experiment 1) were tested by fitting linear mixed models with Gaussian 241 distribution and identity link. The same mixed modelling approach was used to evaluate the 242 effects of Chla and sea temperature on CR and PCIS (Experiment 2), but only considering the 243 main effects of the variables. Additionally, we fitted linear mixed models of predation 244 responses as a function of longitude coordinates to test for spatial patterns. Longitude was 245 used because it describes better the spatial gradient as this coastline runs mostly from west 246 to east. Analyses were done in R software version 3.6.3 (R Core Team 2020) using the 247 package 'nlme' (Bates et al. 2015). All models also included the random effect of 'site' (varying 248 intercept). In case of visual evidence of heterogeneity of variance, models were fitted with 249 different variance structures and selected through AIC score and LR tests (Zuur et al. 2009). 250 Estimates of the parameters of the models were obtained by restricted maximum likelihood 251 (REML). Assumptions of final models were checked through visual inspection of residuals 252 plots (Appendix B: Fig. B1 and B2). Ordinary linear regressions were also used for fitting pertinent relationships between variables (e.g., prey size and Chla, prey size and sea 253 254 temperature). All figures were made using the package 'ggplot2' (Wickham 2016) and edited 255 in the software Inkscape (https://inkscape.org/).

256

257 **Results**

258 Effect of wave exposure and prey density on predator-prey interactions

Mean ambient density of the barnacle prey *Tetraclita stalactifera* showed an increasing trend with wave exposure (Fig. 1D), although the test was marginally non-significant (Linear model on \log_{10} -transformed data: $F_{1,6} = 4.21$, $R^2 = 0.41$, P = 0.08). At ambient densities, barnacles varied on average from 45.0 to 99.3 individuals per 625 cm² in predator inclusion plots and from 36.8 to 103.2 individuals in predator exclusion plots. Reduced prey density plots had on average around 16 barnacles (Fig. 2).

265 Mortality of prey in the absence of predators (i.e., background mortality) was overall 266 very low. Considering all sites, mean mortality rate at ambient prey density was 0.016 against 267 0.005 barnacles per day at reduced prey density. This means that 1 barnacle dies every 62.5 268 and 200 days at ambient and reduced prey density treatments, respectively. Average 269 background mortality was the highest at ambient prey density in Praia Grande (0.031 270 barnacles.day⁻¹ = 1 barnacle in 32 days) and the lowest in reduced prey density in Sta Rita 271 (0.002 barnacles.day⁻¹= 1 barnacle in 500 days) (Appendix A: Fig. A5-A). The overall low 272 background mortality could be a result of cage artefacts attenuating, for example, thermal and 273 desiccation stress.

274 Consumption of the barnacle prey T. stalactifera by the predatory whelk Stramonita 275 brasiliensis showed high variation across replicate plots, ranging from 0 to 0.41 individuals per 276 predator per day. The relationship between wave exposure and consumption rate depended 277 on the prey density treatment. At reduced prey densities, the consumption rate of S. 278 brasiliensis decreased with wave exposure, but there was no effect of wave exposure at 279 ambient prey density (Table 1A, Fig. 4A). Per capita interaction strength (PCIS) of the 280 predatory whelk also varied with wave exposure. PCIS got weaker (i.e., values closer to zero) 281 as wave exposure increased at both prey density treatments, but with different slopes. At 282 reduced prey densities, PCIS got weaker as wave fetch increased with a slope 4 times greater 283 (slope = 0.020) than that in the ambient prey density (slope = 0.005) (Table 1B, Fig. 4B).

284

Large-scale variation in predator-prey interactions and relationships to chlorophyll-a concentration and sea temperature

The mean concentration of satellite derived chlorophyll-a (Chla) showed a general decline northward from Astúrias in the south to Prainha in the north. This general reduction was interrupted, however, due to high values of Chla at two sites, Grumari and Piratininga, which are near to the eutrophic Guanabara bay (Fig. 5; Appendix A: Fig. A1). The mean sea temperature, on the other hand, varied less than 1 °C among sites (from 21.78 °C to 22.60 °C) (Fig. 5). Mean Chla and sea temperature were not correlated (Spearman's rho = 0.28, P = 0.42).

As in Experiment 1, background mortality of the barnacle prey was low during the large-scale manipulations (Experiment 2). Considering the 10 sites, average background mortality was 1 barnacle in 71 days (i.e., 0.014 barnacles.day⁻¹). Values ranged from 0.004 to 0.040 barnacles per day (i.e., 1 dead barnacle in 25 to 250 days), respectively, in Grumari and Piratininga (Appendix A: Fig. A5-B).

299 Both consumption rate and per capita interaction strength of the whelk S. brasiliensis 300 on the barnacle T. stalactifera varied greatly across the studied area. Average consumption 301 rate varied from a minimum of 0.03 to maximum of 0.17 barnacles per whelk per day, in Zimbro 302 and Fortaleza, respectively. Average PCIS was ~8.7 times stronger in Praia Grande (PCIS = 303 -5.93e-03) compared to Grumari (PCIS = -6.83e-04), respectively, the sites with the highest 304 and lowest average. Despite large variation in consumption rate and PCIS, we found no 305 relationship between these measures and either Chla or sea temperature (Table 2, Fig. 6). In 306 fact, there was no clear spatial pattern in either predation response along the studied area as 307 revealed by linear mixed models fitting consumption rate and PCIS as a function of longitude 308 (Appendix A: Table A3, Fig. A6).

309

310 Relationships of prey size with ocean conditions and predation

The size of available prey in the plots for the whelks was not related to satellite Chla (Table 3, Fig. 7A). The size of barnacles consumed by the whelks, on the other hand, increased with the size of barnacles available in the plots and decreased with Chla (Fig. 7B). Sea temperature did not relate to either the size of available or consumed prey. Moreover, both size of the barnacles available and consumed did not affect PCIS, while consumption rate tended to decrease with increasing size of available barnacles (Table 3).

317

318 **Discussion**

319 At a local scale, consumption rate of the predatory whelk Stramonita brasiliensis on 320 the barnacle Tetraclita stalactifera depended on interactive effects of the degree of exposure 321 to wave action and prey density. The effect of wave exposure on whelk's feeding behaviour 322 consistently weakened the per capita interaction strength (PCIS) of this predator on the 323 barnacle but with different rates depending on prey density. These results show the 324 importance of disentangling the effects of covarying factors along environmental gradients to 325 better comprehend community dynamics. In the large-scale experiment, consumption rate and 326 PCIS showed variability, but with no clear spatial pattern, and were not related to chlorophyll-327 a concentration (Chla) nor sea temperature. Little variation in sea temperature during this 328 experiment, however, precludes any dismissal of its effect on this predator-prey system. We 329 consider that large-scale variation in whelk-barnacle interactions was possibly influenced by 330 feeding choice mechanisms linked to other prey features.

In our local experiment, wave exposure decreased the consumption rate of barnacles by the predatory gastropod at reduced density but had no effect at ambient density, partially confirming our expectations. We predicted consumption to decrease with increasing wave exposure as a consequence of impairments on feeding activity of the predator (Menge and Sutherland 1976, 1987; Lamb et al. 2020) and expected this reduction to occur to a greater degree at reduced prey densities. The lack of effect of the wave exposure gradient on consumption rates at ambient prey density is likely linked to enhanced predator-prey 338 encounter rates and stress amelioration underpinned by prey density. From wave-sheltered 339 to exposed sites, barnacle density increases and, consequently, the encounter rate of them 340 by predators (Moran 1985; Dunn and Hovel 2020). Higher barnacle density can also 341 ameliorate effects of wave shock by dissipating water force and creating a more sheltered 342 substrate for whelks (e.g., Dayton 1971; Berlow and Navarrete 1997). This is particularly likely 343 for T. stalactifera, which is a large-bodied species that attaches firmly to the substrate. Thus, 344 whelks from wave-exposed shores at ambient density may be less vulnerable to wave 345 disturbance than those at reduced density, and hence more able to maintain a high 346 consumption rate. These potential explanations corroborate that facilitation, in this case 347 provided by the physical presence of the prey itself, can attenuate the effects of environmental 348 stress on predator-prey interactions (Bruno et al. 2003; Silliman and He 2018). This results 349 also enlighten potential mechanisms affecting within-shore variability in predation rates, as 350 small-scale variability on prey recruitment can result in low density plots even in sites highly 351 exposed to wave action. Our treatment of reduced prey density represents well such a 352 scenario.

353 Understanding how the environmental context affects the strength of ecological 354 interactions is central for advancing community ecology (Agrawal et al. 2007). In that regard, 355 PCIS is considered a key index because many other parameters can derive from it (Laska and 356 Wootton 1998; Berlow et al. 1999). As predicted, there was a clear negative effect of wave exposure on whelk PCIS most likely as a consequence of decreased feeding activity. The 357 358 impact of wave exposure was stronger where the prey was at reduced density owing to 359 density-dependence in the interaction strength indices (Berlow et al. 1999; Wootton and 360 Emmerson 2005). These results confirmed that environmental stress caused by wave 361 exposure can reduce the importance of top-down control (Menge and Sutherland 1976, 1987) 362 but reveals that density-dependent effects can determine the magnitude of the impact (see 363 also Ruesink 1998). Such conclusions apply solely to the component of interaction strength 364 related to predator-exerted mortality of prey in the short-term. In the long run, interaction

strength is also dependent on prey recruitment and growth (Laska and Wootton 1998; Berlow
et al., 1999; Novak and Wootton 2010).

367 Our large-scale experiment did not reveal effects of sea temperature and Chla on the 368 whelk-barnacle interaction. Temperature is expected to affect metabolic rates of species, 369 potentially modifying consumption rate and PCIS (Sanford 1999; O'Connor 2009; Kordas et 370 al. 2011; Carr et al. 2018; Bideault et al. 2019). In our experiment, temperature varied slightly 371 among sites, and, not surprisingly, did not affect any of the responses measured. Seawater 372 temperature across the studied area has a marked temporal variation due to a seasonal wind-373 driven upwelling in the Cabo Frio region (Appendix A: Fig. A1). In the austral summer, 374 upwelling events are frequent generating a southwestern-northeastern thermal gradient in the 375 coastal sea surface (Valentin 2001). However, in the austral winter, when we carried out this 376 experiment, upwelling events are rare and water temperature along this region is more 377 homogeneous (Castro and Miranda 1998). Extending this study to investigate temporal 378 variation in species interactions along the Southeast coast of Brazil incorporating the austral 379 summer may reveal effects of temperature on species interactions.

380 While temperature showed little spatial variation Chla showed a clear pattern, 381 decreasing northward, but with high values associated with proximity to urbanised bays 382 (Santos and Guanabara bay; Appendix A: Fig. A1). The quality of suspension-feeders, such 383 as T. stalactifera, is generally expected to be higher where phytoplankton is more abundant 384 (Bertness et al. 1991; Dahlhoff and Menge 1996), but see Giménez et al. (2017) for a counter 385 intuitive pattern in settling larvae over large scales in the British Isles. We predicted whelks to 386 feed less and to exert a weaker PCIS on barnacles in sites adjacent to Chla rich waters due 387 to higher energetic supply per prey. Our prediction was not confirmed; just as for sea 388 temperature we found no relationship. This result appears to indicate a lack of strong 389 environmental control on species interactions (e.g., Wood et al. 2010; Poore et al. 2013). 390 However, there was evidence of the role of gradients of Chla on whelk behaviour. Despite no 391 variation in barnacle size with Chla, the size of barnacles consumed decreased with increase 392 in Chla. Based on that relationship, it is likely that variability in nutritional quality of prey (e.g., 393 energy content) driven by Chla patterns could affect whelks' feeding choice (Simpson et al. 394 2010; Schmidt et al. 2012). If this holds true, whelks in sites with abundant phytoplankton (high 395 Chla) would choose smaller barnacles, potentially optimizing the trade-offs between handling 396 time and energetic yield or between handling time and risk avoidance (Palmer 1984; 397 Richardson and Brown 1990; Burrows and Hughes 1991; Hughes and Burrows 1991; Rovero 398 et al. 2000). This hypothesis would indicate that environment context affects species 399 interactions through effects on species' traits (e.g., Emmerson and Raffaelli 2004; Poore et al. 400 2013; Contolini et al. 2020) and deserves further attention.

401 An alternative mechanism that might explain the variability in predator-prey 402 interactions across our large-scale experiment is the occurrence of alternative prey to the 403 whelk S. brasiliensis. For example, several studies on the temperate dogwhelk Nucella spp. 404 have shown that they are more efficient in handling and consuming prey with which they have 405 more experience (Dunkin and Hughes 1984; Hughes and Dunkin 1984; Rovero et al. 1999). 406 Along our studied area, T. stalactifera dominates the mid-intertidal zone in most sites, although 407 other prey such as mussels (Mytilaster solisianus and Perna perna) and oysters are abundant 408 in places (López et al. 2010; Martinez et al. 2019). Qualitative observations during fieldwork 409 suggest that the consumption rate of the whelk on *T. stalactifera* was greater where other prey 410 were absent or scarce. This indicates that variability in the abundance of sessile prey along 411 the Southeast coast of Brazil might affect whelk's feeding preferences, potentially modifying 412 any simple relationship between spatial gradients (and associated environmental conditions) 413 and consumption rate/interaction strength (e.g., Wieters and Navarrete 1998; Sanford and 414 Swezey 2008).

In considering patterns in PCIS it is worth considering the implications of conclusions based on a relatively short-term experiment (e.g., Jenkins and Uyà 2016). The 'true' PCIS, i.e., the per capita effect of the predator on the per capita population growth rate of the prey (Laska and Wootton 1998; Berlow et al. 1999; Novak and Wootton 2010), is only really

measured in long term experiments which consider the recovery of prey populations (i.e., 419 420 include recruitment and growth). Considering that recruitment and growth of intertidal sessile 421 invertebrates usually covary with the degree of exposure to wave action (e.g., Menge 1992; 422 McQuaid and Lindsay 2000), the true PCIS of S. brasiliensis on T. stalactifera should correlate 423 to our short-term estimates of PCIS in the Ubatuba area. However, we would expect an even 424 greater reduction in per capita impact of the predator on prey populations along the increasing 425 gradient of wave exposure due to the joint influence of increasing prey recruitment and growth, 426 and wave disturbance. We, however, lack local data on recruitment and growth of this 427 barnacle. For the large-scale experiment, on the other hand, recruitment and growth of this 428 barnacle prey may respond in a complex manner to oceanic-climatic conditions operating over 429 broader spatial scales in SE Brazil (Mazzuco et al. 2015, 2018; Kasten et al. 2019; Pardal et 430 al. 2021). Thus, the way our short-term estimates of PCIS relate to the true PCIS is currently 431 unclear and suggests a useful avenue for future research.

432 We have shown that among-shore variation in the degree of exposure to wave action 433 and prey density interact to determine a subtropical intertidal predator-prey interaction in the 434 short term. These results reveal that disentangling the effects of covarying factors are required 435 to better understand processes driving community dynamics. At a large-scale, we suggest that predator-prey interactions are influenced by whelk's feeding choice driven by size and 436 437 nutritional quality relationships mediated by availability of food for the prey (Chla). Our work 438 contributes to understand the interplay between ecological processes and environmental 439 variability emerging at different spatial scales. To our knowledge, this is one of the few large-440 scale manipulative works along the southwestern Atlantic contributing to recent mensurative 441 efforts in comprehending the structure and functioning of coastal ecosystems over a broad 442 spatial range (e.g., Mazzuco et al. 2015; Kasten et al. 2019; Cruz-Motta et al. 2020; Pardal et 443 al. 2021).

444

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455

456 **Declarations**

457 Ethics approval: Ethics approval was not required for this study according to local legislation458 (UFABC).

- 459 **Consent to participate:** Not applicable
- 460 **Consent for publication:** Not applicable

461 **Availability of data and materials:** Data are fully available in 462 https://github.com/andrepardal/Predator-prey-interactions-rocky-shores-SE-

- 463 Brazil/tree/main/data
- 464 **Code availability:** Codes are fully available in https://github.com/andrepardal/Predator-prey-
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- 468 **Conflict of interest:** The authors declare they have no conflicts of interest.

469

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695 Tables

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697	Table 1. Linear mixed models testing the effect of prey density treatment (ambient, reduced)
698	and wave fetch on the consumption rate and per capita interaction strength (PCIS) of the
699	predatory whelk Stramonita brasiliensis on the barnacle Tetraclita stalactifera. SE = standard
700	error; SD = standard deviation; *P < 0.05; **P < 0.01; ***P < 0.001; ns = not significant.

A - consumption rate										
fixed effects					random effects of 'site'					
parameters	estimate	e SE	t-value	Р	parameters	variance	SD			
intercept	0.357	0.153	2.328	0.022	intercept	8.76e-04	2.96e-02			
treatment = tr	0.272	0.144	1.882	0.063	residual	8.05e-03	8.97e-02			
wave fetch = w	/f -0.044	0.052	-0.854	0.425						
tr:wf	-0.121	0.049	-2.465	0.016*						
effect of wave treatment ¹ :										
ambient	intercept	slope	R ²	reduced	intercept	slope	R ²			
	0.345*	-0.040 ^{ns}	0.02		0.618***	-0.162***	0.47			
B - PCIS										
fixed effects					random effects of	f 'site'				
parameters	estimate	e SE	t-value	P	parameters	variance	SD			
intercept	-0.022	0.006	-3.614	0.000	intercept	4.64e-14	2.15e-07			
treatment = tr	-0.055	0.014	-3.701	0.000	residual	2.01e-05	4.49e-03			
wave fetch = w	/f 0.005	0.002	2.645	0.038						
tr:wf	0.015	0.005	3.038	0.003**						
effect of wave treatment ¹ :	e fetch by pre	y density								
ambient	intercept	slope	R ²	reduced	intercept	slope	R ²			
	-0.022***	0.005*	0.15		-0.077***	0.020***	0.34			
Notes: Both linear mixed models were fitted with different variance structure by prey density										

treatment to meet homoscedasticity assumption. ¹Significance of slopes of regressions were
tested by fitting ordinary linear models for wave fetch and responses (consumption rate and
PCIS) separately per prey density treatment (N = 41). Reported P-values for slopes of such
models were adjusted using Bonferroni correction.

Table 2. Linear mixed models testing the effect of chlorophyll-a concentration (Chla) and seawater temperature on the consumption rate and per capita interaction strength (PCIS) of the predatory whelk *Stramonita brasiliensis* on the barnacle *Tetraclita stalactifera*. SE =

consumption rate											
fixed effects			random effec	ts of 'site'							
parameters	estimate	SE	t-value	Р	parameters	variance	SD				
intercept	-3.30e-01	1.42e+00	-0.23	0.81	intercept	1.48e-03	3.84e-02				
Chla	-1.32e-02	1.72e-02	-0.77	0.47	residual	7.10e-03	8.42e-02				
temperature	2.08e-02	6.49e-02	0.32	0.75							
PCIS ¹											
fixed effects					random effec	ts of 'site'					
parameters	estimate	SE	t-value	Р	parameters	variance	SD				
intercept	3.07e-02	2.01e-02	1.52	0.13	intercept	1.55e-07	3.93e-04				
Chla	1.89e-04	2.88e-04	0.66	0.53	residual	9.37e-05	9.68e-03				
temperature	-1.47e-03	9.17e-04	-1.60	0.15							

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Note: ¹To meet homoscedasticity assumption, the model was fitted with different variance
structure by site (~1|site).

Table 3. Linear models testing the effect of large-scale conditions (Chla, chlorophyll-a concentration; and sea temperature) on the size of available and consumed barnacles and the effect of barnacle size on the consumption rate and per capita interaction strength (PCIS).

716 * P < 0.05; ** P < 0.01; *** P < 0.001; ^{ns}, not significant.

size of available barnacles				
predictor	Ν	intercept	slope	R ²
~ Chla	46	6.80***	-0.15 ^{ns}	0.02
~ sea temperature	46	12.23 ^{ns}	-0.26 ^{ns}	0.00
size of barnacles consumed				
predictor	Ν	intercept	slope	R ²
~ size of available barnacles	37	0.46 ^{ns}	1.00***	0.49
~ Chla	37	8.49***	-0.68**	0.23
~ sea temperature	37	26.57 ^{ns}	-0.88 ^{ns}	0.02
consumption rate				
predictor	Ν	intercept	slope	R ²
~ size of available barnacles	46	0.27**	-0.026*	0.09
~ size of barnacles consumed	37	0.18**	-0.008 ^{ns}	0.02
PCIS				
predictor	Ν	intercept	slope	R ²
~ size of available barnacles	46	-8.55e-03*	9.22e-04 ^{ns}	0.05
~ size of barnacles consumed	37	-7.42e-03*	5.96e-04 ^{ns}	0.04

Notes: A replicate for size of available and consumed barnacles was the average opercular length per plot. The plots that remained in the field for about 30 days were not included in this analysis (4 out of 51) neither the plots with less than 2 barnacles consumed. The size of 'consumed barnacles' was the size of dead barnacles (i.e., empty shells or missing individuals) since background mortality was low and it was not possible to separate it from mortality caused by predation itself. 723 Figure legends

724

Fig. 1. (**A**) Map of the Southeast coast of Brazil showing domain of wave fetch model (proxy to wave exposure). (**B**) Details of the region of Ubatuba in the north coast of São Paulo State where experiments were carried out in 2018 (*Experiment 1*). Size of black circles represents mean wave fetch. (**C**) Wave fetch (mean \pm SE) of sites. (**D**) Ambient density of the barnacle *Tetraclita stalactifera* along the gradient of wave fetch. Black circles are mean values per site (N = 8), line and shaded area are linear prediction \pm 95% confidence interval

731

Fig. 2. Initial density of the barnacle *Tetraclita stalactifera* (mean \pm SE) in the treatments of exclusion or inclusion of the predatory whelk *Stramonita brasiliensis* (–P, +P) and prey density (ambient, reduced) in eight sites in Ubatuba (São Paulo state, SE Brazil) (*Experiment 1*). Grey dashed lines represent the global mean of barnacle density for each prey density treatment

736

Fig. 3. Initial density of the barnacle *Tetraclita stalactifera* (mean \pm SE) in the treatments of exclusion or inclusion of the predatory whelk *Stramonita brasiliensis* (–P, +P) in ten sites along the Southeast coast of Brazil (*Experiment 2*)

740

Fig. 4. (A) Consumption rate and (B) per capita interaction strength (PCIS) of the whelk Stramonita brasiliensis on the barnacle *Tetraclita stalactifera* along a gradient of wave fetch (proxy to wave exposure) and between prey density treatments (ambient, reduced). Small symbols are raw data (N = 82), lines and shaded areas are model predictions \pm 95% confidence interval

746

Fig. 5. Satellite chlorophyll-a concentration (Chla) and sea temperature (mean ± SE) in the
 ten sites where experiments were carried out along the Southeast coast of Brazil (*Experiment*)

749 2). For sea temperature, black and red symbols represent, respectively, satellite SST and in750 situ data from loggers

751

Fig. 6. Relationships among consumption rate and per capita interaction strength (PCIS) of the whelk *Stramonita brasiliensis* on the barnacle *Tetraclita stalactifera* and chlorophyll-a concentration (Chla) and sea temperature in the Southeast coast of Brazil. Small symbols are raw data (N = 51), lines and shaded areas are model predictions \pm 95% confidence interval

756

Fig. 7. Relationships between (**A**) size of barnacles *Tetraclita stalactifera* available to the predatory whelk *Stramonita brasiliensis* and mean satellite chlorophyll-a concentration (Chla) (N = 46) and (**B**) size of barnacles consumed by the predatory whelks and Chla (N = 37). Small circles are averaged opercular length per plot, lines and shaded areas are model predictions \pm 95% confidence interval

Figure 1



Figure 2



Figure 3



Figure 4



Figure 5



Figure 6



Figure 7



Electronic Supplementary Material

Local and large-scale spatial variation in a marine predator-prey interaction in the Southwestern Atlantic

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Fig. A1. Map of the study areas. (**A**) Location of the ten sites along Southeast coast of Brazil where the large-scale experiment was carried out in 2019. (**B**) Detail of the north coast of São Paulo State (Ubatuba municipality) showing the eight sites where experiments were carried out in 2018. Manipulations were done under environmental licence number 58852-4 granted by ICMBio (Ministry of the Environment of Brazil).

Table A1. Information about the plots of predator inclusion treatment in the experiment done in Ubatuba (São Paulo state) in 2018 (*Experiment 1*). *start* = the moment when the experiment was started (month and fortnight: 1, first, or 2, second); *duration* = duration of the experiment in days; *escapes* = number of times that the predator escaped from the cage; *time caged* = percentage of time that the whelk was certainly caged.

site	treatment	plot	start	duration	escapes	time caged (%)
Enseada	ambient	2	jun_2	76	0	100.00
Enseada	ambient	4	jul_2	56	0	100.00
Enseada	ambient	5	jul_2	56	1	75.00
Enseada	ambient	6	jul_2	56	1	69.64
Enseada	ambient	7	jul_2	56	0	100.00
Enseada	reduced	1	jun_2	59	0	100.00
Enseada	reduced	2	jul_2	56	1	69.64
Enseada	reduced	3	jul_2	56	0	100.00
Enseada	reduced	4	jun_2	59	0	100.00
Itaguá	ambient	1	jul_1	61	0	100.00
Itaguá	ambient	2	jun_2	90	0	100.00
Itaguá	ambient	3	jun_2	90	0	100.00
Itaguá	ambient	4	jun_2	58	0	100.00
Itaguá	ambient	5	jun_2	73	1	83.56
Itaguá	ambient	7	jun_2	90	1	83.56
Itaguá	reduced	1	jul_1	61	0	100.00
Itaguá	reduced	3	jun_2	90	0	100.00
Itaguá	reduced	4	jul_1	61	1	72.13
Itaguá	reduced	5	jun_2	73	0	100.00
Itaguá	reduced	7	jul_1	61	0	100.00
Lamberto	ambient	1	jun_1	76	0	100.00
Lamberto	ambient	2	jun_1	76	0	100.00
Lamberto	ambient	3	jun_1	76	1	73.68
Lamberto	ambient	4	jul_1	59	1	76.27
Lamberto	ambient	5	jul_1	59	0	100.00
Lamberto	ambient	6	jun_1	63	0	100.00
Lamberto	reduced	1	jun_1	48	0	100.00
Lamberto	reduced	2	jun_1	63	0	100.00
Lamberto	reduced	3	jul_1	45	1	66.67
Lamberto	reduced	5	jun_1	76	0	100.00
Lamberto	reduced	6	jun_1	63	0	100.00
Lamberto	reduced	7	jun_1	63	1	68.25
Lázaro	ambient	1	jun_1	92	0	100.00
Lázaro	ambient	2	jul_1	61	0	100.00
Lázaro	ambient	3	jul_1	61	0	100.00
Lázaro	ambient	4	jul_1	61	1	70.49
Lázaro	ambient	5	jul_1	61	0	100.00
Lázaro	ambient	6	jun_1	49	0	100.00

site	treatment	plot	start	duration	escapes	time caged (%)
Lázaro	reduced	1	jun_1	64	1	65.00
Lázaro	reduced	2	jun_1	92	0	100.00
Lázaro	reduced	3	jul_1	61	1	73.33
Lázaro	reduced	4	jun_1	64	0	100.00
Lázaro	reduced	5	jul_1	61	0	100.00
Lázaro	reduced	7	jul_1	45	0	100.00
Maranduba	ambient	1	aug_1	59	0	100.00
Maranduba	ambient	2	jun_2	101	0	100.00
Maranduba	ambient	3	jun_2	101	0	100.00
Maranduba	ambient	4	jun_2	101	0	100.00
Maranduba	reduced	1	jun_2	62	0	100.00
Maranduba	reduced	2	jul_2	84	1	70.24
Maranduba	reduced	5	aug_1	59	0	100.00
Maranduba	reduced	6	aug_1	59	1	66.67
P. Grande	ambient	1	jun_2	86	0	100.00
P. Grande	ambient	2	jun_2	86	0	100.00
P. Grande	ambient	3	jun_2	86	0	100.00
P. Grande	ambient	4	jun_2	112	0	100.00
P. Grande	ambient	5	aug_1	59	1	79.31
P. Grande	reduced	2	jun_2	87	1	79.31
P. Grande	reduced	3	jul_1	85	0	100.00
P. Grande	reduced	4	jun_2	87	1	86.21
P. Grande	reduced	6	aug_1	59	0	100.00
P. Grande	reduced	7	aug_1	59	0	100.00
P. Vermelha	ambient	1	jun_2	110	0	100.00
P. Vermelha	ambient	2	jun_2	110	1	85.45
P. Vermelha	ambient	3	aug_1	55	0	100.00
P. Vermelha	ambient	4	aug_1	55	0	100.00
P. Vermelha	ambient	6	jun_2	110	1	85.45
P. Vermelha	reduced	1	jun_2	110	1	85.45
P. Vermelha	reduced	2	aug_1	55	0	100.00
P. Vermelha	reduced	4	jul_2	84	0	100.00
P. Vermelha	reduced	5	aug_1	55	0	100.00
P. Vermelha	reduced	6	jun_2	110	1	88.18
P. Vermelha	reduced	7	jun_2	110	1	76.36
Sta Rita	ambient	1	jun_2	84	0	100.00
Sta Rita	ambient	3	jul_1	58	1	79.31
Sta Rita	ambient	6	jul_1	58	0	100.00
Sta Rita	ambient	7	jun_2	58	0	100.00
Sta Rita	reduced	1	jun_2	84	0	100.00
Sta Rita	reduced	2	jun_2	84	0	100.00
Sta Rita	reduced	3	jun_2	84	0	100.00
Sta Rita	reduced	5	jun_2	84	0	100.00
Sta Rita	reduced	7	jun_2	84	1	79.76

Table A1. Continuation.



Fig. A2. Wave fetch (mean \pm SE) of the ten sites along the Southeast coast of Brazil where the large-scale experiment was done in 2019 (*Experiment 2*). Sites are shown from south to north (see Fig. A1 above).



Fig. A3. Data logger temperature in 6 sites along the Southeast coast of Brazil (*Experiment* 2). Values outside of the range of site average \pm 1.5 SD were excluded to separate seawater from air temperature. Red and blue dots correspond to sea and air temperatures, respectively.



Fig. A4. Match-up between *in situ* and satellite-borne sea surface temperature (SST) measurements from the sites along SE Brazil. For data logger SST, each circle represents daily averages while for satellite SST, each circle is the average of all pixels from an image (4-km resolution, spatial buffer of 3×3 pixels). *Small graph*: Satellite SST bias was calculated as satellite SST minus data logger SST. Small circles are raw data, big circles with error bars are mean \pm SE. Colours represent the same sites in both graphs.

Table /	A2. Linear	model	ls of the i	match	-up be	twe	en s	atellite	and ir	า situ	sea	surfa	ce te	mperat	ture
(SST).	Ordinary	linear	models	were	fitted	for	the	global	data	and	for	each	site	where	we
obtaine	ed both da	ita. *P	< 0.05; *	*P < 0).01, *'	**P -	< 0.0	001; ns	s = no	t sigr	nifica	ant.			

Match-up satellite SST vs. data logger SST										
model	intercept	slope	R ²	Ν	average bias	site corrected				
Global	5.70***	0.76***	0.47	144	+0.35	-				
Iporanga	5.66 ^{ns}	0.76***	0.56	21	+0.11	Astúrias				
Itassucê	5.18 ^{ns}	0.80***	0.66	21	+0.62	Zimbro				
P. Grande	0.86 ^{ns}	0.99**	0.46	18	+0.74	P. Vermelha				
Grumari	7.68 ^{ns}	0.69**	0.30	25	+0.85	-				
Piratininga	12.94***	0.45***	0.46	29	+0.40	-				
Fortaleza	7.60 ^{ns}	0.64*	0.14	30	-0.35	Prainha				



Fig. A5. Mortality of the barnacle prey *Tetraclita stalactifera* in the absence of predators (background mortality) in the experiment done in (**A**) Ubatuba (São Paulo state) in 2018 (*Experiment 1*) and (**B**) along the SE coast of Brazil in 2019 (*Experiment 2*). Small circles are raw data, big circles with error bars are mean \pm SE.

Table A3. Linear mixed models testing the effect of longitude coordinates on the consumption rate and per capita interaction strength (PCIS) of the predatory whelk *Stramonita brasiliensis* on the barnacle *Tetraclita stalactifera*. SE = standard error; SD = standard deviation.

consumption rate											
fixed effects					random effect	ts of 'site'					
parameters	estimate	SE	t-value	Р	parameters	variance	SD				
intercept	2.95e-01	4.50e-01	0.65	0.51	intercept	1.59e-03	3.99e-02				
longitude	4.60e-03	1.01e-02	0.45	0.66	residual	2.17e-02	1.47e-01				
PCIS											
fixed effects					random effect	ts of 'site'					
parameters	estimate	SE	t-value	Р	parameters	variance	SD				
intercept	3.56e-03	7.03e-03	0.50	0.61	intercept	2.24e-07	4.74e-04				
longitude	1.13e-04	1.61e-04	0.70	0.50	residual	8.66e-05	9.31e-03				

Note: To meet homoscedasticity assumption, both models were fitted with different variance structure by site (~1|site).



Fig. A6. Consumption rate and per capita interaction strength (PCIS) of the whelk *Stramonita brasiliensis* on the barnacle *Tetraclita stalactifera* along longitude coordinates of sites from SE Brazil. Longitude coordinates represent better the spatial gradient since this coastline runs mostly from west to east. Small circles are raw data (N = 51), big circles with error bars are mean \pm SE.





Fig. B1. Residuals of the linear mixed models (Gaussian distribution, identity link) testing the effect of wave fetch and prey density treatments (ambient and reduced) on the consumption rate and per capita interaction strength (PCIS) of the whelk *Stramonita brasiliensis* on the barnacle *Tetraclita stalactifera*.



Fig. B2. Residuals of the linear mixed models (Gaussian distribution, identity link) testing the effect of chlorophyll-a concentration (Chla) and sea temperature on the consumption rate and per capita interaction strength (PCIS) of the whelk *Stramonita brasiliensis* on the barnacle *Tetraclita stalactifera*.